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

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Academic dissertation

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

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This thesis is based on the following articles or manuscripts, which are referred to in the text by their Roman numerals:


II  Sihvonen, P. & Kaila, L: Phylogeny and tribal classification of the Sterrhinae with emphasis on delimiting the Scopulini (Lepidoptera: Geometridae). — Submitted.


Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

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INTRODUCTION

What is systematics?

Systematics – what is often called taxonomy - is a field of biology that attempts to reconstruct the evolutionary history, also known as phylogeny, by uncovering the pattern of events that led to the distribution and diversity of life. As put by Lipscomb (1998), systematics is no less than understanding the history of all life. Systematics includes various tasks, such as the practice of recognizing taxa (subject of paper I), and formally specifying those relationships in a hierarchical scheme, called the classification (Simpson 1961, Schuh 2000) (subject of paper III).

The currently practiced zoological taxonomy and classification has its formal beginning in the work of the Swedish botanist and naturalist Carolus Linnaeus (1758), specifically in the monograph called Systema Naturae. The basis for the study of phylogeny, on the other hand, was introduced by Charles Darwin (1859) with the formalization of a theory of organic evolution. He proposed that all of life, no matter how different it may seem, is connected via their evolutionary history rather than being products of divine creation. Curiously, it took over a hundred years after Darwin's publication until an explicit set of methods for resolving the phylogenetic relationships of organisms were produced. The german entomologist Willi Hennig (1950, 1966) argued that only shared derived characters could possibly give us information about the evolutionary history of the taxa under study. This method, cladistics or phylogenetic systematics, uses the principle of parsimony in phylogeny reconstruction. According to Farris (1983): 'Most parsimonious genealogical hypotheses are those that minimise requirements for ad hoc hypotheses of homoplasy.' Due to the analytical nature of these methods (Farris 1983, Kluge 1997), the resulting phylogenetic hypotheses are open for further testing, and, in the case of contradicting evidence, falsifiable. I have used cladistic methods in papers II and III.

Besides cladistics, there are also other schools of taught for resolving phylogenetic relationships and classifying organisms, called phenetics (Sokal & Sneath 1963) and evolutionary taxonomy (Simpson 1961, Mayr 1969). The phenetic point of view incorporates the maximum number of unweighted observations, and groups organisms together on the basis of their overall similarity. It has been shown, however, that grouping of taxa by overall similarity may result in the recognition of artificial classes because mosaic nature of organismal evolution is overlooked (e.g. Hull 1970, Farris 1977). In evolutionary taxonomy the hierarchic level of a taxon in the classification is determined by the amount of its autapomorphic features. This will in many cases lead to recognition of unnatural paraphyletic taxa. The principle of parsimony, as used in the cladistic framework, is not the only optimality criterion that has been used in phylogeny reconstruction. It has been shown, however, that the alternative approaches such as the probabilistic model-based maximum likelihood (Felsenstein 1973, 1978) or three-taxon statements (Nelson & Platnick 1991) have theoretical as well practical problems (Farris et al. 1995, Siddall & Kluge 1997, Wenzel 1997, but see Goloboff 2003). Further, maximum likelihood approach has been considered unsuitable for the analysis of morphological data sets (Schuh 2000).

Description of the study group

I will first introduce the focal group of paper II, the Sterrhinae, and then continue with the largest tribe of the Sterrhinae, the Scopulini, a subject of papers I, III and IV.

The Sterrhinae, a subfamily of the Geometridae moths, or loopers, are often called waves because of the numerous wavy fasciae continuing from forewing to hindwing. They share the typical characteristics of family Geometridae, namely the paired tympanal organs at the base of the abdomen (Cook & Scoble 1992). The monophyly of the subfamily has been challenged (Common 1990, Holloway 1997, Minet & Scoble 1999, Holloway et al. 2001, Hausmann 2001), but within the Sterrhinae, however, there are several possibly monophyletic groups that are more readily diagnosable (Holloway et al. 2001).

Sterrhinae is a diverse group of moths showing great variation of morphology and ecology. The moths are often small in size compared to other Geometridae, with recurrent sexual dimorphism in wing size, shape and pattern. Most species are cryptically coloured and nocturnal, but many are active by day. A few groups are facultatively diurnal, for instance the Neotropical Cyclophora Dalman and its relatives (Covell 1983). Larvae of many species feed on low herbs, but species of the Cyclophora Hübner lineage are arboreal. Polyphagy is widespread, but a number of species are facultatively monophagous (Ebert 2001).

The subfamily includes over 2800 described species, found worldwide, yet the group is mostly tropical (Covell 1983, Heppner 1991, Scoble et al. 1995). The Sterrhinae is often the dominant group of Geometridae in dry habitats. This is possibly explained by the high number of Idaea species that have adapted to use leaf litter and detritus as food, a few species even frequently attack dry herbarium samples (Ebert 2001, Hausmann 2001). The Sterrhinae are poorly represented in higher latitudes and altitudes, although there are differences between biogeographical regions (Hausmann 2001, Brehm 2002).

The Scopulini, i.e. the genus Scopula Schrank and its close relatives, is the largest tribe of the
Sterrhinae, with about 900 described species. The wingspan of the majority of species ranges from 20 to 35 mm, although in few species this may exceed 60 mm. As other Sterrhinae, sexual dimorphism in wing size, shape and pattern is widespread. The males of many species possess secondary sexual characters, such as coremata on the 2nd and 8th sternites, and hairpencils on hindlegs. In most extreme cases male hindleg tarsi are absent, and the swallowed tibia with a hairpencil is not used for walking but primarily for scent-production and distribution (Hashimoto 1992). A majority of species are nocturnal, straw-coloured and cryptic in appearance, yet there are a number of deviations from this type of appearance, especially in the tropical lineages and in the groups that have adapted to a diurnal mode of life. For instance species of the diurnal African genus Aletis Hübner are brightly coloured and are considered to be model species that are mimicked in appearance by butterflies of genus Euphaedra Hübner (Nymphalidae) (Staude & Curle, 1997).

The biology is unknown for the majority of the Scopulini species, but according to better-known western Palaearctic, Japanese and Nearctic faunas, caterpillars of many species are polyphagous feeders on low herbs (McGuffin 1967, Sugi 1987, Ebert 2001). Some specialisation in larval host-plant is evident at the generic level, for instance the species of Problepsis Lederer tend to feed on Oleaceae and those of Antitrygodes Warren on Rubiaceae (Holloway 1997, Robinson et al. 2002). In Scopula a few adults of South East Asian species have adopted an unusual way of life and feed on blood from mammalian wounds, on sweat, and on tears (Bänziger & Fletcher 1985) while a few others are of minor economic importance, attacking tobacco (Sannino & Balbiani 1984, Sannino & Espinosa 1999) and groundnut (Satpathi 1995). Species of Zythos Fletcher have been recorded to visit carrion (Holloway 1997). Typically larvae are narrow and stick-like, and resting posture at a 45 degrees angle is typical (Sugi 1987, Ebert 2001).

The Scopulini are found throughout the world, and have been successful in temperate zones and in open habitats (Holloway 1997). Scopula is the only genus of the Sterrhinae to reach New Zealand (Dugdale 1988) and Polynesia (Holloway 1983a, b).

**Historical review of the classification**

As of yet, there has not been any analytical attempt to solve the tribal relationships of the Sterrhinae, nor the generic relationships of the Scopulini, and the hypotheses put forward are based on regional faunas (Sterneck 1941, Nakamura 1994). Holloway (1997), working on the Bornean fauna, made an effort to place the Sterrhinae species from that area into a broader taxonomic context.

The literature dealing with systematics of the Sterrhinae and the Scopulini are limited. Most data about phylogeny and generic relationships of these groups has to be drawn from check-lists or similar treatments and many family and genus group names have been introduced without descriptions. I will summarize the classification of these moths in chronological order. Only papers with broader systematical importance are discussed.

**Tribal classification of the Sterrhinae**

Application of the widely used family group name Sterrhinae (Serrhidae Meyrick, 1892) is based on usage rather than date priority (Fletcher 1995, Holloway 1997, I).

Pierce (1914), after a detailed study of genitalia structures of the British fauna, recognized three groups that fit the present concept of Sterrhinae: Ptychopodinae (referable to Sterrhini), Acidaliinae (Scopulini) and Cosymbiinae (Cosymbini). He did not consider Ptychopodinae a compact group whereas Acidaliinae was considered a natural group due to its peculiarities, for instance the presence of cerata and mappa on male 8th sternite, not found in any other group of Geometridae. The third group, Cosymbiinae, was considered a compact group including genera Rhodometra, Timandra, Cyclophora, Lythria (Larentiinae) and Parascotia Hübner (Noctuidae). He did not comment on the relationships of these groups.

Prout did not recognize tribes within the Sterrhinae in the first part of his monographic series (1912-16), although he diagnosed three groups around the genera Cyllapoda (referable to Cyllopodini), Acidalia Treitschke (Scopulini) and Cosymbia Hübner (Cosymbini). The Acidalia group contained a majority of the taxa, including, for instance, Rhodostophia Hübner, Timandra, Acidalia (mostly Scopula) and Ptychopoda Curtis (mostly Idaea). The Acidalia group was further divided according to the number of forewing areoles. He discussed shortly the Acidalia and Cosymbia group relationships but was unable to decide which was the derived group. In conjunction with the American Geometridae, Prout (1935-38) recognized one additional group, namely Asellodes Guenée (=Pseudasellodes Warren). In the supplement part to the Palaearctic fauna, Prout (1934-39) diagnosed the Sterrhinae tribes, mainly based on features of the male genitalia and wing venation, and listed the genera according to his earlier findings (Prout 1934-35) and Sterneck’s (1941) system. Two Sterrhinae genera, Asellodes (=Pseudasellodes) and Rhodometra, were treated separately from the previously mentioned groups, but they were not given tribal ranks. Unlike Sterneck (1941), Prout did not recognize Calothysanini (=Timandrinia) as a tribe.
Sterneck (1941), working with Palaearctic material, laid the basis for the still widely used Sterrhinae systematics. His studies relied largely on structures of the male genitalia, and he diagnosed five tribes within the Sterrhinae: Sterrhicæ (-ini), Scopulicæ (-ini), Rhodostrophicæ (-ini), Cosymbicæ (-ini) and Calothysanicæ (Timandrini). He was the first to propose a hypothesis of the tribal relationships. Sterrhini + Cosymbini + Timandrini were considered to form one group, Scopulini and Rhodostrophini were treated as separate lineages. The relationships between these three groups were left unresolved. Singh (1953) recognized two major divisions within Sterrhinae based on differences in larval chaetotaxy. The first of his groups included Traminda mundissima (Walker) and the species of Chrysocraspeda Hampson, which are referable to Timandrini and Cosymbini (Holloway 1997). The second group included Scopulini and Sterrhini.

Covell (1983) reviewed Neotropical Sterrhinae, and gave a list of genera and their associated tribes but did not discuss tribal relationships. Based on eggs (Salkeld 1983), representatives of North American Timandrini and Cosymbini were found to have similar structures. Sterrhini eggs of the genus Idaea did not resemble each other and accordingly they showed affinities either with Scopulini or with Timandrini + Cosymbini.

Hausmann (1993a) suggested that Rhodometrini is associated with Timandrini + Cosymbini lineage based on a longitudinal, ridge-like invagination on the signum of the female genitalia. He also drew attention to the “striate” valve ornamentation seen in the complex, but it is debatable whether these structures are homologous (Holloway 1997).

Nakamura (1994) worked with pupae of Japanese Sterrhinae and divided the fauna into four tribes following Inoue (1956). He concluded that there are two main lineages within Sterrhinae. Cosymbini, and especially the genus Timandra within it, was considered different from the Sterrhini + Scopulini + Rhodostrophini lineage. Scopulini + Rhodostrophini were considered to be most closely related, leaving Sterrhini as a sister group.

The most recent and complete account of Sterrhinae phylogeny, classification and tribal diagnoses is by Holloway (1997) and Holloway et al. (2001). Seven tribes were recognized and arranged into two lineages, based mostly on characters of the male and female abdomen: Timandrini + Rhodometrini + Cosymbini and Sterrhini + Scopulini + Cyllupodini + Rhodostrophini. This division is also supported by larval (Singh 1953) and pupal features (Nakamura 1994), and male secondary sexual characters. The tribes Sterrhini + Scopulini + Cyllupodini + Rhodostrophini all have long scent pencils on the hind tibia that seem to be associated with structures on the second sternite (Hashimoto 1992, Holloway 1997). These structures do not occur in the Timandrini + Rhodometrini + Cosymbini lineage although thick tufts of scales are often present. The Cyllupodini were associated with the Rhodostrophini based on features of the male secondary sexual characters and genitalia. The Rhodometrini have features that make their placement difficult. Features of the signum of the female genitalia (Hausmann 1993a), tympanic organ ansa, a few pupal characters and larval association with Polygonaceae suggest affinity with Timandrini (Holloway 1997). The male genital capsule shape, on the other hand, is similar to Scopula (Scopulini), pupal cremaster resembles those found in Cosymbini and hindwing venation is similar to Larentiinae.

Within the Sterrhinae, the Scopulini have been considered a natural, i.e. monophyletic group, on the basis of unique structures, located mainly on the male 2nd and 8th sternites (Pierce 1914, Sterneck 1941, Holloway 1997, Holloway et al. 2001). Their supposed synapomorphic nature has not been tested analytically.

Larentiinae has been suggested to be the sister group of Sterrhinae based on morphology (Holloway 1997, Fänger 1999). Characters that pull Sterrhinae and Larentiinae together are the distribution of the male secondary sexual organs, structure of signum of the female corpus bursae (Holloway 1997), and features of the tympanal organs (Cook & Scoble 1992). A molecular study by Abraham et al. (2001), based on a very limited taxon sample, did not support the Sterrhinae and Larentiinae relationship. An analysis of chemical structure of sex attractants did not support the Larentiinae connection either; instead, Geometrinae and Sterrhinae were considered to be closely related (Szocs et al. 1991).

Generic classification of the Scopulini

Little has been published on the generic systematics of the tribe Scopulini except for a treatment based on Palaearctic material (Sterneck 1941). The other publications on Scopulini systematics deal with generic or species descriptions focusing mainly on regional faunas. The most important ones are discussed below.

Pierce (1914) was apparently the first to illustrate the genitalia of the genus Scopula (Acidalia), and based on the peculiar structures that were found, he considered it a natural genus.

Prout (1912-16) brought together a number of genera that he called collectively the Acidalia group (Scopulini). Based on the number of forewing areoles alone, it was divided further. The two-areole group contained for instance Somatina Guenée, but also genera that are nowadays considered not to belong to tribe Scopulini, among others Rhodostrophia Hübner.
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Figure 1. Distribution of species per genera for the Scopulini. The majority of genera are small or monotypic, and the largest genus of the tribe, Scopula (at far right), contains alone over 78% of the described species. Numbers of species per genera are taken from Scoble (1999) and the constituent genera of the Scopulini are from II, Table 1.

(Rhodostrophiini). In the context of these groups he discussed the generic relationships and, for example, the one-areole genus Problepsis was considered to be a straight derivate of Somatina. He described four new Scopulini genera, i.e. Glossotrophia, Antilycauges, Holarctias and Oar, the latter three being monotypic. The generic descriptions were based on external morphological features, and for instance the lack of medial spurs on the hind leg of female Glossotrophia were considered an exceptional feature. Later Prout (1934-39) redefined the generic concepts of the Scopulini that were adopted in his earlier works. He included seven genera in the Scopula group, also the genus Cinglis that was earlier referred to the Cosymbia group. The African (1929-35) and Indo-Australian (1920-41) fauna of the Scopulini were treated after his findings on Palaearctic material (Prout 1934-39). The majority of the genera that he associated with the Scopulini are still being treated as such except Discomiosis Prout and Tricentroscelis Prout (II). Prout (1929-35) was the first to discuss the Sterrhinae connection of Aletis and Cartaletis Warren (see II), although he still treated them as Oenochrominae.

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. The majority of genera immediately preceeding and following Scopula in his publication included genera that are still associated with the tribe.

Sterneck (1941) based his explicit hypothesis about the relationships of the Scopulini on a detailed morphological examination of a large number of taxa across the Palaearctic region. 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 the males lack cerata and mappa on the 8th sternite. Cinglis was treated alone because it had the unusual condition of fasciculate male antennae with ventrolateral sensillae arranged in multiple rows and aberrant wing venation. The remaining six genera were combined into two groups on the basis of forewing areoles, aedeagus shape and cerata structure. The first group included Problepsis and Somatina and the second group Antilycauges, Scopula, Glossotrophia and Sigma Alphéraky.

When Hausmann (1994) described two new Scopulini genera, namely Scopuloides and Pseudocinglis, he emphasized the differences of proboscis length, number of hindtibial spurs and wing venation. Scopuloides was considered a close relative of Glossotrophia, although it had several features in common with Scopula, too. Pseudocinglis, on the other hand, was considered to be a genus intermediate between Cinglis and Antilycauges.

Holloway (1997) gave explicit descriptions for Sterrhinae tribes and genera in his treatment of the
Bornean fauna, placing the species from that area into a broader taxonomic context. Problepsini and Aletini were considered to be within the concept of Scopulini, too. He did not discuss the generic relationships, but the order in which he presents them can be inferred to reflect affinities between the genera.

In addition to these, a few taxonomic treatments of single genera, focusing on regional faunas have been published. Those include revisions of Nearctic species of *Scopula* (Covell 1970), various studies on *Glossostrophia* (Hausmann 1993a, b, 1994), Sundanean species of *Zythos* (Yazaki 1996) and *Scopula* species of the Bioko Island (Karisch 2001).

As is evident from the account above, the systematics of the tribe Scopulini has suffered from the regional approach (Sterneck 1941, Nakamura 1994, Holloway 1997). Lack of a broad view of Scopulini taxonomy has resulted in a relatively regional generic scheme and currently the Scopulini is divided into 25 genera (II), 12 of which are monotypic. The distribution of species per genera is distinctly skewed (Fig. 1).

The state of our knowledge about the systematics of these moths is poor enough to substantiate wide scale phylogenetic studies at different hierarchical levels. Further, the Sterrhinae and Scopulini can be considered suitable for applied ecological studies (Pearson 1994, Intachat & Woiwod 1999), and indeed, they have already been used in such studies (e.g. Intachat & Holloway 2000, Brehm 2002). How reliable are the results of such studies if they may be based on unnatural groupings?

**Objectives of the study**

The purpose of this thesis is to study the phylogenetic relationships of the Sterrhinae, especially those of the tribe Scopulini, to classify the extant taxa at the generic level, and to study temporal patterns of species description, spatial distribution and species diversity of the Scopulini on a world wide perspective. I investigated these patterns at different hierarchical levels in order to understand better the study group, the underlying mechanisms of evolution, and, specifically, to get myself a broad view of the tasks and methods that the field of systematics is involved in. The specific objectives of the studies were:

- To revise the taxonomy of the *Scopula cajanderi* group of the Holarctic region (I).
- To test whether the putative synapomorphies of the Scopulini, taken from the literature, support the monophyly of the group; to find additional characters that can be used to delimit the Scopulini; to examine the phylogenetic relationships of Sterrhinae tribes; and to provide preliminary lists of the constituent genera of the tribes (II).
- To examine the phylogenetic relationships of the Scopulini, and to classify and diagnose the world fauna at the generic level (III).
- To describe various temporal and spatial patterns of the species descriptions and distributions of the Scopulini, and to estimate the species diversity of the Scopulini in order to gain an understanding of the state of our knowledge (IV).

**MATERIAL**

The material for these studies was obtained from the following institutes:

- American Museum of Natural History (AMNH), New York, United States
- Australian National Insect Collection, CSIRO Division of Entomology (ANIC), Canberra, Australia
- Canadian National Collection of Insects (CNCI), Ottawa, Ontario, Canada
- Finnish Museum of Natural History (ZMH), Helsinki, Finland
- Institute of Biology and Pedology, Russian Academy of Sciences (IBPV), Vladivostok, Russia
- Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU), Berlin, Germany
- National Science Museum (Natural History) (NSMT), Tokyo, Japan
- The Natural History Museum (BMNH), London, United Kingdom
- Zoological Institute, Russian Academy of Sciences (ZIN), St. Petersburg, Russia
- Zoologische Staatssammlungen (ZSBS), München, Germany.

**METHODS**

**Preparation of specimens**

The genitalia and abdomen of specimens were prepared and stained following routine procedures (Hardwick 1950). A number of specimens were exposed to potassium hydroxide (KOH) treatment, and following maceration, denuded of scales. All preparations were preserved temporarily in glycerol, which allowed for the examination of objects from various perspectives, and were mounted afterwards in euparal. The wing venation slides were prepared in ethanol, and scales were removed from both surfaces of the wings by brushes. Unstained wings were mounted in euparal. The structures were studied with stereo and contrast compound microscopes. The methods of preparation are described in more detail in papers II-III.
Species revisions

To delimit the studied taxa (I), I used the phylogenetic species concept (Nixon & Wheeler 1990, Davis & Nixon 1992) which can be regarded more readily applicable than for example the biological species concept of Mayr (1942, 1963) when working with museum material. Thus the reproductive isolation of the species from other species was inferred indirectly from the observed differences in the morphological features. Special attention was paid to structures of genitalia, but also features of antennae and wing pattern were concerned. Numerous specimens were examined to estimate the amount of intraspecific variation, especially in the form of the male’s 8th sternite, which has been reported to be a region of extensive variation in a few taxa in the genus Scopula (Hausmann 1999).

Phylogenetic analyses

Selection of outgroup and ingroup taxa

For the phylogenetic analysis of Sterrhinae suprageneric lineages (II), altogether five geometrid species from three subfamilies were chosen as outgroups based on recent literature on the relationships among Geometridae subfamilies (II, Appendix 1). Archiearinae are a compact group of diurnal geometrids, unusual in lacking the accessory tympanum (Cook & Scoble, 1992). Geometrinae and Larentiinae have been speculated to be closely related to Sterrhinae or sister groups of it (Szocs et al. 1991, Holloway 1997).

For the phylogenetic analysis of Scopulini genera (III), two species of Sterrhini were used as outgroups, being recovered as such in an earlier study (II). In both studies outgroup taxa were used to root the tree, to polarize the characters and to test the monophyly of the ingroup (Farris 1972, Nixon & Carpenter 1993).

Because it is impractical to include all described species in an analysis of such a species-rich group, the ingroup species for both phylogenetic analyses were chosen using the following guidelines (II, Appendix 1; III, Appendix 1). First, all type species of nominal genera were included, and, if unavailable, it was attempted to include species that were morphologically similar with the type species. Second, more than one species was attempted to be included from all the previously recognized groupings, unless monotypic, in order to reduce the effect of the autapomorphies. Third, it was attempted to cover the morphological diversity of the groupings as exhaustively as possible, and finally, I attempted to include taxa from the less explored areas of the world. For this purpose 650 Scopulini species were studied, including their genitalia, covering over 70% of the described fauna (see III, Appendix 4).

The identity of many studied species (II, III), especially those found in the Holarctic region, is well established and no type material was studied. The identity of many species, on the other hand, was checked against external examination of type specimens.

Selection of characters

I attempted to minimize a priori assumptions regarding the value of characters as a source of systematic information and consequently all characters that could be coded unequivocally, were included.

In the first cladistic analysis of the Sterrhinae, putative characters delimiting the tribe Scopulini (II, Appendices 2 and 4) were taken from the literature (Pierce 1914, Sterneck 1941, Covell 1970, Holloway 1997, Holloway et al. 2001), and coded for the actual specimens. In the second analysis of the Sterrhinae many more characters were analysed, including those used in the first analysis (II, Appendices 3 and 5). In the cladistic analysis of the Scopulini a total of 141 characters were used (III, Appendices 2 and 3).

The majority of the characters were derived from structures of the adult morphology, including many previously unused features from the sclerites of the thorax, and also included were characters from the biology and from the immature stages. Both binary and multistate characters were coded, the latter were treated unordered. A few autapomorphic characters were included in the analysis, if they were known to be synapomorphies of larger groups (Yeates 1992).

Parsimony analysis

All character sets (II, Appendices 4 and 5; III, Appendix 3) were analyzed with the parsimony program NONA (version 2.0, Goloboff 1999), and all characters were weighted equally. The command sequence used for all matrices, using TBR branch swapping, was: ‘hold*, hold/50; mult*200’. The command sequence means that hold as many trees in memory as set by the user (set to 100000); hold 50 starting trees in memory; perform TBR branch-swapping on 200 random-addition replicates). The initial results were then submitted to more exhaustive searches as recommended in the NONA manual (Goloboff 1999): ‘max*’ – ‘swap*’ – ‘altswap*’ – ‘mswap*2’. The trees were saved with ‘sv*’ (meaning that trees were saved in uncollapsed form), read back into NONA and the command ‘best’ was 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 optimisations
Diversity analysis

The study (IV) relies on a computerized database, containing information on all the putatively valid names of the Scopulini species. It is based on a preliminary world check-list of the Scopulini (III). The following information was recorded for each species: generic combination, author, year of description, type locality (country, latitude and longitude), biogeographical region of type locality, number of synonyms, and type specimen depository.

Species were assigned to biogeographical regions according to their type localities, and for practical reasons, rather than their biogeographical reality I followed Wallace’s scheme (see Scoble et al. 1995). When scoring the type specimen depository, I used the depository of the holo- or lectotype, if it was housed in a separate collection than the rest of the type specimens. If type specimens were deposited in more than one museum, and no holo- or lectotype had been designated, the first mentioned depository was used.

The type localities of all known species of each genera were mapped onto a cylindrical projection of the world to give a rough indication of the distribution of the group. The map was divided into equal-area grid squares for intervals of 5°, each square being approximately 152 750 km², and the data was incorporated into maps with the Geographical Information System (GIS) approach.

RESULTS AND DISCUSSION

Species group revision (I)

The Scopula cajanderi species group was found to include three species: Scopula cajanderi, S. mustangensis and S. aegrefasciata. The external appearance of Scopula cajanderi was found to be variable but based on consistent diagnostic characters of the genitalia, including the internal genitalia, three new synonyms were proposed, making it Holarctic in distribution. Scopula mustangensis and S. aegrefasciata were found to be confined to the Palaearctic region, the latter species was described as new. On the species level, the male antenna, the aedeagus and the internal genitalia offered most of the characters to separate the species of the S. cajanderi group, unlike the rather uniform male genitalia capsule. The shape of the male’s 8th sternite was found to be variable, and species delimitations were not based on this character alone.

It was shown that the detailed examination of morphology can yield reliable diagnostic features for a group of closely related species. Based on these findings, it is recommended that the vesica be everted routinely in species of the genus Scopula, because they may offer further taxonomical resolution if other characters fail.

Characters delimiting the Scopulini and the tribal classification of the Sterrhinae (II)

The strict consensus cladogram resulting from the analysis of the literature-based characters only was unresolved, and did not offer any characters that could be used to delimit the tribe Scopulini (Fig. 1). The lack of resolution may have resulted from the fact that the earlier studies have mostly dealt with regional faunas, thus perhaps creating an artificial image that the Scopulini is a distinct tribe and no overlapping with the other tribes exists. It is also possible that there may be many natural, subordinate groups within Scopulini and the characters that can delimit one group may not be applicable to others. Finally, many of the proposed characters delimiting the Scopulini appeared as homoplastic.

The monophyly of the Scopulini was demonstrated in a follow-up analysis, when the characters of the first analysis were supplemented with more data from the adult morphology and ecology (Fig. 12). One of the synapomorphies is characteristic, namely the shape of the signum, although it is absent in a number of species due to the secondary loss. Sterrhini was found to be the sister group of Scopulini.

All previously suggested Sterrhinae tribes were recovered as monophyletic except the Cosymbiini and Rhodostrophiini (Figs. 12, 13). Further, the relationships of these tribes were found to be in accordance to earlier, unanalytical hypotheses (Hausmann 1993a, Holloway 1997). The majority of the recovered synapomorphies supporting the monophyly of the Sterrhinae tribes had been used earlier, but a few novel features were discovered. The monophyly of the Sterrhinae is questionable (also in Holloway 1997) because the two Larentiinae taxa included in our study did not appear as sister groups to Sterrhinae but instead were recovered within the Sterrhinae. The inclusion of these taxa within the present concept of the Sterrhinae may be an artefact resulting from unbalanced taxon sampling, and the result has to be considered preliminary. The putative monophyly of the Sterrhinae was supported by two non-unique synapomorphies: the presence of areoles on the forewings and the absence of anterolateral extensions on the male’s 2nd sternite.

Phylogeny of the Scopulini (III)

A large part of the strict consensus cladogram is well resolved, and it was found that there are two main
lineages in the Scopulini (Figs. 133-135). The male and female genitalia and male secondary sexual structures such as those of the hind legs were found to be areas of great informative variation, and therefore useful at resolving the phylogenetic relationships at the generic level (Table 2). Many characters showed extensive homoplasy, for example the number of forewing areoles, and it is concluded that use of such characters alone would result in artificial groupings.

Generic classification

I recognized groups of species as genera if they were monophyletic and supported by synapomorphies that were unique or had low homoplasy, and on the basis of my personal experience of this group. When recognizing genera, I emphasized similarities rather than differences. I also tried to avoid making new generic synonyms if the material studied was somehow contradictory or if the material was considered insufficient.

Accordingly I recognized seven genera, but no subgenera (Fig. 133, Appendix 4): Scopula is very large, containing about 85% of the described fauna, Somatina s.s. and Problepsis have together almost 100 species, Dithalamia s.s. and Zythos have a few species whereas Isoplenodia and Lipomelia are monotypic. A few taxa were placed incertae sedis but retained in their present generic combinations. Numerous new generic synonyms and new species combinations were proposed.

One could argue that instead of proposing new generic synonyms (Appendix 4), I should have recognized many of the traditional genera. I did not do that, following the reasoning of Kaila (1998), as it would have either left the remaining taxa paraphyletic or the remaining lineages would have had to be extensively split into a large number of small, almost invariably new, genera. Further, a classification with very narrowly delimited genera could lead to an addition of new genera as new species with differing character combinations are discovered. Due to the approach adopted, some recognized genera 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. One could argue that this approach may result in a reduction of taxonomic resolution and information content of the classification. This is not the case, however, because species groups within genera can still be recognized and identified, but there is no need to name them.

Diversity analysis (IV)

Generally taken, the diversity patterns of the Scopulini were found to be similar to those reported earlier in the Geometridae as a whole (Gaston et al. 1995). These include the rate of species description per decade (Figs. 1, 2), the right-skewed distributions of the number of synonyms per valid species (Fig. 4), the numbers of authors describing different numbers of species (Fig. 5), and type specimen depositories (Table 2). Neotropics has been reported to be the most species rich biogeographical area for the Geometridae, but for the Scopulini it was found to be Africa (Table 1).

The synonomy rates, measured as a ratio between the number of putatively valid species that have associated synonyms, was found to be highest in the New Zealand and Nearctic regions and lowest in Madagascar. When the relationship between the number of synonyms and the numbers of valid Scopulini species names for different biogeographical regions were considered, we found that these are broadly correlated (Fig. 3). In other words, the more valid names there are, the more synonyms there are.

The Scopulini was found to be cosmopolitan in distribution but the distribution of type localities is uneven. The most species-rich squares were located in sub-Saharan Africa and in northern India. Many of the most speciose squares of the Scopulini have also been identified earlier as biodiversity hotspots, based on non-invertebrate taxa (Myers et al. 2000). In other areas, virtually no species have been described from the interior parts of the Nearctic and Neotropics. When latitudinal patterns were investigated, it was found that the majority of the species have been described from low latitudes and numbers decrease steadily towards higher latitudes (Fig. 6). Our result contradicts the earlier view that Scopulini have been successful in temperate zones (Holloway 1997).

The taxonomical effort has been very uneven between biogeographical regions, and changes in the numbers of described species are likely to occur. For example, it remains unknown whether the notably low species number of the Neotropics and the fact that no species have been described from the region since the 1950s, is a true phenomenon or an artefact resulting from an insufficient exploration of the fauna. When estimating the world species diversity of the Scopulini it is important to take into account the synonymy. Currently 19% of the valid species have associated synonyms but this figure is likely to rise if the fauna becomes the subject of modern revisions.

CONCLUSIONS AND CHALLENGES FOR THE FUTURE

The Scopulini are the most species rich group of the Sterrhinae, and they are cosmopolitan in distribution (IV). The majority of the species have been described from the low latitudes, sub-Saharan Africa being the hot spot of species diversity. The taxonomical effort has been uneven among biogeographical regions,
however, and changes in the proportions of described species between biogeographical regions are likely.

The phylogenetic relationships of the tribes of the Sterrhinae were found to be similar to earlier hypotheses. However, due to the specific aims of the study (II), taxon sampling was uneven among its constituent tribes and the tribal relationships of the Sterrhinae need to be investigated further. In addition, the systematic position of many genera of the Sterrhinae still remains uncertain at the tribal level (II, Table 1), and the monophyly of the Sterrhinae is challenged.

It was shown that the putative synapomorphies of the tribe Scopulini, taken from the literature, failed to support the monophyly of the group in a broader taxonomical context. When the putative characters were combined with additional morphological evidence, a few characters appeared as synapomorphies of the Scopulini (II). A worldwide investigation of the genera of the Scopulini revealed many new generic synonyms (III). The majority of the synonymized genera were monotypic. Extensive species level revisions of the Scopulini are necessary, including the study of their generic combinations, as was indicated by a few examples (III).

Many morphologically distinct species groups within the genus Scopula can be identified, such as the S. cajanderi group (I), but the relationships between species groups may be best resolved with the aid of sequence level data.

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