



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

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Academic dissertation

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Pasi Sihvonen

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

- I** Sihvonen, P. 2001: Revision of the *Scopula cajanderi* (Lepidoptera: Geometridae, Sterrhinae) species group with description of a new species. — Canadian Entomologist 133: 467–486.
- II** Sihvonen, P. & Kaila, L: Phylogeny and tribal classification of the Sterrhinae with emphasis on delimiting the Scopulini (Lepidoptera: Geometridae). — Submitted.
- III** Sihvonen, P: Phylogeny and classification of the Scopulini moths (Lepidoptera: Geometridae, Sterrhinae). — Submitted.
- IV** Sihvonen, P. & Siljander, M. Diversity of Scopulini moths on a worldwide scale: spatial and temporal patterns (Lepidoptera: Geometridae, Sterrhinae). — Submitted.

Contributions

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

	I	II	III	IV
Original idea	LK	PS, LK	LK	PS
Study design	LK, PS	LK, PS	LK, PS	PS
Material and methods	PS	PS	LK, PS	PS, MS
Data gathering	PS	PS	PS	PS
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Original articles

- I. Revision of the *Scopula cajanderi* (Lepidoptera: Geometridae, Sterrhinae) species group with description of a new species
- II. Phylogeny and tribal classification of the Sterrhinae with emphasis on delimiting the Scopulini (Lepidoptera: Geometridae)
- III. Phylogeny and classification of the Scopulini moths (Lepidoptera: Geometridae, Sterrhinae)
- IV. Diversity of the Scopulini moths on a worldwide scale: spatial and temporal patterns (Lepidoptera: Geometridae, Sterrhinae)

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 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 thought 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 *Cylophoda* 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 (Sterrhidae Meyrick, 1892) is based on usage rather than date priority (Fletcher 1995, Holloway 1997, II).

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 (Cosymbiini). 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 *Cyllopoda* (referable to Cyllopodini), *Acidalia* Treitschke (Scopulini) and *Cosymbia* Hübner (Cosymbiini). 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 (= Timandrini) 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: Sterrhicae (-ini), Scopulicae (-ini), Rhodostrophicae (-ini), Cosymbicae (-ini) and Calothysanicae (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 Cosymbiini (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 Cosymbiini 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 + Cosymbiini.

Hausmann (1993a) suggested that Rhodometrini is associated with Timandrini + Cosymbiini 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. Cosymbiini, 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 + Cosymbiini and Sterrhini + Scopulini + Cyllopodini + Rhodostrophini. This division is also supported by larval (Singh 1953) and pupal features (Nakamura

1994), and male secondary sexual characters. The tribes Sterrhini + Scopulini + Cyllopodini + 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 + Cosymbiini lineage although thick tufts of scales are often present. The Cyllopodini 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 Cosymbiini 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

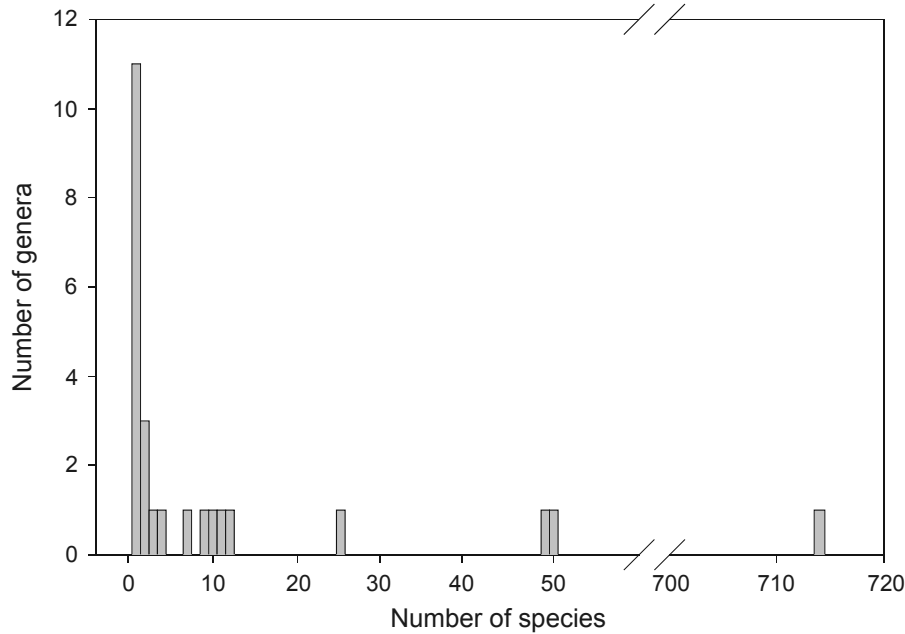


Figure 1. Distribution of species per genera for the Scopulini. The majority of genera are small or monotypic, and the largest genus of the tribe, *Scopula* (at far right), contains alone over 78% of the described species. Numbers of species per genera are taken from Scoble (1999) and the constituent 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 derivative 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 preceding 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 *Stigma* 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. Proplepsini 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 *Glossotrophia* (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

were studied using WinClada (version 1.00.08, Nixon 2002).

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 depositary.

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 depositary, I used the depositary 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 depositary 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 synonymies were proposed, making it Holarctic in distribution. *Scopula mustangensis* and *S. aegrefasciata* were found to be confined to the Palearctic 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, *Dithalama s.s.* and *Zyθος* 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 homogenous. 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 synonymy 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 (III). 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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REFERENCES

- Abraham, D., Ryrholm, N., Wittzell, H., Holloway, J. D., Scoble, M. J. & Löfstedt, C. 2001: Molecular phylogeny of the subfamilies in Geometridae (Geometroidea: Lepidoptera). *Molecular Phylogenetics and Evolution* **20**: 65-77.
- Brehm, G. 2002: *Diversity of geometrid moths in a montane rainforest in Ecuador*. Ph.D. thesis, Universität Bayreuth, Bayreuth.
- Bänziger, H. & Fletcher, D. S. 1985: Three new zoophilous moths of the genus *Scopula* (Lepidoptera: Geometridae) from South-east Asia. *Journal of Natural History* **19**: 851-860.
- Common, I. F. B. 1990: *Moths of Australia*. Melbourne University Press.

- Cook, M. A. & Scoble, M. J. 1992: Tympanal organs of geometrid moths: a review of their morphology, function and systematic importance. *Systematic Entomology* **17**: 219-232.
- Covell, C. V. 1970: A revision of the North American species of the genus *Scopula* (Lepidoptera, Geometridae). *Transactions of the American Entomological Society* **96**: 101-221.
- Covell, C. V. 1983: The state of our knowledge of the Neotropical Sterrhinae (Geometridae). *Second Symposium on Neotropical Lepidoptera Arequipa, Peru 1983. Supplement 1*: 17-23.
- Darwin, C. 1859: *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. John Murray, London.
- Davis, J. I. & Nixon, K. C. 1992: Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic Biology* **41**: 421-435.
- Dugdale, J.S. 1988: *Lepidoptera - annotated catalogue, and keys to family-group taxa*. Fauna of New Zealand 14.
- Ebert, G. 2001: Sterrhinae. In: Ebert, G. (ed.), *Die Schmetterlinge Baden-Württenbergs, Nachtfalter VI, Band 8 (Geometridae)*: 74-210. Verlag E. Ulmer, Stuttgart.
- Farris, J. S. 1972: Estimating phylogenetic trees from distance matrices. *American Naturalist* **106**: 645-668.
- Farris, J. S. 1977: On the phenetic approach to vertebrate classification. In: Hecht, M., Goody, P. & Hecht, B. (eds.), *Major patterns in Vertebrate evolution*: 823-850. Plenum Press, New York.
- Farris, J. S. 1983: The logical basis of phylogenetic analysis. In: Platnick, N. I & Funk, V. A. (eds.), *Advances in Cladistics*, vol. 2: 7-36. Columbia University Press, New York.
- Farris, J. S., Källersjö, M., Albert, V. A., Allard, M., Anderberg, A., Bowditch, B., Bult, C., Carpenter, J. M., Crowe, T. M., De Laet, J., Fitzhugh, K., Frost, D., Goloboff, P., Humphries, C. J., Jondelius, U., Judd, D., Karis, P. O., Lipscomb, D., Luckow, M., Mindell, D., Muona, J., Nixon, K., Presch, W., Seberg, O., Siddall, M. E., Struwe, L., Tehler, A., Wenzel, J., Wheeler, Q. & Wheeler, W. 1995: Explanation. *Cladistics* **11**: 211-218.
- Felsenstein, J. 1973: Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. *Systematic Zoology* **22**: 240-249.
- Felsenstein, J. 1978: The number of evolutionary trees. *Systematic Zoology* **27**: 27-33.
- Fletcher, D. S. 1995 (reprint): *The generic names of moths of the World, volume 3: Geometroidea*. The Natural History Museum, London.
- Fänger, H. 1999: Comparative morphology of tergal phragmata occurring in the dorsal thoraco-abdominal junction of ditrysian Lepidoptera (Insecta). *Zoomorphology* **119**: 163-183.
- Gaston, K.J, Scoble, M.J. & Crook, A. 1995. Patterns in species description: a case study using the Geometridae (Lepidoptera). *Biological Journal of the Linnean Society* **55**: 225-237.
- Goloboff, P. 1999: *NONA*. Program and documentation. Version 2.0.
- Goloboff, P. 2003: Parsimony, likelihood, and simplicity. *Cladistics* **19**: 91-103.
- Hardwick, D. F. 1950: Preparation of slide mounts of Lepidopterous genitalia. *Canadian Entomologist* **82**: 231-235.
- Hashimoto, S. 1992: Tibial scent organ and its related structures in the genera *Idaea* and *Scopula* of the subfamily Sterrhinae (Lepidoptera: Geometridae). *Akitu* **130**: 1-7.
- Hausmann, A. 1993a: *Heterolocha xerophilaria* Püngeler, 1902 – ein Synonym von *Pseudosterrha rufistrigata* (Hampson, 1896), comb. n., mit weiteren Anmerkungen zur Systematik der Sterrhinae (Lepidoptera, Geometridae). *Nota Lepidopterologica* **16**: 23-33.
- Hausmann, A. 1993b: Der Aussagewert struktureller Unterschiede im 8. Sternit. Revision der in Italien vorkommenden Arten der Gattung *Glossotrophia* PROUT, 1913. *Atalanta* **24**: 265-297.
- Hausmann A. 1994: Dritter Beitrag zur Revision der Gattung *Glossotrophia* Prout, 1913 nebst Beschreibung zweier neuer Gattungen (Lepidoptera: Geometridae, Sterrhinae. *Nota lepidopterologica* **16**: 195-211.
- Hausmann, A. 1999: Falsification of an entomological rule: Polymorphic genitalia in Geometrid moths. *Spixiana* **22**: 83-90.
- Hausmann, A. 2001: *The Geometrid moths of Europe*, vol. 1. Introduction, Archiearinae, Orthostixinae, Desmobathrinae, Alsophilinae, Geometrinae. Apollo Books, Stenstrup.
- Hennig, W. 1950: Grundzüge einer Theorie der Phylogenetischen Systematic. Deutscher Zentralverlag, Berlin.
- Hennig, W. 1966: *Phylogenetic systematics*. University of Illinois Press, Urbana.
- Heppner, J. B. 1991: Faunal regions and the diversity of Lepidoptera. *Tropical Lepidoptera 2, Supplement 1*: 1-84.
- Holloway, J. D. 1983a: The biogeography of the macrolepidoptera of south-eastern Polynesia. *GeoJournal* **7**: 517-525.

- Holloway, J. D. 1983b: On the Lepidoptera of the Cocos-Keeling Islands in the Indian Ocean, with a review of the *Nagia linteola* complex (Noctuidae). *Entomologia generalis* **8**: 99-110.
- Holloway, J. D. 1997: The Moths of Borneo: Family Geometridae, subfamilies Sterrhinae and Larentiinae. *Malayan Nature Journal* **5**: 1-242.
- Holloway, J. D., Kibby, G. & Pegg, D. 2001: *The families of Malesian moths and butterflies*. Fauna Malesiana handbook, vol. 3. Brill, Leiden.
- Hull, D. 1970: Contemporary systematic philosophies. *Annual Review of Ecology and Systematics* **1**: 19-54.
- Inoue, H. 1956: *Check list of the Lepidoptera of Japan* **3**: 219-364. (In Japanese).
- Intachat, J. & Woiwod, I. P. 1999: Trap design for monitoring moth biodiversity in tropical rainforests. *Bulletin of Entomological research* **89**: 153-163.
- Intachat, J. & Holloway, J. D. 2000: Is there stratification in diversity or preferred flight height of geometroid moths in Malayasian lowland tropical rainforest? *Biodiversity and Conservation* **9**: 1417-1439.
- Janse, A. J. T. 1933-1935: *The moths of South Africa, Vol. 2: Geometridae*. EP. & Commercial Printing Co. Ltd, Durban.
- Kaila, L. 1998: Classification of the Elachistidae (Lepidoptera: Gelechioidea). Academic dissertation, University of Helsinki.
- Karisch T. 2001: Zur Geometridenfauna von Bioko (Lepidoptera: Geometridae). *Lambillionea* **101**: 161-184.
- Kluge, A. G. 1997: Testability and the refutation and corroboration of cladistic hypotheses. *Cladistics* **13**: 81-96.
- Linnaeus, C. 1758: *Systema Naturae*. 10th ed. Stockholm.
- Lipscomb, D. 1998: *Basics of cladistic analysis*. George Washington University, Washington D.C.
- Mayr, E. 1942: *Systematics and the origin of species*. Columbia University Press.
- Mayr, E. 1963: *Animal species and evolution*. Harvard University Press, Cambridge, Massachusetts.
- Mayr, E. 1969: *Principles of systematic zoology*. McGraw-Hill, New York.
- McGuffin, W. C. 1967. Guide to the Geometridae of Canada (Lepidoptera). 1. Subfamily Sterrhinae. *Memoirs of the Entomological Society of Canada* **50**: 1-67.
- Meyrick, E. 1892: On the classification of the Geometrina of the European fauna. *Transactions of the Entomological Society of London* **1892**: 53-140.
- Minet, J. & Scoble, M. J. 1999: The Drepanoid/Geometroid Assemblage. In: Kristensen, N. P. (ed.), *Handbook of Zoology*, part 35: Lepidoptera, moths and butterflies, Volume 1: Evolution, systematics, and biogeography: 301-320. W. de Gruyter, Berlin.
- Myers, N., Mittermeier, R.A., da Fonseca, G.A.B. & Kent, J. 2000: Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858.
- Nakamura, M. 1994: Pupae of Japanese Geometridae (II). *Transactions of the Shikoku Entomological Society* **20**: 247-256.
- Nelson, G. & Platnick, N. I. 1991: Three-taxon statements: a more precise use of parsimony? *Cladistics* **7**: 351-366.
- Nixon, K. C. 2002: *WinClada*, Version 1.00.08. Published by the author: Ithaca, New York.
- Nixon, K. C. & Wheeler, Q. 1990: An amplification of the phylogenetic species concept. *Cladistics* **6**: 211-223.
- Nixon, K. C. & Carpenter, J. M. 1993: On outgroups. *Cladistics* **9**: 413-426.
- Nixon, K. C. & Carpenter, J. M. 1996: On consensus, collapsibility, and clade concordance. *Cladistics* **12**: 305-321.
- Pearson, D. L. 1994: Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **345**: 75-79.
- Pierce, F. N. 1914: *The genitalia of the group Geometridae of the Lepidoptera of the British Islands*. Northern Publishing Company, Liverpool.
- Prout, L. B. 1912-16: Die Spanner des Palaearktischen faunengebietes. In: Seitz, A. (ed.), *Die Gross-Schmetterlinge der Erde*, vol. 4: 1-479. Verlag A. Kernen, Stuttgart.
- Prout, L. B. 1920-41: Die indoaustralischen Spanner. In: Seitz A. (ed.), *Die Gross-Schmetterlinge der Erde*, vol. 12: 1-356. Verlag A. Kernen, Stuttgart.
- Prout, L. B. 1929-35: Die Afrikanischen Spanner. In: Seitz A. (ed.), *Die Gross-Schmetterlinge der Erde*, vol. 16: 1-152. Verlag A Kernen, Stuttgart.
- Prout, L. B. 1934-35: Geometridae: Subfamilia Sterrhinae. In: Strand, E. (ed.), *Lepidopterorum Catalogus*, pars 61, 63, 68: 1-486. W. Junk, Berlin.
- Prout, L. B. 1934-39: Die Spanner des Palaearktischen faunengebietes. In: Seitz, A. (ed.), *Die Gross-Schmetterlinge der Erde*, supplement zu band 4: 1-253. Verlag A. Kernen, Stuttgart.
- Prout, L. B. 1935-38: Die Amerikanischen Spanner. In: Seitz, A. (ed.), *Die Gross-Schmetterlinge der*

- Erde*, vol. 8: 1-144. Verlag A. Kernen, Stuttgart.
- Robinson, G. S., Ackery, P. R., Beccaloni, G. W., Kitching, I. J. & Hernandez, L. M. 2002: *HOSTS – The Natural History Museum's database of the hostplants of the moth and butterfly caterpillars of the world*, <http://flood.nhm.ac.uk/cgi-bin/perth/hosts/>.
- Salkeld, E. H. 1983: A catalogue of the eggs of some Canadian Geometridae (Lepidoptera), with comments. *Memoirs of the entomological society of Canada* **126**: 1-271.
- Sannino, L. & Balbiani, A. 1984: *Scopula ochroleucaria* H.S. (Lepidoptera, Geometridae) injurious to tobacco in Campania (South Italy). *La difesa delle piante* **5-6**: 289-300.
- Sannino, L. & Espinosa, B. 1999: Morphological and ethological aspects of *Scopula turbidaria* (Lepidoptera: Geometridae). *Fragmenta Entomologica* **31**: 377-395.
- Satpathi, C. R. 1995: Insects infesting groundnut (*Arachis hypogaea*) in West Bengal. *Annals of Entomology (Dehra Dun)* **13**: 97-98.
- Schuh, R. T. 2000: *Biological systematics: principles and applications*. Cornell University Press, Ithaca and London.
- Scoble, M.J., Gaston, K.J. & Crook, A. 1995. Using taxonomic data to estimate species richness in Geometridae. *Journal of the Lepidopterists' Society* **49**: 136-147.
- Siddall, M. E. & Kluge, A. G. 1997: Probabilism and phylogenetic inference. *Cladistics* **13**: 313-336.
- Simpson, G. 1961: *Principles of animal taxonomy*. Columbia University Press, New York.
- Singh, B. 1953: Immature stages of Indian Lepidoptera No. 8 – Geometridae. *Indian Forest Records, N. S.* **8**: 67-158.
- Sokal, R. & Sneath, P. 1963: *Principles of numerical taxonomy*. W. H. Freeman, San Francisco.
- Staude, H. S. & Curle, A. I. 1997: A classification of visual-signals emanating from the wings of Afrotropical Lepidoptera. *Metamorphosis, Supplement* **3**: 156-188.
- Sterneck, J. 1941: Versuch einer Darstellung der systematischen Beziehungen bei den palaearktischen Sterrhinae (Acidaliinae). Studien über Acidaliinae (Sterrhinae) IX. *Zeitschrift des Wiener Entomologen-Vereines* **26**: 248-262.
- Sugi, S. (ed.) 1987: *Larvae of Larger Moths in Japan*. Kodansha, Tokyo.
- Szocs, G., Ronkay, L., Vojnits, A. & Toth, M. 1991: Does the chemical structure of sex attractants reflect taxonomical position of Geometrid species (Lepidoptera)? In: *Proceedings of the Conference on Insect Chemical Ecology*, Tábor, 1990: 75-79. Academia Prague and SPB Academic Publishing, The Hague.
- Wenzel, J. W. 1997: When is a phylogenetic test good enough? In: Grandcolas, P. (ed.), *The origin of biodiversity in insects: Phylogenetic tests of evolutionary scenarios*. Mémoires du Muséum National d'Histoire Naturelle, Paris **173**: 31-54.
- Yazaki K. 1996. The genus *Zythos* (Lepidoptera, Geometridae) of Wallacea. *Transactions of the Lepidopterological Society of Japan* **47**: 49-56.
- Yeates, D. 1992: Why remove autapomorphies? *Cladistics* **8**: 387-389.