Primitive (non-ditrysian) Lepidoptera of the Andes: diversity, distribution, biology and phylogenetic relationships

Ebbe S. Nielsen

Division of Entomology, CSIRO, G.P.O. Box 1700, Canberra, A.C.T., 2601, AUSTRALIA

Abstract. The families of primitive Lepidoptera represented in South America are reviewed with special reference to those occuring in the Andes. Of the twenty-two extant families of primitive Lepidoptera, fourteen are reported from South America and two (Heterobathmiidae and Neotheoridae) are endemic there. The diversity, distribution, biology and phylogenetic relationships of the South American primitive Lepidoptera are outlined.

Resumen. Se reexamina las familias de lepidópteros primitivos presentes en América del Sur, con especial referencia a aquellas que ocurren en los Andes. De las 22 familias de lepidópteros primitivos existentes en la actualidad, 14 han sido registradas para Sudamérica, y dos de ellas (Heterobathmidae y Neotheoridae) son endémicas del subcontinente. Se hace referencia a la diversidad, distribución, biología y relaciones filogenéticas de los lepidópteros primitivos de América del Sur.

Introduction

The Lepidoptera are one of the most successful insect orders and thus one of the most successful groups of animals. The order contains more than 140,000 described species, but the total number of species may well exceed 200,000. Most species of Lepidoptera, approximately 99%, belong to the infraorder Ditrysia, while the rest, the so-called primitive Lepidoptera, belong to several small sub- and infraorders. Hennig (1953) produced the first cladogram of the Lepidoptera. According to Hennig, the successful Ditrysia have developed through the process termed 'additive typogenesis' (Hennig, 1981): the derived characters in the Ditrysia have not arisen at the same time but through a sequence of events. Each 'nodal point', branching point, where the lineage leading to the successful group (the lineage leading to the Ditrysia) has acquired one or more of its advanced characters, 'enabling mechanisms', has also given rise to a less successful group without this character (one of the non-ditrysian lineages). The non-ditrysian groups can therefore be arranged in a sequence according to the

number of ditrysian characters they have acquired. In short, it can be said that the scheme outlined by Hennig still is recognized, but his relatively simple picture has become modified and much more complicated by the considerable amount of new information which has become available during the last two decades. Much of this novel information on primitive Lepidoptera is the result of recent field studies on the South American fauna, especially that of the southern Andes. This field work has led to several important discoveries which have contributed to our understanding of the evolutionary pathways in the Lepidoptera, has provided much new information on several little known primitive groups, and has led to the finding of new primitive families.

The primitive families of Lepidoptera found in South America, particularly those occurring in the Andes, are reviewed here with emphasis on their diversity, distribution and biology and with a summary of the phylogenetic (cladistic) relationships of the South American representatives of each family.

Phylogeny and Classification of the Primitive (non-ditrysian) Lepidoptera

All known and recognized families of non-ditrysian Lepidoptera are presented in the cladogram in Figure 1 and the current classification outlined in Table 1, in which the families represented in South America are marked with an asterisk and those known only from South America with two asterisks. Figure 1 and Table 1 summarize our current knowledge of the phylogeny and classification of the primitive Lepidoptera and are based mainly on the following recent studies: non-Glossata: Kristensen & Nielsen (1983), Kristensen (1984). Glossatan non-Myoglossata: Common (1973), Davis (1978), Kristensen & Nielsen (1981) and Kristensen (1984). Position of Neopseustidae: Davis & Nielsen (1980), Kristensen & Nielsen (1981). Exoporian families: Common, 1975; Gibbs, 1979; Kristensen, 1978a, b; Kristensen & Nielsen, unpublished. Heteroneuran families: Nielsen, 1982b, in press, and unpublished.

The interrelationships between the families are dealt with in these papers and are not discussed below.

Micropterigidae

The Micropterigidae, the only family in the suborder Zeugloptera after the Heterobathmiinae were removed to a suborder of their own (Kristensen & Nielsen, 1983), are now known from all zoogeographical regions. The family contains about one hundred species in about ten genera. The largest genus is the Palaearctic *Micropterix* Hübner, 1825 which probably is the sister-group to all other genera, the circum-Pacific and South African *Sabatinca*-group of genera.

Diversity and distribution. Since the Micropterigidae are well rep-

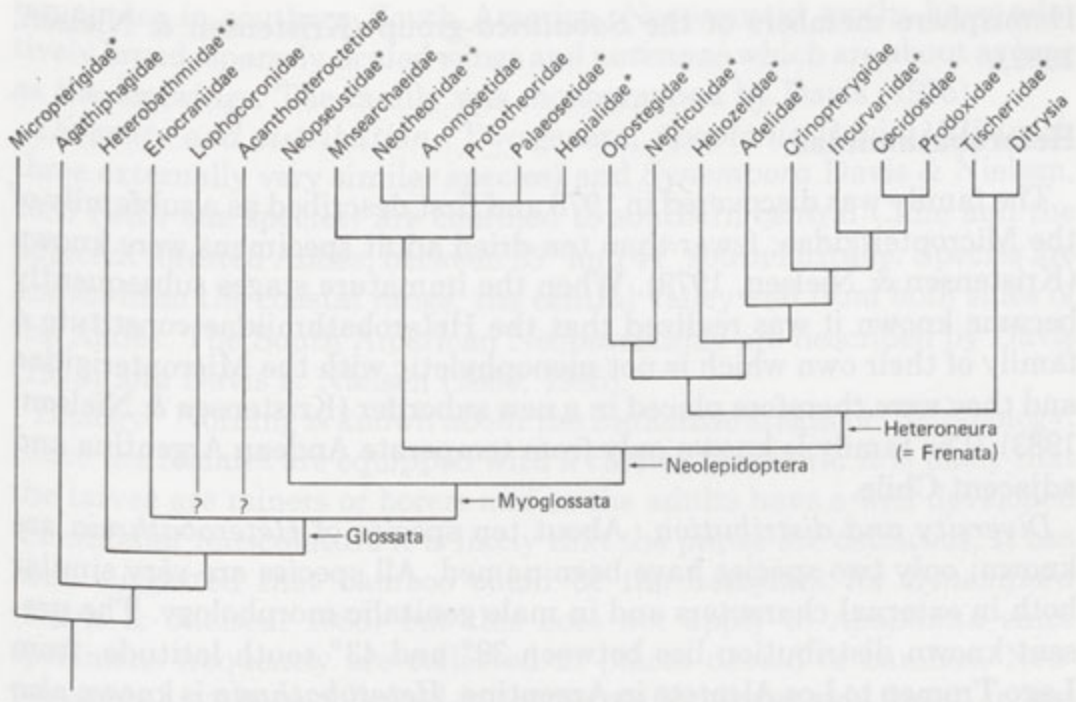

Fig. 1. Proposed phylogeny of the primitive lepidopteran families. One asterisk (*) indicates families represented in South America; two asterisks (**) indicate families endemic to South America. The literature upon which the present cladogram is based is listed in the section on 'Phylogeny and classification of the primitive Lepidoptera'.

resented in Australia, New Caledonia and New Zealand and occur in South Africa their occurrence in South America has long been expected. However, only recently could their presence in the form of two new monobasic genera be reported from the Neotropical region. Both genera are from the Andes (Kristensen & Nielsen, 1982). The genus *Hypomartyria* is known only from Osorno province in southern central Chile, where 7 specimens have been collected in dense, humid Valdivian forest localities. The genus *Squamicornia* is represented by a single specimen from Napo province in northern Ecuador. It was collected at an altitude of 2600 m in an area rich in primary forest.

Biology. Adult micropterigids are day fliers and most species occur in humid forest localities. The adults feed on pollen and spores. The larvae feed on liverworts, in rotten logs and on lower parts of grasses and other herbaceous plants (Carter & Dugdale, 1982; Gibbs, 1984). Nothing is known of the biology of the South American species, but the localities conform well to those known from New Zealand and Australia. All specimens of *Hypomartyria* were collected by sweeping on sunny days.

Phylogeny. Both *Hypomartyria* and *Squamicornia* belong to the *Sabatinca* group of genera, the phylogeny of which is still poorly understood. *Hypomartyria* is closely related to *Sabatinca* s. lat. The closest relatives of *Squamicornia* may well be the Old World Southern

Hemisphere members of the *Sabatinca*-group (Kristensen & Nielsen, 1982).

Heterobathmiidae

The family was discovered in 1978 and first described as a subfamily of the Micropterigidae; fewer than ten dried adult specimens were known (Kristensen & Nielsen, 1979). When the immature stages subsequently became known it was realized that the Heterobathmiidae constitute a family of their own which is not monophyletic with the Micropterigidae and they were therefore placed in a new suborder (Kristensen & Nielsen, 1983). The family is known only from temperate Andean Argentina and adjacent Chile.

Diversity and distribution. About ten species of *Heterobathmia* are known; only two species have been named. All species are very similar both in external characters and in male genitalic morphology. The present known distribution lies between 39° and 43° south latitude, from Lago Tromen to Los Alcerces in Argentina. *Heterobathmia* is known also from three localities in Chile in the Valdivia and Osorno provinces. Since *Heterobathmia* is known to feed on deciduous *Nothofagus* its range might be much larger and could coincide with that of the deciduous *Nothofagus* which in South America ranges from the latitude of Santiago to Tierra del Fuego.*

Biology. The biology is outlined by Kristensen & Nielsen (1983): the adults fly during the late winter and early spring; the flight is diurnal and is restricted to days with sunshine. Adults have been observed feeding on *Nothofagus* flowers and they are therefore most likely pollen-feeders. Several species of deciduous *Nothofagus* are hostplants. The eggs are deposited on the underside of the leaf of the host and the larvae develop as leaf miners. When mature, after only ten days, the larvae drop to the ground and diapause in the soil during the summer, autumn and most of the winter in a strong silken cocoon 8-15 cm below the surface.

Phylogeny. The Heterobathmiidae share specialized characters with the Aglossata, Zeugloptera and/or Glossata, but six synapomorphies shared by *Heterobathmia* and Glossata are particularly weighty so a sister-group relationship between *Heterobathmia* and the Glossata is the best hypothesis, given our present information (Kristensen & Nielsen, 1983; Kristensen, 1984).

Neopseustidae

The Neopseustidae are a small family with four genera and eleven species. Two genera with seven species occur in southeast Asia and the

*Footnote added in press. *Heterobathmia* has now been collected in several places with deciduous *Nothofagus* north and south of Santiago in Chile (Nielsen, unpublished).

remainder in southern South America. Neopseustid moths have relatively broad, sparsely-scaled wings and antennae which are about as long as the forewings. The family was monographed by Davis (1975).

Diversity and distribution. Two genera, *Apoplania* Davis, 1975 (with three externally very similar species) and *Synempora* Davis & Nielsen, 1980 (with one species) are confined to southern central Chile and the adjacent forested Andes, between 35° and 44° south latitude. Species are known from the coastal range, the central valley and from both sides of the Andes. The South American Neopseustidae are described by Davis (1975) and Davis & Nielsen (1980, 1985).

Biology. Nothing is known about the immature stages or their biology. Since the females are equipped with a cutting ovipositor it is likely that the larvae are miners or borers and as the adults have a well developed mandibular musculature it is likely that the pupae are decticous. It has been suggested that bamboo could be the hostplant for *Synempora* (Davis & Nielsen, 1980) but this does not apply to *Apoplania* since specimens frequently are collected in places devoid of bamboo. Neopseustids have been collected in temperate Valdivian rain forest, in wet *Nothofagus dombeyi-Chusquea* forest, in wet *Nothofagus-Araucaria* forest, and in secondary *Nothofagus* forest. Only one species, *Apoplania chilensis* Davis, 1975 occurs in the drier and warmer deciduous *Nothofagus* forest. *Synempora* has been observed flying actively during the day; this has not been seen for *Apoplania*. While *Synempora* rests with the wings steeply reflexed, *Apoplania* rests with the wings completely flattened (Davis & Nielsen, 1980, 1985).

Phylogeny. The two South American genera are regarded as being monophyletic and their sister-group is most likely the Asian *Neopseustis* Meyrick, 1909 (Davis & Nielsen, 1980).

Neotheoridae

This family was described by Kristensen (1978a) on the basis of a single specimen of *Neotheora chiloides* Kristensen, 1978 from Brazil, Matto Grosso. The family Neotheoridae is described in detail and its systematic position discussed by Kristensen (1978a, b; 1984). No information is available on its biology. The single specimen was collected at light in late September.

Palaeosetidae

This family which otherwise occurs in Australia, Taiwan and Assam is represented in South America by a single species *Osrhoes coronta* Druce, 1900 (Nielsen & Robinson, 1983). *Osrhoes* is in many aspects phenetically similar to the other members of the family, but recent observations cast strong doubts on the monophyly of the family Palaeosetidae (Kristensen & Nielsen, unpublished). Nothing is known of the biology of

Osrhoes. The species is known only from Colombia, Sierra del Libane, at an altitude of 1800 m.

Hepialidae

The 'ghost moths' or 'swifts' are by far the most successful family of non-Heteroneura, being distributed worldwide and comprising approximately 80 genera with more than 500 species.

Distribution and phylogeny. The recent checklist of the South American hepialids recognizes 18 genera and 130 species, with more than one-third of the species in *Aepytus* Herrich-Schäffer, 1858 (Nielsen & Robinson, 1983), but only the hepialid fauna of forested southern South America (from Coquimbo to Tierra del Fuego) can be said to be well known. There are eight genera and 30 species in this area, and all, apart from *Druceiella basirubra* (Schaus, 1901) are endemic. The two large genera of the area, *Dalaca* Walker, 1856 and *Callipielus* Butler, 1882 each contain ten species. Four species of hepialids occur in Tierra del Fuego and three species north of Santiago in Chile. The highest diversity is reached in deciduous *Nothofagus* forest and in Valdivian forest. No hepialids have been collected above the tree line (Nielsen & Robinson, 1983). Little is known of the hepialids of the Andes north of the southern forested area, but species of the following genera occur there: *Druceiella* Viette, 1949, *Pfitzneriana* Viette, 1952, *Aepytus, Phialuse* Viette, 1961, and *Pfitzneriella* Viette, 1950.

Biology. Larvae of most hepialids tunnel in the soil and either feed on roots or emerge from the tunnel at night and feed on herbaceous plants. The larvae of a few American, African, Asian, and Australian genera tunnel in the stem of shrubs and trees. Very little information is available on the biology of the immature stages of the South America Hepialidae, but several species are now being studied in Argentina. Larvae of *Dalaca* tunnel in the soil and feed on roots of grasses.

Phylogeny. The phylogeny of the family is little understood. Nielsen & Robinson (1983) could not establish any close phylogenetic relationships between any of the southern South American genera and genera occurring elsewhere.

Nepticulidae

Although the Nepticulidae include the smallest lepidopterans they are currently one of the best studied families of microlepidoptera and our knowledge of this family is increasing rapidly. Scoble (1983) has produced a valuable review of the classification of the family. He recognizes two subfamilies, the Pectinivalvinae and the Nepticulinae. The former is restricted to Australia and the latter occurs worldwide.

Diversity and distribution. Only ten species were named from South America by Zeller, Meyrick and Forbes. Zeller's species are both from

Colombia and several of Meyrick's species are from high altitude Peru. Only one species has been described from the southern forested Andes. Recent collecting in that area has produced not less than 30 species. A few species have also been collected in the Patagonian steppe.

Biology. The egg is deposited on the hostplant; the larvae of most species form mines in leaves, but some mine in bark, leaf petioles or buds. When mature the larva drops to the ground where it pupates in an oval cocoon; a few species pupate within the mine. The Nepticulidae feed on a wide range of Angiosperms. The southern South American species have been found on the following hosts: several species of *Nothofagus* (Fagaceae), several species of Myrtaceae, *Azara microphylla* (Flacourtiacae), *Schinus* sp. (Anacardiaceae) and *Discaria serratifolia* (Rhamnaceae). A group of large coppery species make characteristic mines in the leaves of *Myrceugenia planipes* in wet Valdivian forest localities.

Phylogeny. The South American Nepticulidae are still little collected and studied and so nothing can be said either about which genera are represented or about the affinities of the South American nepticulids.

Opostegidae

This little studied family occurs worldwide except for New Zealand. It apparently reaches its greatest diversity in the SE Palaearctic region, east Asia and Australia. The monophyly of the family and its sister-group relationship to the Nepticulidae seems well established (Nielsen, in press).

Diversity and distribution. From South America eighteen species are named in two genera: *Opostega* Zeller, 1839 with 17 species and *Enteucha* Meyrick, 1915 with one species. *Enteucha cyanochlora* Meyrick, 1915 was described from Guyana (British Guiana); *Enteucha* may well be a synonym of *Opostega*.* Five of the South American *Opostega* species are described from the Caribbean, five from Mexico, one from Guyana, two from lowland Brazil, one from northern Argentina, and only four are described from the Andean region: one from Colombia, two from Ecuador, and one from Peru. No species are described from the southernmost parts of South America, but a relatively large, blackish species occurs in *Nothofagus* forests in the coastal range around Valdivia (Carey et al., 1978). It is to be named by D. R. Davis, Washington, D.C. This species has been searched for in the Andes, in appropriate *Nothofagus* localities on both sides, but was not found. Otherwise no species of Opostegidae are known from the southernmost part of South America, including the Patagonian steppe.

Biology. The biology of the Opostegidae is little known and even for the

*Footnote added in press. D. R. Davis has now examined the single specimen of *Enteucha cyanochlora*; it belongs to the family Nepticulidae (D. R. Davis, in press. A re-examination of *Enteucha cyanochlora* Meyrick and its subsequent transfer to the Nepticulidae (Lepidoptera: Nepticulidae)).

common European species there is still no precise information available. The Hawaiian *Opostega* species are the best documented with regard to the biology of the immature stages: they are leaf-miners in *Pelea* (Rutaceae) and their mines may be circular, spiral-shaped, long and threadlike or serpentine-shaped. The mature larvae drop to the ground where they form a dense oval silken cocoon (Zimmerman, 1978: 245). Other species are cambium miners: one North American species mines the cambium of *Ribes* (Grossulariaceae) (Zimmerman, 1978: 246), one Japanese species mines in the trunk of *Betula* (Betulaceae) (Kumata, pers. comm.). The biology of the many Australian species is little known.

The biology of the unnamed species from Valdivia was studied by Carey (1975) and a short summary was published by Carey et al. (1978): the larvae make cambium mines up to one metre long in the trunk and branches of *Nothofagus dombeyi* (Fagaceae); the larva mines upwards in a zig zag pattern and when mature in the late spring it turns round and makes a short mine parallel to the first; from the second gallery it makes several lateral chambers in one of which the larva estivates. In the autumn the larva drops to the ground and spins a cocoon. The adults fly during the early spring and come to light.

Phylogeny. So far nothing can be said about the interrelationships within the family. A review of the New World fauna is being prepared by D. R. Davis, Washington, D.C.

Heliozelidae

The Heliozelidae are a relatively large family, absent from New Zealand, but otherwise distributed worldwide. Owing to their very small size and specialized flying behaviour (only in sunshine) they are both little collected and little studied. Nielsen (unpublished) recognizes 13 genera in the family, several of which remain to be described. The family probably reaches its greatest diversity in SE Asia.

Diversity and distribution. Fewer than 20 species are named from South America and few of these are described from the Andes. Only one is from the southern Andes. An ongoing study of the heliozelid fauna of southern forested South America shows that at least three genera with approximately 20 species occur in that area, though the family is still little collected.

Biology. The larvae are leaf-miners and finally cut out an oval flat case from the mine. In most genera the case drops to the ground but in a few the case is attached to a twig of the hostplant. Pupation takes place in the case. Only one genus is known to mine in herbaceous plants, all the others mine in leaves of trees and bushes. Little is known of the biology of the southern South American heliozelids: species of one unnamed genus undoubtedly feed in deciduous *Nothofagus* and species of another unnamed genus are associated with myrtaceaous shrubs and trees.

Phylogeny. The three genera occurring in southern South America are all unnamed. One of those (feeding on Myrtaceae) is related to *Heliozela* Herrich-Schäffer, 1853, and has a wide distribution outside southern South America, including southern Africa and Australia. Another genus, feeding on *Nothofagus*, is related to the North American *Coptodisca* Walsingham, 1895, the European *Holocacista* Walsingham & Durrant, 1909, and the Pacific *Ischnocanaba* Bradley, 1961, which all have a male retinaculum consisting of a series of hook-shaped bristles. The most interesting taxon, however, is a primitive heliozelid genus with rough head vestiture, the epicranial suture present, five segmented maxillary palpus and hindwing with basally free 1A and 2A. This genus, which is not found outside southern South America, is important for our understanding of the phylogeny of the heliozelids and systematic position of the family.

Adelidae

Most species of the 'fairy moth' family have antennae which are 2-3 times as long as the forewing. The family is absent from New Zealand but occurs otherwise worldwide. The metallic coloured dayflying adelids (the *Adela* group) are probably most numerous in the E. Palaearctic area while the greyish or yellowish duskfliers (the *Ceromitia* group) reach their greatest diversity in southern Africa and South America. The *Adela* group is absent from South America except for Central America: Guatamala and Mexico.

Diversity and distribution. Although only 15 species are described (eight from Brazil, one from Paraguay, five from Argentina and one from Chile), the *Ceromitia* group is much more diverse in central and southern South America and the total number of species may well exceed 40 (Davis, pers. comm.). *Ceromitia* species are known from Costa Rica to the southern Andes. The group is little collected outside southern forested Andean South America, where it is a conspicious element of the fauna. Pastrana (1961) recognized five species from this area, but many more species are now known to occur.

Biology. Little is known of the biology of the species of the *Ceromitia* group. The eggs of the Palaearctic genus *Nematopogon* Zeller, 1839, are laid in herbaceous plants, which the newly hatched larva leaves to construct a case from dead leaves and litter, the larvae most likely feeding on dead leaves. Elongate flat cases with *Ceromitia* larvae are frequently found in leaf-litter on the forest floor in the Andes, but nothing further is known of the biology of the larvae. Adults fly at dusk and dawn and come to light, often in vast numbers.

Phylogeny. The phylogeny of the Southern Hemisphere genera of the *Ceromitia* group is little understood. *Ceromitia* s. lat. occurs in Australia, Africa and South America, and is probably monophyletic since all its members have a resting posture which is not observed in other adelids.

The South American species have been placed in two genera, *Ceromitia* Zeller, 1852, and *Trichorrhabda* Meyrick, 1912, and a revision is being prepared by D. R. Davis, Washington, D.C.

Incurvariidae

The family comprises approximately thirteen genera worldwide. It is found in all zoogeographic regions, but is absent from New Zealand and is poorly represented in the tropics and sub-tropics. It reaches its greatest diversity in Australia with five genera and more than 60 species (Nielsen, unpublished).

Diversity and distribution. The South American incurvariid fauna was recently revised (Nielsen & Davis, 1981). Four species in two new genera (*Basileura* and *Simacauda*) were recognized, occurring in southern Argentina (provinces Neuquen, Rio Negro) and southern central Chile (provinces Osorno, Llanquihue). Recent collecting has produced specimens from Chubut province in Argentina and Valdivia province in Chile.

Biology. Larvae of most Incurvariidae first mine in leaves and then cut out an oval flat case which the larva uses as shelter when feeding within a new mine or leaf-skeletonizing. Pupation takes place inside the case on the ground. All incurvariids are restricted to woodlands and feed on broad-leaved trees and shrubs, especially of the families Myrtaceae, Proteaceae and Fagaceae. The South American species occur in Valdivian forest and *Nothofagus dombeyi* forest. Nielsen & Davis (1981) assumed that Myrtaceae are the hostplants for the species of both *Basileura* and *Simacauda*. This assumption has since been further substantiated for *Simacauda* as collecting around myrtaceaeus shrubs has produced many additional specimens of all three species. Moreover, empty incurvariid mines have been found on the same shrubs. *Basileura*, however, has been found to be associated with the evergreen *Nothofagus dombeyi*. No larvae have been reared but careful observations have shown that adults always occurred in places with *N. dombeyi* and could be collected by sweeping the foliage of that tree.

Phylogeny. Nielsen & Davis (1981) discussed the affinities of the two South American genera: *Basileura* and *Simacauda* were regarded as each others closest relatives and it was assumed that they represent the sister-group of all North Hemisphere Incurvariidae. The sister-group of the South American + North Hemisphere genera are most likely one or two yet unnamed large Australian genera with larvae feeding on Myrtaceae (*Eucalyptus*). There is no close relationship between the South American genera and the only South African genus *Protaephagus* Scoble, 1980.

Cecidosidae

The Cecidosidae (=Ridiaschinidae) are, together with some yucca moths, the only incurvarioids which have invaded arid and semi-arid

areas. The family is restricted to southern South America and southern Africa. There are two genera currently recognized in South Africa and four in South America (Nielsen, unpublished).

Diversity and distribution. The taxonomy of the South American Cecidosidae has been little studied since Brèthes (1916) but a revision of the family is in progress by D. R. Davis and E. S. Nielsen. Becker (1977) discussed the South American Cecidosidae and synonymized two of the genera, *Cecidoses* Curtis, 1835, and *Eucecidoses* Brèthes, 1916. His study was based on two species and additional material now seems to indicate that the two genera are probably distinct (Nielsen, unpublished). The other South American genera are *Oliera* Brèthes, 1916, and *Dicranoses* Kieffer & Jörgensen, 1910 (=*Ridiaschina* Brèthes, 1916). The four genera contain about ten species which are distributed from southern Brazil to Estrecho de Magellanes and from the Andes to the Atlantic coast. None of the genera seems restricted to the Andes, but there are records of *Oliera* from the Andes and species of both *Cecidoses* and *Eucecidoses* occur in arid areas adjoining the Andes.

Biology. All species of Cecidosidae for which the biology is known are gall makers in Anacardiaceae. One of the South African species makes galls on *Rhus*; the galls later drop to the ground where they become 'jumping beans'. Most of the South American species are gall-makers in *Schinus* and one species is reported to make galls in *Duvana*. The galls of *Cecidoses* are large and spherical, those of *Eucecidoses* and *Oliera* are smaller and spherical while the galls of *Dicranoses* are elongate and slender and clustered in large colonies. It is characteristic that one or few bushes of *Schinus* can be heavily infested with *Cecidoses* galls while nearby bushes are completely unaffected. Several papers of which Wille (1926) is the most extensive, describe the biology of *Cecidoses*.

Phylogeny. The Cecidosidae have been included variously in the families Incurvariidae or Prodoxidae by different authors. However, the six genera now recognized in the group display a remarkable suite of specialized traits and the monophyly of the taxon is not in dispute. It is best treated as a distinct family. The Cecidosidae seem most closely related to the Prodoxidae as these two groups are the only incurvarioids with endophagous larvae. Both the South African and South American genera seem to represent monophyletic entities within the family. Among the South American genera *Oliera* and the highly specialized *Dicranoses* (entirely with piliform scales, spurs 0-2-2, pretarsus without claws) are most closely related, as they both have the maxilla absent and pupa with a prominent, beak-like projection ('gall-cutter') (Nielsen, unpublished).

Prodoxidae

The North American yucca moths, the Prodoxinae of Davis (1967), are by far the best known representatives of the Prodoxidae. Some large North Hemisphere incurvarioid genera such as *Lampronia* Stephens,

1829 and *Greya* Busck, 1907 also belong to the Prodoxidae as currently defined (Nielsen, 1982a), and the family was until recently regarded as exclusively Holarctic. However, recent collecting in Valdivian rain forest in Argentina and Chile has produced a single new species in a new genus of prodoxids to be described elsewhere by Nielsen & Davis (in preparation).

Distribution. The first Southern Hemisphere prodoxid is known only from a rather small area of Valdivian forest on both sides of the Andes including the Rio Negro Province in Argentina and the Osorno province of Chile.

Biology. Larvae of prodoxids are internal feeders in twigs, buds and seeds of herbs and shrubs; they do not construct a case. Nothing is known of the biology of the South American taxon but the adults were always collected flying around or near myrtaceaous shrubs.

Phylogeny. The systematic position of the South American prodoxid is not yet fully analyzed, but it seems likely that it represents the sister-group of all other Prodoxidae. It is phenetically very distinct but possesses both prodoxid autapomorphies listed by Nielsen (1982a).

Tischeriidae

The Tischeriidae are another little studied family which occurs worldwide except for Australia and New Zealand. There are fewer than 100 described species in the family and all are currently placed in the genus *Tischeria* Zeller, 1839. The largest number of species is named from North America where the family seems to be relatively diverse (Braun, 1972). Nonetheless, the number of species in the western Palaearctic and SW Asia might well prove to be higher than that occurring in North America.

Diversity and distribution. The Tischeriidae seem weakly represented in South America with only seven named species so far: one from Mexico, two from the Caribbean, one from Guyana, one from the Buenos Aires province of Argentina and two from Peru. However, species of Tischeriidae are small and elusive moths and this low number might not do justice to the South American fauna. Recent collecting activity has however not produced any Tischeriidae from the southern Andes or southern Chile, but a few species have been collected in the western parts of the Patagonian steppe in the Argentinian provinces Rio Negro and Neuquen. Some undescribed species are known from Brazil.

Biology. All species for which the biology is known are leaf-miners in herbs, shrubs and trees of the families Fagaceae, Rosaceae and Malvaceae. Pupation takes place inside the mine. Nothing is known about the biology of any of the South American species.

Phylogeny. The family is little studied and nothing can yet be said about the systematic position of the South American species within the family.

Conclusion

The neopseustid *Apoplania chilensis* Davis was the only palaeolepidopteran known from South America until 1979. Since then several have been discovered: two genera of Micropterigidae, the new family Heterobathmiidae and a new genus and three species of Neopseustidae. Notable findings in the Neolepidoptera include the new exoporian family Neotheoridae and the first South American representatives of the families Palaeosetidae and Prodoxidae. It is therefore not surprising that an additional new family of primitive heteroneurans recently has been discovered independently by D. R. Davis and E. S. Nielsen. The family includes several species and is mainly confined to the Valdivian rainforest. The South American representatives are being dealt with by D. R. Davis. The family has been recognized recently in Australia (Nielsen, unpublished).

Acknowledgments. Mr. E. D. Edwards and Dr. M. Horak, Division of Entomology, CSIRO, Canberra, Australia, provided valuable comments on the manuscript. Unpublished manuscripts and information was made available by Dr. D. R. Davis, Washington, D.C., USA; Dr. G. W. Gibbs, Wellington, New Zealand; Dr. N. P. Kristensen, Copenhagen, Denmark; Dr. T. Kumata, Sapporo, Japan, and Mr. P. B. McQuillan, Hobart, Australia.

Literature Cited

BECKER, V. O., 1977. The taxonomic position of the Cecidosidae Brèthes (Lepidoptera). Polskie Pismo ent. 47:79-86.

BRAUN, A. F., 1972. Tischeriidae of America north of Mexico (Microlepidoptera). Mem. Am. ent. Soc. 28:1-148.

BRÈTHES, J., 1916. Estudio fito-zoologico sobre algunos Lepidopteros argentinos productores de agallas. An. Soc. cient. argent. 81:113-140.

CAREY, P., 1975. Biologia del minador del cambium de *Nothofagus dombeyi* (Mirb.) Oerst. 59 pp. - Universidad Austral de Chile, Valdivia.

———, C. SCOTT, L. CERDA M. & R. I. GARA, 1978. Ciclo estacional de un minador de coigue (*Nothofagus dombeyi*). Turrialba, 28:151-153.

CARTER, D. J. & J. D. DUGDALE, 1982. Notes on collecting and rearing *Micropterix* (Lepidoptera: Micropertigidae) larvae in England. Entomologist's Gaz. 33:43-47, pl. 2.

COMMON, I. F. B., 1973. A new family of Dacnonypha (Lepidoptera) based on three new species from southern Australia, with notes on Agathiphagidae. J. Aust. ent. Soc. 12:11-23.

———, 1975. Evolution and classification of the Lepidoptera. A. Rev. Ent. 20:183-203.

DAVIS, D. R., 1967. A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae). Bull. U.S. nat. Mus. 255:1-170.

———, 1975. Systematics and zoogeography of the family Neopseustidae with the proposal of a new superfamily (Lepidoptera: Neopseustoidea). Smithson. Contr. Zool. 210:i-iii, 1-45.

———, 1978. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae

(Lepidoptera). Smithson. Contr. Zool. 251:i-iv, 1-131.

_____ & E. S. NIELSEN, 1980. Description of a new genus and two new species of Neopseustidae from South America, with discussion of phylogeny and biological observations (Lepidoptera: Neopseustoidea). Steenstrupia, 6:253-289.

_____, 1985. The South American neopseustid genus *Apoplania* Davis: a new species, distribution records and notes on adult behaviour (Lepidoptera: Neopseustina). Ent. scand. 15:497-509.

GIBBS, G. W., 1979. Some notes on the biology and status of the Mnesarchaeidae (Lepidoptera). N.Z. Ent. 7:2-9.

_____, 1983. Evolution of Micropterigidae (Lepidoptera) in the S.W. Pacific Geo Journal 7:505-510.

HENNIG, W., 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. Beitr. Ent. (Suppl.), 3:1-85.

_____, 1981. Insect Phylogeny. xi + 514 pp. - John Wiley & Sons.

KRISTENSEN, N. P., 1978a. A new familia of Hepialoidea from South America, with remarks on the phylogeny of the suborder Exoporia (Lepidoptera). Ent. Germ. 4:272-294.

_____, 1978b. Observations on *Anomoses hylecoetes* (Anomosetidae), with a key to the hepialoid families (Insecta: Lepidoptera). Steenstrupia, 5:1-19.

_____, 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). Steenstrupia 10:141-191.

_____ & E. S. NIELSEN, 1979. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). Steenstrupia, 5:69-147.

_____, 1981. Intrinsic proboscis musculature in non-ditrysian Lepidoptera - Glossata: structure and phylogenetic significance. Ent. scand. Suppl. 15:299-304.

_____, 1982. South American micropterigid moths: two new genera of the *Sabatinca*-group (Lepidoptera: Micropterigidae). Ent. scand. 13:513-529.

_____, 1983. The *Heterobathmia* life history elucidated: Immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). Z. Zool. Syst. EvolForsch. 21:101-124.

NIELSEN, E. S., 1982a. Incurvariidae and Prodoxidae from the Himalayan area (Lepidoptera: Incurvarioidea). Insecta matsum. 26:187-200.

_____, 1982b. Review of the higher classification of the Lepidoptera, with special reference to lower heteroneurans. Butterfl. Moths, 33:98-101.

_____, in press. The monotrysian heteroneuran phylogeny puzzle: a possible solution (Lepidoptera).

_____ & D. R. DAVIS, 1981. A revision of the Neotropical Incurvariidae s.str., with the description of two new genera and two new species (Lepidoptera: Incurvarioidea). Steenstrupia, 7:25-57.

_____ & G. S. ROBINSON, 1983. Ghost moths of southern South America (Lepidoptera: Hepialidae). Entomonograph, 4:1-192.

PASTRANA, J. A., 1961. La familia Adelidae (Lep.) en la Republica Argentina. Physis B. Aires, 22:191-201.

SCOBLE, M. J., 1983. A revised cladistic classification of the Nepticulidae (Lepidoptera) with descriptions of new taxa mainly from South Africa. Monogr. Transv. Mus. 2:i-xi, 1-105.

WILLE, J., 1926. *Cecidoses eremita* Curt. und ihre Galle an *Schinus dependens* Ortega. Z. Morph. Okol. Tiere, 7:1-101.

ZIMMERMAN, E. C., 1978. Microlepidoptera. Part 1. Monotrysia, Tineoidea, Tortricoidea, Gracillarioidea, Yponomeutoidea, and Alucitoidea. Insects Hawaii, 9(1):i-xx, 1-881, pls. 1-8.

Table 1. Proposed classification of the primitive Lepidoptera. One asterisk (*) indicates families represented in South America; two asterisks (**) indicate families endemic to South America.

LEPIDOPTERA

ZEUGLOPTERA
- Micropterigoidea
  - Micropterigidae*

AGLOSSATA
- Agathiphagoidea
  - Agathiphagidae

HETEROBATHMIINA
- Heterobathmioidea
  - Heterobathmiidae**

GLOSSATA

DACNONYPHA s.lat.
- Eriocranioidea s.lat.
  - Eriocraniidae
  - Lophocoronidae
  - Acanthopteroctetidae

NEOPSEUSTINA
- Neopseustoidea
  - Neopseustidae*

EXOPORIA
- Mnesarchaeoidea
  - Mnesarchaeidae
- Hepialoidea
  - Neotheoridae**
  - Anomosetidae
  - Prototheoridae
  - Palaeosetidae*
  - Hepialidae*

HETERONEURA

NEPTICULINA (=NANNOLEPIDOPTERA)
- Nepticuloidea
  - Nepticulidae*
  - Opostegidae*

INCURVARIINA
- Incurvarioidea
  - Heliozelidae*
  - Adelidae*
  - Crinopetrygidae
  - Incurvariidae*
  - Cecidosidae*
  - Prodoxidae (=Lamproniidae)*

TISCHERIINA
- Tischerioidea
  - Tischeriidae*

DITRYSIA