A review of wing reduction in Lepidoptera

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CONTENTS

SYNOPSIS. In Lepidoptera, wing reduction associated with loss of flight has evolved in many independent lineages in 25 of about 120 currently recognized families; however, less than one per cent of all known species are affected, reduction usually being confined to the female sex. The phenomenon of wing reduction is here examined throughout the Lepidoptera, the literature on the subject is reviewed, implications of flightlessness are discussed and the major hypotheses on the evolution of wing reduction are critically evaluated. A systematic list of family-group taxa in which wing reduction occurs is provided together with a list of all Microlepidoptera, including Pyralidae, known to be wing-reduced. An overview of the 25 families with wing-reduced taxa is given and a number of examples are illustrated.

INTRODUCTION

The acquisition of wings suitable for sustained directional flight undoubtedly played a crucial part in the evolution of insects and is a major reason for their success. The advantage of flight lies in greatly enhanced possibilities for the location of food sources for the adults and host-substrates for their early stages, mate location, dispersal and escape from predators. The possible

role of the wings in maintaining the thermal balance of an insect by providing a large surface area for the exchange of heat with the environment must also be considered. Yet in spite of such seemingly obvious benefits, a smaller or larger number of species within most major insect orders, for example Hemiptera, Coleoptera, Hymenoptera, Diptera, Neuroptera and Lepidoptera, have secondarily lost the ability to fly, sometimes in only one sex, whilst the wings have undergone various degrees of reduction culminating in their complete loss.

The Lepidoptera are characterised by two pairs of scale-covered wings, but within the order a considerable degree of wing shape diversity can be observed. The most primitive Lepidoptera have broadly lanceolate wings with a short fringe; fore and hind wings are of the same shape and size and have similar (homoneurous) venation. In higher, heteroneurous Lepidoptera the number of wing veins is somewhat reduced and, as the hind wing has lost more veins than the fore wing, both pairs are dissimilar. In many Microlepidoptera, for example Nepticulidae, Gracillariidae and Coleophoridae, the hind wing is very narrow, but this reduction is compensated by a greatly extended fringe. Similarly in Alucitidae and Pterophoridae both pairs of wings are divided into narrow branches which are connected and surrounded by long fringes. If the wings play a significant part in heat regulation such modifications of their shape may be a means of reducing the heat-exchanging wing surface without losing the aerodynamic benefits of the larger wing area. In numerous groups of Lepidoptera some genuine reduction of one pair of wings, usually the hind wings, can be observed, for example in the males of the Australian genera *Tympanota* Warren and *Sauris* Guenée (Geometridae) (Dugdale, 1980). Amongst the more extreme examples are the Indian himantopterine Zygaenidae with filiform hind wings and the male of the South American *Diptilon culex* Draudt (Arctiidae, Ctenuchinae) with hind wing vestiges so small that they are concealed in the metathoracic hair cover. However, as such specialisations, even when extreme, do not render the affected insects flightless, this phenomenon is not pursued further in this paper. By contrast, the presence of fully developed, seemingly functional wings is no indication that they are actually used, and there is ample evidence that some species are more active fliers than others. Females especially are frequently sluggish and those of many species rarely take to the air before they have mated and deposited at least part of their egg complement; but flightlessness without wing reduction is also outside the scope of this review.

In the Lepidoptera flightlessness coupled with some degree of wing reduction, usually brachyptery, is an exception and affects less than one per cent of the currently known 150,000–200,000 species. Nevertheless, wing-reduced species are recorded in 25 out of the 120 or so currently recognised families, representing 11 of the 38 superfamilies. In the primitive, non-ditrysian families wing reduction is unknown except in a few Hepialidae; it is also unknown in the ditrysian superfamilies Cossoidea, Castniodea, Sesioidea, Immoidea, Alucitoidea, Pterophoroidea, Calliduloidea, Hedyloidea, Hesperioidea, Papilionoidea, Mimallonoidea and Sphingoidea.

Although wing reduction in Lepidoptera is not a uniform phenomenon, and each case should be looked at on its own merit, a number of general principles are recognizable. It has evolved many times independently and is a positive strategy, not an evolutionary blind alley that leads to early extinction. There is no apparent phylogenetic predisposition to such reduction; it can evolve in any family, provided specific preconditions are met. Wing reduction is almost exclusive to the female sex, but in rare instances has evolved in both sexes. Reduced wings are frequently correlated with reduced mouthparts and, where applicable, reduced tympanal organs; in females there is also a correlation with an extension of the ovaries into the thorax. In most instances reduction has occurred either as a consequence of sedentary habit or in response to certain environmental factors. Species of the first category have more or less reduced legs whilst those of the second category have retained full use of their legs and are able to run and sometimes jump. Wing reduction in response to environmental conditions occurs mainly in species that are endemic to small oceanic islands, or inhabit the alpine zone of high mountains, or have their adult activity period in the cold season.

According to Dierl & Reichholf (1977: 30) wing reduction mainly occurs within small systematic units such as genera or groups of genera in which it affects all or most species. Examples in support of this contention are *Diurnea* Haworth and *Cheimophila* Hübner (Oecophoridae), *Ceuthomadarus* Mann (Lecithoceridae) and many genera of Geometridae. However, an analysis on a world basis indicates that wing-reduced species are more frequently the exception within large genera of fully winged species, for example *Pharmacis* Hübner (Hepialidae); *Tinea* Linnaeus, *Eudarcia* Clemens (Tineidae); *Kessleria* Nowicki (Yponomeutidae); *Ethmia* Hübner, *Thyrocopa* Walsingham, *Borkhausenia* Hübner, *Pleurota* Hübner (Oecophoridae); *Elachista* Treitschke (Elachistidae);

Symmoca Hübner (Symmocidae); *Kiwaia* Philpott, *Ephysteris* Meyrick, *Caryocolum* Gregor & Povolný, *Stomopteryx* Heinemann (Gelechiidae); *Oxypteron* Staudinger (Tortricidae); *Synaphe* Hübner, *Catoptria* Hübner, *Orocrambus* Purdie (Pyralidae); *Xanthorhoe* Hübner, *Elophos* Boisduval (Geometridae); *Orgyia* Ochsenheimer (Lymantriidae); *Xestia* Hübner, *Agrotis* Ochsenheimer (Noctuidae) and others. It should therefore not be assumed automatically that wing reduction affects all members of a genus if it is known to occur in one of them. For example, Dierl (1983: 141) implies that the females of all species of *Estimata* Kozhanchikov (Noctuidae) are brachypterous, although those of all but one species are still unknown.

In almost all cases wing reduction is restricted to the female sex whilst the male retains fully developed wings and the ability to fly. Wing reduction in both sexes is extremely rare; it is recorded in 10 different families and affects only about 25 species, most of them inhabitants of southern ocean islands. Flightlessness with wing reduction affecting solely the male sex is so far unknown in Lepidoptera.

Terminology

Depending on the state of their wings and the degree of reduction, Lepidoptera can be classified as macropterous, brachypterous, stenopterous, micropterous or apterous; however, these are not clear-cut categories and the terminology is often applied loosely, in particular the term brachyptery, which may encompass stenoptery and microptery. The classification is restricted to the wing itself and disregards the associated flight musculature and the actual ability to fly. See also Hackman (1966: 2).

Macropterous — species with fully developed wings (e.g. Figs 1, 3, 5, 9). Macropterous species are usually but not always capable of flight. For example the macropterous female of *Lymantria dispar* (L.) (Lymantriidae) is more or less flightless.

Brachypterous — species showing various degrees of wing reduction (e.g. Figs 2, 4, 6–8, 12). In a living brachypterous moth the wings are usually exceeded to a greater or lesser extent by the abdomen. The wing shape is broadly lanceolate and one or more veins are lost, although some tubular veins are retained, at least in the fore wing. The hind wing may be further reduced than the fore wing and may have lost all tubular veins (for example in *Sattleria* ♀), but often retains the frenulum. Brachypterous moths are incapable of sustained flight.

Stenopterous — species with the fore wing strongly reduced in width but without any significant reduction in length. The hind wing is also reduced and may be vestigial although the frenulum is usually present. Stenoptery is very rare but is observed, for example, in the females of *Pleurota marginella* (Denis & Schiffermüller) (Oecophoridae) (Fig. 10; Spuler, 1910: 341, pl. 88, fig. 69b, as *P. rostrella* Hübner) and *Spartopteryx kindermannaria* (Staudinger) (Geometridae) (Fig. 45; Wehrli, 1941: 466, pl. 41b). Stenopterous moths are incapable of flight.

Micropterous — species with both pairs of wings reduced to small unstructured lobes (Figs 32, 60). All tubular veins are lost and the upper and lower wing membranes are often separated. The hind wing vestige has also lost the frenulum, for example, *Erannis defoliaria* (L.) (Geometridae); *Chondrostega* species (Lasiocampidae).

Apterous — species without any external remnants of wings. Aptery is very rare and, where it occurs, is confined to the females; no species with apterous males is known. Certain species sometimes referred to in the literature as 'apterous' or 'wingless' still have external wing vestiges, for example some geometrid winter moths. An example of true aptery is the female of *Cheimoptena pennigera* Danilevsky (Danilevsky, 1969a: 182, fig. 10).

Phases of wing reduction

In various Lepidoptera sexually dimorphic wing shapes can be observed. Such dimorphism may reflect the different flight requirements of the sexes resulting, for example, from their different body weight; however, even if small, it may be the first indication of a trend towards wing reduction in the female.

The reduction of the wings follows a distinct evolutionary (but not phylogenetic) sequence and examples of all intermediate stages between macroptery and aptery are found. Initially the distal half of the fore wing becomes narrower; if a distinct tornus was present this is reduced until the wing margin (dorsum and termen) is an even curve from base to apex and the formerly triangular wing has become broadly lanceolate. Simultaneously the hind wing changes shape and in broad-winged forms also becomes lanceolate.

The slight sexual wing dimorphism in *Chionodes pergrandella* (Rebel) (Gelechiidae) (Burmann, 1977: figs B2 ♂, B3 ♀, as *C. decolorella*) from the European Alps and Central Asia is seen as an example of an early stage in the development of female brachyptery (Sattler, 1986: 258–259). In

the male the costal and dorsal margins of the fore wing diverge towards the termen, and the wing is distinctly wider at two-thirds than at one-third whereas in the female both margins run almost parallel and the wing is not wider at 2/3. The hind wing termen of the female is more oblique than that of the male and the apex is more pointed.

In *Thyrocopa apatela* (Walsingham) (Oecophoridae, Xyloryctinae) (Figs 7, 8; Zimmerman, 1978: figs 645, 650, ♀) from Hawaii wing reduction is further advanced. Both wings have become lanceolate and the venation in the distal half is much condensed. In the fore wing R4 and R5 are almost coincident and one M vein is lost; in the hind wing M3 and CuA1, which are usually connate in *Thyrocopa* Meyrick, have migrated onto a common stalk. The hind wing is significantly smaller than the fore wing, whereas in other members of this genus they are of about equal size.

Further simplification of the venation is followed by withdrawal of the veins from the wing margin (accompanied by loss of the marginal sensilla campaniformia) and gradual loss of the tubular structure of the remaining veins (Baus, 1936: 45). For example, in the fore wing of *Areniscythris brachypteris* Powell (Scythrididae) from California only part of Sc, the R stem with traces of R5 and sometimes R4, and the partly obsolete M3 and 2A are present whilst the hind wing venation is reduced to just traces of Rs and 2A (Powell, 1976b: figs 2, 3, ♀).

With the loss of the tubular veins the upper and lower membranes of the wing vestiges become separated and the sensilla campaniformia are lost except for some of those on the wing base (Baus, 1936: 45). This stage is reached in the vestigial wings of *Erannis defoliaria* (L.) (Geometridae) female. Complete loss of the wings is known in the females of certain Psychidae (Dierl, 1973) and Heterogynidae (Daniel & Dierl, 1966, figs 2, 3) but is also recorded, for example in *Cheimoptena pennigera* Danilevsky (Geometridae) (Danilevsky, 1969a: 183, fig. 10), *Orgyia ericae* (Germar) and *O. dubia* (Tauscher) (Lymantriidae) (Heitmann, 1934: 180). No cases of aptery in male Lepidoptera are known.

The frenulum is lost at a very late stage in the reduction process. It is still present on the rudimentary hind wings of *Pleurota marginella* (Denis & Schiffermüller) (= *rostrella* Hübner) (Oecophoridae) and *Sattleria* Povolný (Gelechiidae), which have lost all tubular veins, but is absent from the hind wing vestiges of *Erannis defoliaria* (L.) and others.

The reduction of the hind wing and its venation progresses faster than that of the fore wing. For example the stenopterous female of *Pleurota marginella* (Denis & Schiffermüller) and brachypterous females of *Sattleria* spp. retain still most of their original venation in the fore wings whilst the vestigial hind wings have lost all tubular veins.

Correlation between the reduction of wings and reduction in other organs

The correlation between wing reduction and reduction of the mouthparts was investigated and discussed in detail by Naumann (1937). A tendency towards reduction of the mouthparts is widespread in the Lepidoptera, and examples of a reduced proboscis are found in most families, although there are fewer in groups of strong fliers such as the Sphingidae and Noctuidae and, as to be expected, very few in the butterflies, for example some African Lycaenidae of the subfamily Lipteninae (Eliot, 1973: 394). In fully winged species the mouthparts are mostly developed equally in both sexes whereas in those with wing reduction in the female the male has a longer proboscis. Nevertheless, in such species the male proboscis (in relation to the body length) is shorter than in related fully winged species, which indicates that mouthpart reduction affects both sexes, even though it is distinctly more advanced in the female. Differences in the length of the proboscis between macropterous males and wing-reduced females raise the question whether in some instances the former may still feed whilst the latter no longer do so.

A close correlation between wing reduction and the reduction of the tympanal organs in Geometridae, Lymantriidae, Arctiidae and Noctuidae was observed and discussed in detail by Heitmann (1934) and Gohrbandt (1938) (see also p. 250).

Teratological wing reduction

In most macropterous Lepidoptera individuals with imperfectly developed wings are occasionally observed. Failure to expand the wings properly, following emergence from the pupa, is usually the result of mechanical damage or other unfavourable influences, such as lack of moisture during the pupal or perhaps larval stage. According to some observers the females are more susceptible to such damage than the males. Crippled individuals frequently result from pupae that were kept too dry, and even the condition of the host-plant during the larval stage may be significant. For example, Loritz (1952) considered casual brachyptery in females of *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Thaumetopoeidae) reared in captivity to be the result of desiccated larval food.

Apart from the failure to expand an otherwise normally developed wing completely, the loss of one or more wings, usually a hind wing, is also known and is commonest in the Geometridae. During a mass occurrence of *Eulype hastata* (L.) (Geometridae) in Finland in 1947 Hackman (1966: 2) observed that for an unknown reason about 25% of all specimens lacked one or both of their hind wings. Burmann linked a similar observation on *Semiothisa clathrata* (L.) (Geometridae) in Austria to the influence of an unidentified herbicide on the host-plants of the larvae. Many of the *clathrata* examined in a locality near Innsbruck lacked one or rarely both of their hind wings (Burmann, 1973: figs 1–5); two individuals of *Perizoma blandiata* (Denis & Schiffermüller) (Geometridae) with the same defect were also observed. Amongst the defective individuals both sexes were represented in about equal numbers and the affected wings were lost completely, without any trace of external rudiments. The F1 generation reared from one normal and two defective *clathrata* females had normal wings.

Knatz (1891) assumed accidental deformation of the wings, resulting from unfavourable influences during the larval or pupal period, to be the primary cause of wing reduction. Males thus affected would simply perish without a chance of finding a mate, whereas females rendered flightless would still be fertilized. Continued over long periods this effect would be increased and finally lead to wing reduction in the female. As a result the thorax would become smaller and the abdomen larger with the ovaries increasing in size. The mouthparts of the males of such species would be reduced because the male would have to spend more time in search of the non-motile female and consequently would have less time for feeding. Moreover, its chances of meeting the (non-motile) female at the food source would be diminished. However, it is unlikely that accidental wing deformation has played a significant role, if any at all, in the evolution of flightlessness and wing reduction because no selective advantage to the female can be demonstrated.

Feeding and flight

For reasons of longevity, slow progressive maturing of the ova after emergence of the female from the pupa, energy-intensive courtship, search and dispersal flights, migration etc., many adult Lepidoptera must feed to supplement the energy that was stored at the larval stage. They take energy in the form of pollen, nectar, decaying fruit and other plant material, sap from injured trees and other usually liquid substances, and flight plays so important a part in the search for such non-ubiquitous food sources that non-feeding must be considered one of the preconditions for the evolution of flightlessness. It is therefore not surprising to find that certain species with wing reduction were pre-adapted in that respect, because they are members of generally non-feeding families in which mouthpart reduction is a family characteristic, for example Hepialidae, Psychidae, Lasiocampidae and Lymantriidae. However, other wing-reduced species, although themselves having reduced mouthparts, are more or less closely related to taxa which have fully developed apparently functional mouthparts. For example, in *Apocheima* Hübner and *Lycia* Hübner, both genera with wing-reduced females, the mouthparts are reduced, whereas in the closely related but fully macropterous genus *Biston* Leach (Geometridae) they are well developed.

Similarly, in *Ethmia charybdis* Powell (Oecophoridae, Ethmiinae), a species with brachypterous females, the mouthparts are reduced (Powell, 1971: 31) whereas in other species of *Ethmia* Hübner they are well developed. For example, in *E. aurifluella* (Hübner) and *E. lineatonotella* (Moore), both sexes fully winged, the distal portion of the proboscis bears characteristic sensilla styloconica (Sattler, 1967: pls 12, 13), which are chemoreceptors, possibly sensitive to sucrose (Städler *et al.*, 1974: 63). Their presence suggests that such species may feed; however, within *Ethmia* various degress of reduction of the proboscis and the labial and maxillary palpi are known (Sattler, 1967: 10, pl. 11) and indicate that there may be a general shift away from feeding. It is possible that even a somewhat reduced proboscis is still used to take in water, which is readily available as rain or condensation in most habitats, to counteract desiccation. Non-feeding may have been an important pre-adaptation in certain moths that facilitated a shift of their adult activity period to the cold season with its absence of flowers and paucity of other energy sources.

According to Tweedie (1976) abstention from feeding as an adult is the main cause of wing reduction in the female. A non-feeding female will have a heavy abdomen as a consequence of having to store enough nutrient in the larval stage for its full egg complement. This causes reduction of flight activity and eventually results in reduction of unused flight organs. However, whilst non-feeding is a precondition to flightlessness, it is unlikely to be the main factor in its evolution, because there are successful strategies available to maintain the ability to fly when the body weight is increased.

Courtship and flight

The importance of flight in the courtship process of the Lepidoptera and the crucial role of the male in mate locating must be seen as the major reason why flightlessness and wing reduction are usually restricted to the female and are only found exceptionally in the male (see p. 251). In most Lepidoptera the male alone is responsible for finding a mate. It is usually guided to its target by pheromones emitted by a stationary female, and tacking against the wind, often flying close to the ground, is the most effective means of scanning a large area for a pheromone plume. Even in those groups in which the female is attracted to the male at some stage in the courtship process, flight remains essential for the latter to fulfil its role, for example by congregating with other males on flowers, where the sexes meet (Micropterigidae), performing courtship dances (Hepialidae), forming courtship swarms (Adelidae) or setting up and defending territories (butterflies) to which the females are attracted. Intrasexual competition in that process acts as a powerful effective barrier against flightlessness in the male, whereas in most Lepidoptera no such constraints act upon the female. Similarly, a mate locating system that requires active participation of the female is an obstacle to the evolution of flightlessness in that sex.

Oviposition and flight

Most Lepidoptera live in a non-homogeneous environment where flight is essential or at least highly advantageous to the female in locating a suitable oviposition site. The larvae of many species, in particular those of most Microlepidoptera, are highly host-specific. They often feed on annual plants and other non-permanent, discontinuous food sources, and their respective host-plants are not always available in the immediate vicinity of a freshly emerged female. For example, annual plants die off during the winter, and fresh plants may have appeared elsewhere when the female emerges from an overwintered pupa. Some larvae also undergo a change of diet, as a consequence of which pupation may take place at some distance from their initial host-plant. For example, the first instar larvae of Adelidae mine the leaves of certain living plants whilst later instars are scavengers amongst leaf litter on the ground. In all such instances the female has to find the host-plant of the first instar larva for oviposition, and the selective advantage of flight in this process is so great that flightlessness would only have a chance to evolve in a habitat that is

sufficiently permanent and continuous to allow non-selective oviposition. Such a condition is met in species with larvae that are omnivorous (*Pringleophaga* Enderlein, Tineidae), scavengers (various Tineidae, Psychidae, Oecophoridae, Lecithoceridae, Symmocidae), polyphagous (most cold season Oecophoridae and Geometridae; Lymantriidae) or host-specific but inhabiting single species plant communities or sites in which their host-plant dominates.

A number of species with brachypterous females or with wing reduction in both sexes inhabit grassland, which constitutes a permanent, continuous habitat. Their larvae feed on roots or green tissue, often apparently without specialization on a particular grass species. Grassland inhabitants are *Pharmacis* spp. (Hepialidae), *Embryonopsis halticella* Eaton (Yponomeutidae), *Pleurota marginella* (Denis & Schiffermüller) (Oecophoridae), *Elachista* spp. (Elachistidae), *Megacraspedus* spp. and probably *Ephysteris* spp. (Gelechiidae), *Catoptria* spp. and *Exsilirarcha graminea* Salmon & Bradley (Pyralidae, Crambinae, Scopariinae) and others. A few cold season species are apparently monophagous on certain trees, e.g. *Exapate duratella* (Heyden) (Tortricidae) on *Larix* and the Geometridae *Erannis ankeraria* (Staudinger) on *Quercus* and *Alsophila quadripunctaria* (Esper) on *Acer*, and it is likely that a single tree of adequate size can act as an island large enough to sustain a viable population over many years.

Flight as an escape mechanism

Many Lepidoptera react to disturbance of their immediate vicinity, for example vibrations caused by an approaching person or animal, by flying away. The question has to be asked whether flight is essential in avoiding danger or whether a species could adequately protect itself by other means were it to lose the ability to fly. The greatest danger to adult Lepidoptera is predation, primarily by vertebrates (insectivorous birds, mammals and reptiles), but whilst flying undoubtedly provides an important escape mechanism, there are also numerous other successful strategies. These include living under conditions of naturally reduced predator pressure as they prevail, for example, on low diversity oceanic islands (Gressitt, 1970: 316), possibly on high mountains, or during the cold season of the northern hemisphere (Dierl & Reichholf, 1977: 33). When at rest individuals can hide in inaccessible places such as scree, dense vegetation, under bark etc., or rely on cryptic coloration. Many species are protected by unpalatable or poisonous hairs or

substances and advertise this fact by aposematic coloration. The loss of flight still leaves other forms of motility such as running, jumping or simply dropping to the ground, often followed by feigning death. All these strategies, individually or in combination, are widely and successfully employed in Lepidoptera and indicate that the need to avoid predators would be no insurmountable obstacle to flightlessness. There is even evidence that the wing-reduced sex sometimes may be better protected from predators than the fully winged one. For example, in the Alps, Pinker (1953: 179) and Burmann (1956) observed very heavy bird predation on the macropterous males of *Lycia alpina* (Sulzer) (Geometridae) whilst the equally common brachypterous females were apparently ignored by the predators.

Sedentary habit and locomotion in wing-reduced moths

Without the need to fly for purposes of feeding, mating or ovipositing the females of certain species, for example Psychidae, Heterogynidae, Lymantriidae and Artiidae, have become more or less sedentary, in extreme cases even followed by a partial reduction of their legs. The sedentary females remain near, on or inside the pupal cocoon; those of certain Psychidae do not even emerge from the pupa, for example *Thyridopteryx ephemeraeformis* (Haworth) (Davis, 1964: 11, figs 144, 145) or *Megalophanes viciella* (Denis & Schiffermüller) and others (Dierl, 1973: 3). Mating takes place in situ and the eggs are deposited in one batch on the pupal cocoon (*Orgyia* Ochsenheimer, Lymantriidae), in the larval/pupal case (many Psychidae) or in the pupal exuviae (some Psychidae; Heterogynidae). By contrast, the brachypterous females of most other species have retained some degree of motility and normally are capable of running and climbing. The larvae of many cold season moths, such as *Diurnea* Haworth (Oecophoridae), *Exapate congelatella* (Clerck) (Tortricidae) and many Geometridae, are polyphagous on deciduous trees and pupate on the ground. After emerging from the pupae such females are able to find and ascend a tree, where mating and ovipositing take place. In sparsely vegetated alpine habitats with limited stands of the host-plant, flightless females of the motile type are able to move between plants and disperse their egg complement. For example, in the almost barren habitat of *Sattleria melaleucella* (Constant) in the Lechtaler Alpen the main host-plant in that locality, *Saxifraga biflora* subsp. *macropetala*, grows in clusters which are often too small to accommodate

all the offspring of one female so that some motility is advantageous.

Several observers have specifically commented on the remarkable ability of certain brachypterous moths for making short jumps, covering distances of about 5 cm or more; however, jumping is sometimes also observed in species that normally fly. Petry (1904: 6) described the movements of the males of *Acompsia dimorpha* Petry (Gelechiidae), which approached a freshly emerged female in early morning, as more hopping than flying ('mehr hüpfend als fliegend'). Jumping as an escape mechanism was observed in *Scythris inspersella* (Hübner) (Scythrididae), a fully winged species that normally flies; the adults visit various flowers from which they jump to the ground rather than fly away when disturbed (Sattler, 1981: 16). As a regular behaviour jumping is known in both sexes of the fully winged but nevertheless flightless Gelechiidae *Gnorimoschema bodillum* Karsholt & Nielsen from Denmark (Karsholt & Nielsen, 1974: 96) and *Scrobipalpula* sp. from the Falkland Islands (Kirke, pers. comm.); exceptionally it also occurs in the male of *Sattleria melaleucella* (Constant) (pers. obs.), which is capable of normal flight. Jumping as a regular means of locomotion or in response to disturbance has been recorded in the brachypterous females of *Kessleria zimmermanni* Nowicki (Yponomeutidae); *Thyrocopa apatela* (Walsingham) (both sexes), *Atomotricha ommatias* Meyrick, *Pleurota marginella* (Denis & Schiffermüller) (Oecophoridae); *Elachista galatheae* (Viette) (Elachistidae) (both sexes); *Kiwaia jeanae* Philpott (both sexes), *Caryocolum laceratella* (Zeller), *Sattleria* species (Gelechiidae); *Areniscythris brachypteris* Powell (Scythrididae) (both sexes); *Sorensenata agilitata* Salmon & Bradley (probably both sexes, female unknown), *Sphaleroptera alpicolana* (Frölich) (Tortricidae); *Campbellana attenuata* Salmon & Bradley (Carposinidae) (both sexes) and *Exsilirarcha graminea* Salmon & Bradley (Pyralidae) (both sexes). The presence of this habit in at least eight different families, representing the superfamilies Yponomeutoidea, Gelechioidea, Tortricoidea, Copromorphoidea and Pyraloidea, is an indication that it may have evolved many times independently from the moths' normal take-off mechanism for flying.

Although widespread in wing-reduced Lepidoptera, jumping appears to be restricted to species that live on the ground in places with exposed soil and sparse vegetation, for example *Thyrocopa apatela* (Walsingham), *Sattleria* species, *Areniscythris brachypteris* Powell, or in dense grass, for example *Elachista galatheae* (Viette), *Pleurota marginella* (Denis & Schiffermüller), *Exsilirarcha*

graminea Salmon & Bradley, sometimes *Sattleria* species. This habit is not developed in motile tree-living moths such as *Diurnea* species and the various geometrid winter moths (*Alsophila* Hübner, *Operophtera* Hübner, *Erannis* Hübner and others), nor in the Psychidae and the females of heavy-bodied moths (Lasiocampidae, Lymantriidae, Arctiidae), many of which are sedentary. According to Harper (1990: 44) the brachypterous female of *Diurnea fagella* (Denis & Schiffermüller), when disturbed while at rest on a tree trunk, drops slowly, its fall apparently controlled by the outstretched wings. Although the descent is not vertical but proceeds at an angle it cannot be described as true gliding. Little is known about locomotion in the wing-reduced Noctuidae on southern ocean islands, but it would not be surprising if at least the micropterous *Dimorphinoctua cunhaensis* Viette were capable of jumping.

Whilst in the wing-reduced females of certain Psychidae, Heterogynidae, Lasiocampidae, Lymantriidae and Arctiidae the legs are more or less strongly reduced as a consequence of their sedentary habit, there is little evidence that in wing-reduced but motile species the legs are better adapted to running or jumping than in their fully winged close relatives that fly. According to Powell (1976*b*: 328) *Areniscythris brachypteris* Powell (brachypterous in both sexes) possesses longer tarsi and a 1.5 times thicker hind femur than several other Scythrididae of comparable size; however, those differences are relatively slight. Moreover, the systematic position of *Areniscythris* Powell is still somewhat unclear and it is therefore uncertain whether the examined *Scythris* species are systematically close enough for a meaningful comparison. The legs of *Thyrocopa apatela* (Walsingham) (brachypterous in both sexes) do not differ noticeably from those of fully winged *Thyrocopa* species and there are no appreciable differences in leg structure between the macropterous flying males and brachypterous running and jumping females of *Sattleria* species. No comparative studies of the leg musculature in jumping and non-jumping moths are available, but if we consider jumping as merely a behavioural remnant of the normal take-off for flight, the absence of special adaptions for that means of locomotion would not be surprising.

Ovarial development and flightlessness

In broad agreement with several previous authors (Naumann, 1937; Eggers, 1939; Downes, 1964; Hackman, 1966) the crucial initial factor in the process that leads to flightlessness and wing reduction in the females is seen in the degree of maturity the eggs have reached when the adult emerges from the pupa. Those species in which they mature gradually after the female has left the pupa must be relatively long-lived and depend on feeding to sustain themselves and obtain extra energy for the development of the eggs. The importance of flight in the search for food sources makes it unlikely that flightlessness evolves in such moths or, for the same reason, in many butterflies. By contrast, females that emerge from the pupa with a fully mature egg complement are able to mate and oviposit immediately, before the first flight, if other conditions permit. For example, if the male is attracted to the female and the larvae are generalist rather than specialist feeders, oviposition can take place more or less on the spot without the female having to search for a mate or a specific host-plant and therefore without gaining any significant advantage from the ability to fly. Such species can afford to be short-lived and thus need not feed. A short adult life span would also reduce the exposure of the egg-laden female to predators.

An increase in the number of fully developed eggs is accompanied by an increase in ovarial size, and the growing ovaries gradually displace the tracheal air sacs and tympanal organs, where present, resulting in a heavier abdomen. The main function of the tympanal organs being the detection of ultrasonic cries of insectivorous bats (Spangler, 1988), the loss of that organ is of little consequence to non-flying moths, whilst conversely it is advantageous to a moth that has lost its hearing ability to avoid flying and thus not expose itself to such predators. With a further increase in size the ovaries of various species extend more or less deeply into the thorax, for example in *Orgyia* Ochsenheimer (Lymantriidae) (Heitmann, 1934: 174–180) and *Ocnogyna* Lederer (Arctiidae) (Heitmann, 1934: 180–183), until they finally fill the entire cavity of the thorax, for example in *Heterogynis penella* (Hübner) (Heterogynidae) (Dierl, 1966: 459) and *Erannis defoliaria* (L.) (Geometridae) (Heitmann, 1934: 165). Some reduction of the flight musculature was observed in the brachypterous females of *Agrotis fatidica* (Hübner) and *Ulochlaena hirta* (Hübner) (Noctuidae) (Gohrbandt, 1938: 18) and can be expected whenever the ovaries extend a significant distance into the thorax. It is thus likely that the ability to fly is adversely affected not only by the increasing body weight, which may lead to decreasingly favourable wing loading (i.e. wing: body ratio) and consequently less sustained flight, but also by direct interference of the expanding ovaries with the flight musculature. With decreasing readiness to fly, the trend towards early mating and oviposition

becomes stronger and the females of various species deposit most of their egg complement before the first flight takes place, for example the genus *Setina* Schrank (Arctiidae) (Burmann, 1957, as *Endrosa* Hübner). Continuation of this trend leads eventually to flightlessness and sedentary behaviour with progressive reduction of the wings and legs as observed in families such as Psychidae, Heterogynidae and Lymantriidae and Arctiidae where the females no longer leave the pupation site.

Wing reduction in males

As a result of the division of functions between male and female the sexes have different flight requirements and consequently are subjected to different selective pressures with regard to their flight organs and their ability to fly. This is immediately obvious from the fact that wing reduction rarely occurs in the male. An analysis of those species that are wing-reduced in both sexes shows that they are all inhabitants of mostly small oceanic islands or restricted coastal habitats. The effect of continuous strong winds has long been invoked to explain the high incidence of wing reduction in island insects and provides also the most plausible explanation for brachyptery in Lepidoptera males. The most important activity of the male involving flight is the search for a mate; however, continuous high wind speeds, as they prevail for example on the small sub-Antarctic islands, make directional flight impossible. Individuals attempting to fly will be carried out of their habitat without much chance of regaining it (Gressitt, 1970: 364). Moreover, very strong winds must rapidly disperse the pheromones emitted by a female to such an extent that no pheromone trail would develop for the male to follow. Under such circumstances there would be no attraction over long distances whilst over short distances, for example in the shelter of grass tussocks and other dense, low-growing vegetation, alternative means of locomotion, such as jumping or running, are more effective. In an environment where high wind speeds are the norm a shift from flying to jumping and a reduction of the wing area exposed to the wind becomes advantageous because they increase the ability of the moth to stay in control of its movements. At the same time the reduced wings probably fulfil also an important function as stabilizers during a jump, and the greater need of the male for speed and manoeuvrability in the competitive courtship process may be the reason why the male wings are occasionally less reduced than those of the female. Both male and female sometimes show a tendency

towards stenoptery, for example *Exsilirarcha graminea* Salmon & Bradley (Pyralidae) (Fig. 40; Salmon & Bradley, 1956: figs 24, 27), and it is likely that stenopterous wings are more effective stabilizers to a jumping moth than are broader wings. The resistance of the male to flightlessness is so great that even in windswept alpine and arctic habitats no brachyptery has evolved in that sex. Significantly, wing reduction in both sexes of a species restricted to high mountain habitats above the tree line (oreal species) is known only in the two oceanic island species *Thyrocopa apatela* (Walsingham) (Oecophoridae, Xyloryctinac) (Hawaiian Islands, Maui) (Figs 7, 8; Zimmerman, 1978: 937, fig. 560) and *Ephysteris* sp. (Gelechiidae) (Madeira) (Sattler, 1988: 232). It is noteworthy that *Ephysteris curtipennis* (Zerny) (Morocco, High Atlas), which is closely related to the Madeiran species and occurs under similar environmental conditions, has macropterous males (Zerny, 1936: 138). However, the reasons for that difference may be connected with the smaller population and limited size of the habitat on the oceanic island, because a flying male that is removed from its habitat by the force of strong winds is unlikely to find an alternative population as it might in the much larger continental habitat.

Although Salmon (1956: 62) and Viette (1959: 22) accept the strong winds as the prime cause of flightlessness in sub-Antarctic island Lepidoptera, they additionally assume a genetic predisposition to brachyptery. If this were so, one would expect to find some tendency towards wing reduction elsewhere amongst the nearest relatives of such species, particularly where these occur in environments that normally favour brachyptery. One example in support of this view is the genus *Asaphodes* Meyrick (Geometridae) with two brachypterous sub-Antarctic island species, originating from New Zealand stock, and several 'mainland' species, some of them with brachyptery. However, other species on sub-Antarctic and other oceanic islands are clearly the only brachypterous members of large, widespread genera of macropterous species without the tendency towards wing reduction elsewhere in the world (for example *Elachista* Treitschke, *Borkhausenia* Hübner, *Udea* Guenée, *Peridroma* Hübner). Considering all types of wing reduction in the Lepidoptera, and the many different lineages in which brachypterous forms have arisen independently, it appears likely that many species would in time respond in that way to appropriate environmental pressures.

The low temperature on sub-Antarctic islands is sometimes also invoked to explain the reluctance of insects to fly in such habitats. However, the cold cannot account for male flightlessness in the

Lepidoptera, because there are several successful strategies that enable, for example, northern hemisphere winter-active Geometridae and Noctuidae to fly in much lower ambient temperatures, even below freezing. Moreover, several Lepidoptera with male brachyptery occur in high temperature environments, for example *Ambloma brachyptera* Walsingham (Symmocidae) and *Areniscythris brachypteris* Powell (Scythrididae) in coastal sand dunes on the Canary Islands and in California respectively, where other factors must be responsible.

Wing reduction in cold season moths

The largest category with environmentally induced wing reduction in the female sex is that of the northern hemisphere cold season species ('winter moths') which are univoltine and have an adult activity period somewhere between about late October and April. Examples of this category are known in the Eriocottidae, Tineidae, Oecophoridae (Ethmiinae, Chimabachinae), Tortricidae, Somabrachyidae and possibly Lasiocampidae and Arctiidae; they are particularly numerous in the Geometridae (Oenochrominae, Larentiinae, Ennominae). The severe conditions of continental winters usually act as a strict barrier that sharply divides the cold season moths into a 'late' (moths emerging October-December) and an 'early' (moths emerging January-April) group; however, in the mild oceanic winter climate of the British Isles both groups may overlap and blend into each other. Even under extreme low temperatures the break is not always absolute as is demonstrated by *Cheimoptena pennigera* Danilevsky (Geometridae), an inhabitant of the Central Asiatic deserts, with an adult activity period that extends from December till February (see below).

There is so far only moderate evidence of a comparable southern hemisphere cold season element, for example in New Zealand the genus *Atomotricha* Meyrick (Oecophoridae), which has several winter species with adult activity periods in about August-September, and a few diurnal Tortricidae (Dugdale, pers. comm.) and *Zermizinga indocilisaria* Walker (Geometridae; also found in Australia).

A significant minority of the Lepidoptera in the temperate zone of the northern hemisphere pass the cold season as adults, and species overwintering in that stage are known in many families, for example Opostegidae, Gracillariidae, Yponomeutidae, Lyonetiidae, Oecophoridae (Depressariinae), Momphidae, Gelechiidae, Tortricidae, Alucitidae, Pterophoridae, Pyralidae, Pieridae, Nymphalidae and Noctuidae. Because of their longevity both sexes of such species depend on an intake of energy; they have fully developed mouth parts and feed. Many overwintering moths are capable of flying at low ambient temperatures. The importance of flight in the search for food sources, hiding places and oviposition sites acts against flightlessness in such species, and no example of wing reduction in Lepidoptera overwintering as adults is known. Other species are active in autumn and into the colder part of the year (for example *Agrochola* Hübner) or emerge very early in the year but extend their activity period into the warmer months (for example *Orthosia* Ochsenheimer). In common with the overwintering moths these species feed, for example early Noctuidae of the genus *Orthosia* Ochsenheimer at *Salix* catkins, and show no tendency towards flightlessness.

The group in which wing reduction in females has evolved comprises those species that emerge in late autumn, frequently after the first frost, winter or early spring and complete their adult life in the cold season. Both sexes of such species are short-lived; they do not feed and their mouth parts are usually reduced. The males are capable of flying in very low air temperatures, often below 0°C. The females of certain species are fully winged, albeit with a more or less strong tendency towards flightlessness, for example *Semioscopis oculella* (Thunberg), *S. avellanella* (Hübner) (Oecophoridae); *Poecilocampa populi* (L.), *Eriogaster lanestris* (L.) (Lasiocampidae); *Lemonia vallantini* (Oberthür) (Lemoniidae); however, those of most species show various degrees of wing reduction, from brachypterous half-sized wings in *Protalcis* Sato to micropty or aptery in *Erannis* Hübner (Geometridae) (for example Inoue, 1982: pl. 98). They are motile with normal functional legs and are capable of walking, climbing and sometimes running, but they do not jump. The females emerge from pupae on the ground with their egg complement fully developed; those of the flightless species ascend tree trunks, where they soon attract the males and mating takes place. The eggs are then deposited without much delay high up in the canopy of the same trees. As the larvae of most cold season moths are polyphagous, usually on deciduous trees, there is no need for flight in search of an appropriate host-plant on which to lay the eggs, and an important barrier to flightlessness and wing reduction in the female is removed. The female's loss of the ability to disperse is at least in part compensated by a dispersal phase in the larval stage when the young larvae actively migrate from the oviposition site to other parts of the plant or are passively transported through the air, ballooning on silken threads. Such passive transport accounts for the

presence of larvae on isolated bushes or on trees that had been protected from ascending females by sticky bands. The suggestion that the female may be carried to such isolated sites by the male during copulation, a claim often made with reference to the winter moth *Operophtera brumata* (L.) (e.g. Porritt, 1913), was never supported by direct observation and has long been discredited (Chapman, 1913: 81, 1917: 63).

Many cold season moths are nocturnal, for example *Alsophila* Hübner, *Operophtera* Hübner, *Apocheima* Hübner, *Lycia alpina* (Sulzer), *Agriopis* Hübner and *Erannis* Hübner, and their activity frequently begins shortly after sunset; however, several species with more or less fully winged females, for example *Semioscopis oculella* (Thunberg), or brachypterous females, for example *Dasyethmia hiemalis* Danilevsky, *Cheimophila salicella* (Hübner), *Exapate duratella* (Heyden), *Synnoma lynosyrana* Walsingham, *Chondrosoma fiduciarium* Anker, *Lycia zonaria* (Denis & Schiffermüller), *Cheimoptena pennigera* Danilevsky and *Ocnogyna* spp., are diurnal, with the male courtship flight usually taking place in sunshine.

Lepidoptera are capable of flight only within a certain range of ambient temperatures. If the temperature drops below a critical point the insect is no longer able to maintain the minimum thoracic temperature necessary for its flight muscles to operate. In contrast, if the ambient temperature exceeds the critical upper limit, not enough excess heat is discharged to the environment. In either case the duration of the flight is curtailed as the critical temperature is approached until flight ceases altogether. During flight many Lepidoptera are homoeothermic; they have their specific operating temperature which is more or less constant and largely independent of the ambient temperature. For example, the in-flight thoracic temperature of many Noctuidae is maintained at about 30°–35°C (Heinrich, 1987: 319–320, fig. 6) and similar temperatures have been measured in butterflies (Heinrich, 1981: 249). The heat required to reach and maintain the operating temperature of the flight musculature can be generated endothermically by the insect's own metabolism. Many nocturnal Lepidoptera, for example Noctuidae and Sphingidae, raise their thoracic temperature in a mandatory preflight warm-up by a process of 'shivering', i.e. rapid contractions of the flight muscles accompanied by low amplitude wing vibrations (Kammer, 1981: 132–138), but this method of warm-up has not been recorded for the males in any of the cold season species with flightless females. During flight the operating temperature in the thorax is maintained through insulation, which reduces convective heat loss,

and a counter-current heat exchange system that diminishes the loss of heat from the thorax to the head and abdomen (Heinrich, 1987).

Field observations on the flight behaviour of some diurnal cold season species (Burmann, 1953, 1965; Danilevsky, 1969a, 1969b) suggest that they may also be homoeothermic in flight but raise the temperature of their flight musculature to an operational level by acquiring heat ectothermically from solar radiation. It has been argued that the wings act as highly effective solar heat collectors which absorb and transport the energy to the thorax with the aid of haemolymph circulating through the wing veins (Clench, 1966); however, this has been disputed on the grounds that the haemolymph flow is insufficient to be effective (Kammer, 1981: 307). Instead, it has been suggested that warm air accumulates under the wings of basking Lepidoptera (such as dorsal baskers amongst the butterflies) and enables heat exchange with the body by convection (Casey, 1981: 96–99). The latter explanation is also plausible for diurnal moths that maintain a roof-like wing posture during warm-up rather than spread their wings to give them maximum exposure to the sun. The effect of the wings in such a resting position is then that of a greenhouse and is apparently adequate to allow the males of certain cold season species to commence their courtship flight soon after sunrise during the coldest hour of the day. For example, the mating flight of *Semioscopis oculella* (Thunberg) (= *anella* Hübner) (Oecophoridae), a species with a fully winged but almost flightless female, and *Exapate duratella* (Heyden) (Tortricidae), a species with a brachypterous female, begins soon after the sun reaches their habitat, even when the air temperature is still well below freezing (Burmann, 1953, 1965).

In contrast to the homoeothermic species, nocturnal cold season Geometridae are poikilothermic in flight, i.e. their body temperature is variable and depends on the ambient temperature. Because their heat production is low and convective heat loss of their small bodies to the environment is high, their in-flight thoracic temperature is maintained within a few degrees of the ambient temperature (Casey & Joos, 1983). Their low wing loading, i.e. a large wing area in relation to the body mass, permits them to fly at low wing stroke frequencies. Although such flight is slow and poorly controlled it has the advantage that it is instant over a wide range of ambient temperatures, without the mandatory preflight warm-up of species which have a high wing loading and a better flight performance such as Sphingidae and Noctuidae. Most importantly, the energy required to generate the minimum power for lift-off and

flight is low and the flight musculature is able to operate effectively at a low temperature. Consequently, winter moths such as the North American *Alsophila pometaria* (Harrison) and *Operophtera bruceata* (Hulst) are able to sustain themselves in flight at thoracic muscle temperatures as low as −3°C (Heinrich & Mommsen, 1985).

The main selective advantage of a shift of the adult activity period to the cold season is seen in the reduced predator pressure at a time when arthropod predators are dormant, insectivorous mammals in hibernation, migratory insectivorous birds absent and resident populations of birds at low density whilst some of them (for example *Parus* spp.) have switched their diet from insects to seeds (Dierl & Reichholf, 1977: 33–34).

Several hypotheses have been offered to account for the prevalence of wing reduction amongst cold season species. According to Hudson (1912: 274) flightlessness prevents the female from straying so far from the host-plant of its larva that it would be unable to regain it were it overcome by the cold whilst some distance away. Chapman (1917: 62) suggested that the female, once removed from its host-plant, would be unable to locate a substitute by chemical cues ('scent') at a time when the vegetation is leafless and dormant. Hering (1926: 214) argued that the seasonal storms in the northern temperate zone in autumn and spring would carry females out of reach of a suitable oviposition site if they attempted to fly. All three of those explanations see the selective advantage of flightlessness in the cold season in a better chance of the female in finding an oviposition site. However, the selection of such a site is hardly critical enough in this context because the larvae of most cold season species are polyphagous and often have an early dispersal phase that further aids in locating a host-plant. Were flight essential in this process, the problem of low temperatures would have been overcome by the female adopting one of the strategies successfully employed by winter-flying males. The wind factor can hardly be invoked in this case either, because the seasonal storms are never as continuous as, for example, on the sub-Antarctic islands so that conditions suitable for flight would exist at least at some time during the normal lifespan of an individual. Were strong winds responsible in the way suggested by Hering, then both sexes would be equally affected because the difficulty of a female in locating a host-plant is no greater than that of a male in finding a mate.

Based on an analysis of the Winter Moth, *Operophtera brumata* (L.) (Geometridae), Dierl & Reichholf (1977) argued that cold season brachyptery is an energy conservation measure

that protects the egg-bearing female from excessive loss of heat to a low temperature environment. The larger the wing area in relation to body size, the greater the loss of heat to the environment and the greater obviously the benefits of energy saving through wing reduction. However, as the role of the wings as heat exchangers is disputed and may be negligible (Kammer, 1981: 307) that explanation is not entirely satisfactory and it is more likely that environmental factors other than a low temperature are responsible for cold season wing reduction. To a host-specialist in a stable but patchy environment it is advantageous to be long-lived and motile because that increases its chances of locating a scarce, scattered food resource on which to deposit its eggs. In contrast, under unpredictable environmental conditions, as they prevail during the cold season with sudden drastic weather changes, it must be of selective advantage if the vulnerable adult stage is short. This presupposes that the female is instantly ready for mating and ovipositing when environmental cues, for example temperature, humidity or barometric pressure, signal favourable ambient conditions and trigger its emergence from the pupa. But, as discussed on p. 250, the entire mature egg complement can only be accommodated simultaneously if the ovaries are extended more or less far forward into the thorax, where they interfere with the flight musculature and thus cause flightlessness. In such circumstances it is of advantage to the female to shed the burden of the wings, over which it has diminished control, and redirect the energy saved into egg development.

Wing reduction in oreal moths

Another group with a high incidence of wing reduction in the female sex is that of the oreal species, i.e. species that inhabit high mountains above the tree line. Oreal species with brachypterous females are found in the Hepialidae, Tineidae, Yponomeutidae, Blastobasidae, Symmocidae, Gelechiidae, Lecithoceridae, Tortricidae, Pyralidae, Geometridae, Arctiidae and Noctuidae. Most of the known species occur in the Palaearctic region (Atlas mountains, European mountains, Central Asian mountains), a small number in tropical Africa (Kilimanjaro, Ruwenzori), South America (Andes), Australia and New Zealand. Unspecified high altitude Gelechiidae were recorded from North America (Colorado Rocky Mountains) (Hodges, 1986: 6) and further discoveries in this category, particularly amongst the Microlepidoptera, can be expected in various parts of the world in poorly explored alpine habitats. For example, several as yet unidentified

strongly brachypterous females, including some Blastobasidae, were recently collected by Karsholt in the Peruvian Andes at altitudes of 3500–4300 m.

Thyrocopa apatela (Walsingham) (Oecophoridae, Xyloryctinae), endemic to the Hawaiian island of Maui (Figs 7, 8; Zimmerman, 1978: 937, fig. 650), and an undescribed *Ephysteris* species (Gelechiidae), endemic to the Atlantic island of Madeira (Sattler, 1988: 232), inhabit oreal habitats but are brachypterous in both sexes (see p. 251).

The brachypterous females of oreal species are usually motile; they are able to walk and run, for example *Agrotis fatidica* (Hübner) (Noctuidae), and often also jump, for example *Kessleria* Nowicki (Yponomeutidae), *Thyrocopa apatela* (Walsingham) (Oecophoridae, Xyloryctinae) (both sexes), *Caryocolum laceratella* (Zeller), *Sattleria* Povolný (Gelechiidae) and *Sphaleroptera alpicolana* (Frölich) (Tortricidae). In some species the mouth parts are sufficiently well developed that they might be functional; however, neither sex of such species was ever observed on flowers or other potential food sources and it is likely that feeding, if it takes place, is restricted to the intake of water to counteract desiccation.

Some authors have compared flightlessness in oreal species to the same phenomenon in cold season species on the grounds that the adults of both groups may be exposed to very low temperatures (Hudson, 1912: 273; Dierl & Reichholf, 1977: 30). However, an important difference with regard to the temperature factor is that the cold season species must be able to operate in very low ambient temperatures whilst the adults of most oreal species are summer-active, when conditions allow flight within a temperature range that is normal for Lepidoptera. Thus various nocturnal oreal species fly only when it is relatively warm, and their flight ceases well above the freezing point. Nevertheless many oreal species are diurnal. The males of several species with wing-reduced females fly in the sunshine and cease flying as soon as the sun is obscured by clouds, for example *Pharmacis pyrenaicus* (Donzel) (Hepialidae) and *Sphaleroptera alpicolana* (Frölich) (Tortricidae) (pers. obs.). In common with the males of some diurnal winter moths those of several oreal species such as *Acompsia dimorpha* Petry (Gelechiidae) (Petry, 1904: 6) and *Sphaleroptera alpicolana* (Frölich) (Tortricidae) (Burmann, 1958: 1) commence their courtship flight early in the morning when they probably absorb the rays of the rising sun for a preflight warm-up. Having ruled out exposure to low temperatures as critical, the common factor that links oreal species with cold season species is seen here in an uncertain environment. Even in summer the alpine zone of high

mountains is often subjected to strongly fluctuating weather conditions, not unlike those in the cold season, sometimes with sudden snowfall, which would favour short-lived species with their potential for wing reduction in the female.

It should be noted that there are some oreal cold season species. *Lycia alpina* (Sulzer) (Geometridae), which occurs in the European Alps at altitudes of about 1500–2500 m, is the first moth to emerge along the edges of the receding snow from late April till mid-July, depending on the altitude and exposure of the habitat to the sun. Like the males of other true cold season species those of *L. alpina* are crepuscular to nocturnal and fly at ambient temperatures around freezing point (Pinker, 1953: 179; Burmann, 1956). It can be assumed that in common with other cold season Geometridae they operate at thoracic temperatures near the ambient temperature whilst most other oreal species can be expected to have a high operating temperature. *L. alpina* is closely related to other cold season species such as *L. zonaria* (Denis & Schiffermüller) and *L. pomonaria* (Hübner) which are restricted to lower altitudes, but whilst the adults of the lowland species are active at a time of lowest predator pressure (Dierl & Reichholf, 1977: 33–35), those of oreal species such as *L. alpina* emerge after the arrival of the migratory birds and sometimes suffer from heavy bird predation (Pinker, 1953: 179; Burmann, 1956: 256).

Flight in a high temperature environment

Having established that certain environmental conditions can induce wing reduction and having identified strong winds on small oceanic islands and sudden weather changes in the cold season or in oreal habitats as potential factors, it is worth considering whether other extreme or unusual environmental factors could have a similar effect. Although low temperature was rejected as a significant factor, it is imaginable that an extreme high temperature environment could favour the evolution of wing reduction because in a high ambient temperature moths would not be able to discharge into the environment enough of the excess heat generated by their flight musculature. Consequently their flight would be curtailed and eventually cease altogether, particularly in the heavier female sex, and such enforced flightlessness could give rise to wing reduction. However, most of the summer-active species with wing-reduced females occur in the temperate regions where temperatures do not consistently rise for any significant length of time above the critical levels beyond which Lepidoptera are no longer

able to fly. Although much still remains to be discovered in the tropics, there is as yet no evidence of wing reduction linked to high temperature.

Wing reduction in forest moths

A number of Lepidoptera with wing-reduced females, including Psychidae, Oecophoridae, Tortricidae, Geometridae and Lymantriidae, are inhabitants of northern hemisphere broad-leaved forests. According to Barbosa *et al.* (1989), who investigated forest-dwelling Lepidoptera in eastern North America, flightlessness in such species arose as a response to ecological pressures from the forest environment. Although forests provide favourable conditions for flightless species because they constitute a permanent, continuous habitat with stable food sources, an analysis of forest-inhabiting wing-reduced species indicates that the factors critical for the evolution of flightlessness and wing reduction may not be inherent in the specific ecological conditions of the forest environment.

Flightlessness is a family strategy in Psychidae (p. 262) and is common in Lymantriidae (p. 277). Thus it is likely that the affected forest-dwelling species in these families evolved from ancestors that were already flightless when entering the forest environment. In contrast, flightlessness and wing-reduction in Geometridae, Oecophoridae and Tortricidae may have evolved in the forest; however, all the forest-inhabiting wing-reduced members of those families are cold season species for which unpredictable seasonal weather conditions are seen as the critical evolutionary factor (p. 254).

Wing reduction in steppe and desert moths

Some instances of brachyptery have been interpreted as a response to environmental conditions in steppes and deserts. Zerny & Beier (1936: 1568) suggested that in xerothermic habitats the female would be unable to locate suitable plants for oviposition at times when flowers and leaves were dried up. Under such circumstances it would be advantageous if the female were prevented from straying too far from the host-plant of its own larva. However, there is no evidence of an increased incidence of brachyptery in steppe and desert Lepidoptera to suggest an inherent factor favouring the evolution of wing reduction in that environment. Moreover, the examples given by Zerny & Beier can be interpreted more convincingly by other factors; *Somabrachys* Kirby (Somabrachyidae), *Lambessa* Staudinger (= *Lasiocampa* Schrank) (Lasiocampidae) and *Ocnogyna* Lederer (Arctiidae) are cold season

forms whereas wing reduction in summer-active *Chondrostega* Lederer (Lasiocampidae) is the result of sedentary habit.

Wing reduction in aquatic moths

A number of Lepidoptera, mostly Pyralidae of the subfamily Nymphulinae, have adapted to an aquatic way of life with their larvae living on or in the submerged parts of water plants. However, the adults of all species leave the water and are capable of flying with the exception of a female morph of *Acentria ephemerella* (Denis & Schiffermüller), which remains submerged throughout its adult life and has reduced wings adapted for swimming (see p. 274). It is obvious that any shift of the adult stage from air into water would require significant modification of the wings including a reduction in their size.

Flightlessness in cavernicoles

Wing reduction is one of the morphological adaptations characteristic of many obligate cavernicoles amongst the insects (Howarth, 1983: 374) but is so far unknown in cave-dwelling Lepidoptera. Many cavernicolous Lepidoptera are probably at best troglophiles, i.e. species with permanent cave-dwelling populations which also occur above the ground in comparable microhabitats, whilst the number of troglobites, i.e. species which complete their life cycle in caves and are unable to survive outside the hypogaean environment, is very small. As the larvae of most Lepidoptera depend for their food on the live tissue of green plants, most species with permanent cave-dwelling populations are members of the tineid subfamily Tineinae, the larvae of which utilize as their energy source various kinds of animal detritus such as bird and bat guano and associated arthropod remains. The habits and distribution of many cavernicolous Tineidae are still inadequately known and it is difficult to establish their ecological status; however, at least one species, *Tinea microphthalma* Robinson from the Philippines, has significantly reduced eyes typical of true troglobites but is macropterous in the male whilst the female is still unknown (Robinson, 1980: 111, figs 35, 47). Another group of troglobitic Lepidoptera are species of the genus *Schrankia* Hübner (Noctuidae) inhabiting lava tubes in the Hawaiian Islands. Lava tubes are frequently so close to the surface that they can be invaded by the roots of native trees such as *Metrosideros polymorpha* (Myrtaceae) (Howarth, 1973: 144, fig. 1) which are the food source for the *Schrankia* larvae. Whilst *Schrankia* males are weak fliers, the females,

which are usually found near their cocoons, are flightless but not appreciably wing-reduced (Howarth, 1983: 376).

Flightlessness in a butterfly inhabiting the communal nest of its larvae

Geiger *et al.* (1989: 32) recently recorded an interesting case of incipient wing reduction in the Mexican *Eucheira socialis* Westwood (Pieridae) resulting from the unusual biology of this species. Its gregarious larvae spin large communal nests from which they emerge only for nocturnal feeding and in which they eventually pupate. Whilst the adults of *E. socialis westwoodi* Beutelspacher from the north-western part of central Mexico leave the shelter and are capable of weak flight, those of *E. socialis socialis* from southern Mexico cannot fly at all and remain permanently in the nest where they mate and oviposit. According to Geiger *et al.* most females lay only a few eggs, thus obviating the need for feeding in order to acquire energy from external sources for additional egg production. Populations are only sustainable at such low reproduction rates if excessive losses from predation, parasitism or unfavourable environmental conditions can be prevented; therefore it may be assumed that the communal nests in conjunction with the nocturnal feeding habit of the larvae provide adequate protection. Although the wings of the adults appear to be full size, Geiger *et al.* observed some reduction of the venation in the female and it is easy to visualize how, with time, brachyptery could evolve under the special conditions of nest-living. Almost certainly wing reduction in this instance would not be confined to the female but would also affect the male; in other groups of Lepidoptera wing reduction occurring in both sexes of a species has arisen only under the influence of strong winds.

E. socialis demonstrates that loss of flight can evolve in butterflies and that there is even potential for wing reduction. Nevertheless, butterflies are a group that offers poor candidates because, in many species, a mate-locating system involving active participation of the male and female is an effective barrier against the evolution of flightlessness in either sex. Other aspects of butterfly biology provide similarly effective barriers. For example, in some *Heliconius* species (Nymphalidae, Heliconiinae) males are attracted to female pupae which they guard until they are able to mate with the freshly emerge female (Gilbert, 1976: 420). However, as the female does not leave the pupa with a fully developed egg complement it must retain its ability to fly in search of food sources in order to produce energy for further egg development. Moreover, host-specificity of the larvae, which requires more or less extensive searches for oviposition sites, makes further demands on the motility of the female.

Flight in Saturniidae

It is surprising that there is no record of flightlessness in females of Saturniidae, many species of which appear to be singularly pre-adapted to loss of flight and even wing reduction. Adult Saturniidae are short-lived and do not feed; most species have non-functional, reduced mouthparts. The female emerges from the pupa with its total egg complement fully developed and thus is instantly ready to mate and oviposit. Effective long-ranging pheromones guide the male to the female so that the latter does not have to participate actively in the mate-locating process. As the larvae of many species are polyphagous, oviposition can take place unselectively without flight playing a critical role in the search for oviposition sites. The saturniid wings with bright warning coloration suggest that such species are unpalatable and thus enjoy some protection from diurnal vertebrate predators without having to resort to flying as a means of escape. Conspicuous eye spots on the wings of many species fulfil a similar defensive role. Consequently there appears to be no necessity for the females to fly for purposes of feeding, mate-finding, ovipositing or escaping from predators and one might therefore have expected some tendency towards wing reduction or at least sedentary behaviour; however, no evidence of this has been found. The females of Saturniidae have succeeded in retaining their ability to fly by avoiding the loss of flight musculature and maintaining a sufficiently low wing loading. To accommodate a large egg complement the volume of the abdomen has been greatly increased thus obviating the need to extend the ovaries forward into the thoracic cavity where, in many flightless Lepidoptera, they displace the flight musculature. The consequent problem of wing loading, which would be adversely affected by an increasing body weight, has been solved by enlargement of the wing area, and it is probably no coincidence that most Saturniidae are very large moths. It is not clear at this stage what kinds of selective pressure have prevented flightlessness in Saturniidae and it is interesting to note that wing reduction did evolve under apparently similar conditions in certain Lasiocampidae, Lymantriidae and Arctiidae.

Check list of family-group taxa in which wing reduction occurs

Wing reduction is usually restricted to the female sex; taxa in which it is recorded in both sexes are marked with an asterisk (*).

HEPIALOIDEA
  Hepialidae
TINEOIDEA (*)
  Eriocottidae
  Psychidae
  Tineidae (*)
YPONOMEUTOIDEA (*)
  Yponomeutidae (*)
  Glyphipterigidae
GELECHIOIDEA (*)
  Oecophoridae (*)
    Depressariinae
    Ethmiinae
    Xyloryctinae (*)
    Oecophorinae (*)
    Chimabachinae
  Elachistidae (*)
  Blastobasidae
  Symmocidae
  Cosmopterigidae
  Gelechiidae (*)
    Aristoteliinae
    Gelechiinae (*)
      Gnorimoschemini (*)
    Anacampsinae
  Lecithoceridae
  Scythrididae (*)
TORTRICOIDEA (*)
  Tortricidae (*)
    Tortricinae (*)
    Olethreutinae
ZYGAENOIDEA
  Heterogynidae
  Zygaenidae
    Procridinae
  Somabrachyidae
COPROMORPHOIDEA (*)
  Carposinidae (*)
PYRALOIDEA (*)
  Pyralidae (*)
    Pyralinae
    Crambinae
    Acentropinae
    Pyraustinae (*)
    Scopariinae (*)
GEOMETROIDEA
  Geometridae
    Oenochrominae
    Ennominae
      Semiothisini
      Bistonini
      Gnophini
    Larentiinae
      Xanthorhoini
      Operophterini

BOMBYCOIDEA
  Lasiocampidae
NOCTUOIDEA (*)
  Lymantriidae
  Arctiidae
    Lithosiinae
    Arctiinae
    Ctenuchinae
  Noctuidae (*)
    Acronictinae
    Cucullinae
    Hadeninae
    Noctuinae (*)

Check list of the Microlepidoptera species, including Pyralidae, with wing reduction

An attempt is made to list all species of Microlepidoptera, including the Pyralidae, in which wing reduction is known. Species with merely slight sexual wing dimorphism that may be an indication of the beginning of wing reduction in the female are excluded. The species of Psychidae, Heterogynidae and Somabrachyidae are not individually listed because most or all members of those families are affected. As far as possible the taxa are arranged in a systematic sequence. The valid name of each species is followed by an indication of the wing-reduced sex (a sex symbol in square brackets indicates that an as yet unknown sex is likely to be wing-reduced) and the general area of distribution. For oreal species the mountain range is added in parentheses and for oceanic island species the island group. Northern hemisphere cold season species are identified by the months of their adult activity period given in Roman numerals in parentheses.

Hepialidae
Pharmacis pyrenaicus (Donzel, 1838) ♀ Europe (Pyrenees)
Pharmacis anselminae (Teobaldelli, 1977) ♀ Europe (Alps)
Pharmacis bertrandi (Le Cerf, 1936) ♀ Europe (Alps)
Aoraia senex (Hudson, 1908) ♀ New Zealand (1100–1700 m)
Aoraia species ♀ New Zealand (1100–1500 m)

Eriocottidae
Deuterotinea auronitens Lucas, 1956 [♀] Morocco (xi)
Deuterotinea axiurga (Meyrick, 1922) [♀] Syria (?)
Deuterotinea balcanica Zagulajev, 1972 [♀] Bulgaria (xi-i)
Deuterotinea casanella (Eversmann, 1844) ♀ South Russia (ix, x)
Deuterotinea instabilis (Meyrick, 1924) [♀] Cyprus (xii-iii)
Deuterotinea maracandica Zagulajev, 1988 [♀] Uzbekistan (?)
Deuterotinea palaestinensis Rebel, 1901 [♀] Israel (?)

Deuterotinea paradoxella (Staudinger, 1859) ♀ Spain (xi-i)

Deuterotinea stschetkini Zagulajev, 1972 ♀ Turkmeniya, Tadzhikistan (xi)

Psychidae
Most species ♀ World-wide

Tineidae
Tinea allomella Bradley, 1965 ♀ East Africa (Ruwenzori)

Eudarcia brachyptera (Passerin d'Entrèves, 1974) ♀ Italy

Eudarcia gallica (Petersen, 1962) ♀ Europe, France

Pringleophaga crozetensis Enderlein, 1905 ♂, ♀ South Indian Ocean (Crozet Is)

Pringleophaga kerguelensis Enderlein, 1905 ♂, ♀ South Indian Ocean (Kerguelen Is)

Pringleophaga marioni Viette, 1968 ♂, ♀ South Indian Ocean (Marion I.)

Proterodesma turbotti (Salmon & Bradley, 1965) ♂, ♀ South Pacific (Antipodes Is, Bounty I.)

Pararhodobates syriaca (Lederer, 1857) ♀ Central Asia – China (x, i-iv)

Yponomeutidae
Kessleria zimmermanni Nowicki, 1864 ♀ Europe (Carpathians)

Kessleria species ♀ Europe (Alps)

Kessleria pyrenaica Friese, 1960 ♀ Europe (Pyrenees)

Embryonopsis halticella Eaton, 1875 ♂, ♀ South Indian Ocean (Kerguelen Is)

Glyphipterigidae
Glyphipterix rugata Meyrick ♀ New Zealand

Oecophoridae
Depressariinae

Proteodes clarkei Philpott, 1926 ♀ New Zealand
Ethmiinae

Ethmia discrepitella (Rebel, 1901) ♀ U.S.S.R., southern Ural (iv-v)

Ethmia charybdis Powell, 1973 ♀ U.S.A., California (xi-xii)

Dasyethmia hiemalis Danilevsky, 1969 [♀] U.S.S.R., Kazakhstan (i)
Xyloryctinae

Thyrocopa apatela (Walsingham, 1907) ♂, ♀ Pacific Ocean (Hawaiian Is, Maui, 3000–4000 m)
Oecophorinae

Borkhausenia falklandensis Bradley, 1965 ♂, ♀ South Atlantic (Falkland Is)

Tinearupa sorenseni sorenseni Salmon & Bradley, 1965 ♂, ♀ South Pacific (Campbell I.)

Tinearupa sorenseni aucklandica Dugdale, 1971 ♂, ♀ South Pacific (Auckland Is)

Chersadaula ochrogastra Meyrick, 1923 ♀ New Zealand

Atomotricha ommatias Meyrick, 1884 ♀ New Zealand

Atomotricha chloronota Meyrick, 1914 ♀ New Zealand

Atomotricha sordida (Butler, 1877) ♀ New Zealand

Atomotricha oeconoma Meyrick, 1914 ♀ New Zealand

Atomotricha versuta Meyrick, 1914 ♀ New Zealand

Pleurota marginella (Denis & Schiffermüller, 1775) ♀ South-eastern Europe
Chimabachinae

Diurnea fagella (Denis & Schiffermüller, 1775) ♀ Europe (iii-v)

Diurnea phryganella (Hübner, 1796) ♀ Europe (x-xi)

Diurnea issikii Saito, 1979 ♀ Japan (iv)

Diurnea cupreifera (Butler, 1879) ♀ Japan (iii-iv)

Diurnea soljanikovi Lvovsky, 1986 [♀] East Asia (iv)

Cheimophila salicella (Hübner, 1796) ♀ Europe (iv)

Cheimophila kurentzovi Lvovsky, 1990 [♀] East Asia (v)

Cheimophila fumida (Butler, 1879) ♀ East Asia (iii-iv)

Elachistidae
Biselachista brachypterella Klimesch, 1990 ♀ Europe (Alps)

Elachista galatheae galatheae (Viette, 1954) ♂, ♀ South Pacific (Campbell I.)

Elachista galatheae antipodensis (Dugdale, 1971) ♂, ♀ South Pacific (Antipodes Is)

Elachista hookeri (Dugdale, 1971) ♂, ♀ South Pacific (Auckland Is)

Elachista pumila (Dugdale, 1971) ♂, ♀ South Pacific (Auckland Is)

Elachista holdgatei (Bradley, 1965) ♂, ♀ South Atlantic (Falkland Is)

Blastobasidae
Unidentified taxon ♀ South America, Peru (Andes)

Symmocidae
Symmoca (*Parasymmoca*) *profanella* (Zerny, 1936) ♀ North Africa, Morocco (Haut Atlas)

Symmoca (*Symmoca*) *signella* (Hübner, 1796) ♀ Europe (Alps)

Ambloma brachyptera Walsingham, 1908 ♂, [♀] Atlantic Ocean (Canary Is)

Cosmopterigidae
Vulcaniella extremella (Wocke, 1871) ♀ Southern Europe

Gelechiidae
Aristoteliinae

Megacraspedus dolosellus (Zeller, 1839) ♀ Europe

Megacraspedus separatellus (Fischer von Roeslerstamm, 1843) ♀ Europe

Megacraspedus subdolellus Staudinger, 1859 ♀ Europe

Megacraspedus lanceolellus (Zeller, 1850) ♀ Europe

Megacraspedus monolorellus Rebel, 1905 ♀ Turkey (Erciyas Dagi)

Megacraspedus binotellus (Fischer von Roeslerstamm, 1843) ♀ Europe

Megacraspedus imparellus (Fischer von Roeslerstamm, 1843) ♀ Europe

Megacraspedus culminicola Le Cerf, 1932 ♀ North Africa, Morocco (Moyen Atlas)

Daltopora felixi Povolný, 1979 ♀ Mongolia

Eulamprotes libertinella (Zeller, 1872) ♀ Europe (Alps)
Gelechiinae (Gnorimoschemini)

Kiwaia glaucoterma (Meyrick, 1911) ♀ New Zealand

Kiwaia jeanae Philpott, 1930 ♂, ♀ New Zealand

Kiwaia plemochoa (Meyrick, 1916) ♀ New Zealand

Gnorimoschema elbursicum Povolný, 1984 ♀ Iran (Elburz Mts)

Paraschema detectendum Povolný, 1990 ♀ South America, Bolivia (Andes)

Ephysteris curtipennis (Zerny, 1936) ♀ North Africa, Morocco (Haut Atlas)

Ephysteris species ♂, ♀ Atlantic Ocean (Madeira, 1400 m)

Ephysteris kasyi Povolný, 1968 ♀ Afghanistan (Dasht-i-Newar, 3000 m)

Caryocolum laceratella (Zeller, 1868) ♀ Europe (Alps)

Sattleria arcuata Pitkin & Sattler, 1991 ♀ Europe (Pyrenees)

Sattleria pyrenaica (Petry, 1904) ♀ Europe (Pyrenees; Basses Alpes)

Sattleria angustispina Pitkin & Sattler, 1991 ♀ Europe (Pyrenees)

Sattleria breviramus Pitkin & Sattler, 1991 ♀ Europe (Alps)

Sattleria melaleucella (Constant, 1865) ♀ Europe (Alps)

Sattleria basistrigella (Müller-Rutz, 1934) ♀ Europe (Alps)

Sattleria styriaca Pitkin & Sattler, 1991 ♀ Europe (Alps)

Sattleria dzieduszyckii (Nowicki, 1864) ♀ Europe (Carpathians)
    Anacampsinae

Acompsia dimorpha Petry, 1904 ♀ Europe (Pyrenees)

Stomopteryx mongolica Povolný, 1975 ♀ Mongolia

Lecithoceridae

Ceuthomadarus viduellus Rebel, 1903 ♀ South-eastern Europe

Ceuthomadarus rungsi (Lucas, 1937) [♀] North Africa, Morocco (Atlas Mts)

Ceuthomadarus atlantis Gozmány, 1978 ♀ North Africa, Morocco (Atlas Mts)

Ceuthomadarus funebrella (Chrétien, 1922) ♀ North Africa, Morocco (Atlas Mts)

Ceuthomadarus naumanni Gozmány, 1987 [♀] Afghanistan (Nuristan, 2500 m)

Tegenocharis species ♀ Nepal (Himalaya)

Scythrididae

Areniscythris brachypteris Powell, 1976 ♂, ♀ U.S.A., California

Tortricidae
    Tortricinae

Sorensenata agilitata Salmon & Bradley, 1956 ♂, ♀ South Pacific (Campbell I.)

Exapate congelatella (Clerck, 1759) ♀ Europe (x-xi)

Exapate duratella (Heyden, 1864) ♀ Europe, Alps (x-xi)

Oxypteron impar Staudinger, 1871 ♀ South-eastern Europe, Asia Minor (ix-x)

Oxypteron homsana (Amsel, 1954) [♀] Syria, Jordan (xi-xii)

Oxypteron exiguana (de la Harpe, 1860) ♀ Southern Europe, North Africa

Sphaleroptera alpicolana (Frölich, 1830) ♀ Europe (Alps, Pyrenees)

Synnoma lynosyrana Walsingham, 1879 ♀ South-western U.S.A. (x-xi)
    Olethreutinae

Olethreutes orestera Bradley, 1965 ♀ East Africa (Ruwenzori)

Heterogynidae

Heterogynis Rambur, all species ♀ Southern Europe, North Africa

Zygaenidae
    Procridinae

Pollanisus calliceros Turner, 1926 ♀ Australia (New South Wales, Tasmania; mountains)

Somabrachyidae

Somabrachys Kirby, all species ♀ North Africa - Syria (ix-xi)

Carposinidae

Campbellana attenuata Salmon & Bradley, 1956 ♂, ♀ South Pacific (Campbell I.)

Pyralidae
    Pyralinae

Synaphe punctalis (Fabricius, 1775) ♀ Europe, North Africa

Synaphe amuralis (Hampson, 1900) ♀ East Asia

Synaphe bombycalis (Denis & Schiffermüller, 1775) ♀ Europe

Synaphe moldavica (Esper, 1794) ♀ Europe

Synaphe oculatalis (Ragonot, 1885) ♀ Spain, North Africa, Jordan
    Crambinae

Catoptria digitella (Herrich-Schäffer, 1849) ♀ Europe (Pyrenees)

Catoptria biformella (Rebel, 1893) ♀ South-eastern Europe (mountains)

Catoptria majorella (Drenowski, 1925) ♀ South-eastern Europe (mountains)

Orocrambus crenaeus (Meyrick, 1885) [♀] New Zealand (mountains)

Orocrambus lindsayi Gaskin, 1975 ♀ New Zealand (Mount Ida)

Kupea electilis Philpott, 1920 [♀] New Zealand (coastal)

Crambus reductus Viette, 1959 ♀ South Indian Ocean (Amsterdam I.)
    Acentropinae

Acentria ephemerella (Denis & Schiffer-müller, 1775) ♀ Europe, North America
    Pyraustinae

Udea hageni Viette, 1952 ♂, [♀] South Atlantic (Tristan da Cunha)
    Scopariinae

Exsilirarcha graminea Salmon & Bradley, 1956 ♂, ♀ South Pacific (Auckland Is, Campbell I.)

Protyparcha scaphodes Meyrick, 1909 ♀ South Pacific (Auckland Is)

DISCUSSION OF WING REDUCTION IN DIFFERENT FAMILIES

Hepialoidea

1. Hepialidae

The Hepialidae are the only non-ditrysian family of Lepidoptera with examples of wing reduction. Slight to moderate reduction is recorded in the females of two oreal *Aoraia* species occuring in the alpine zone of New Zealand's South Island at altitudes of about 1100–1700 m: *A. senex* (Hudson)

(Dumbleton, 1966: 935) and an undescribed species (Patrick, 1989: fig. 3). Distinct brachyptery has evolved in the females of three oreal *Pharmacis* species (Figs 1, 2; Teobaldelli, 1977: fig. 1; Freina & Witt, 1990: pl. 9) in European mountains (Pyrenees, Alps). *Pharmacis* males are diurnal and fly in the sunshine close to the ground in search of 'calling' females (pers. obs. on *P. pyrenaicus* (Donzel); Teobaldelli, 1977: 41, on *P. anselminae* (Teobaldelli)). Mate-finding by the male is very widespread in the Lepidoptera and appears to be almost universal in nocturnal species; however, in some Hepialidae, for example *Hepialus humuli* (Linnaeus) and *Phymatopus hecta* (Linnaeus), the males form courtship groups at dusk to which the females are visually and chemically attracted (Mallet, 1984; Wagner, 1985). It is evident that brachyptery could not have evolved in species in which the females participate actively in the process of mate locating.
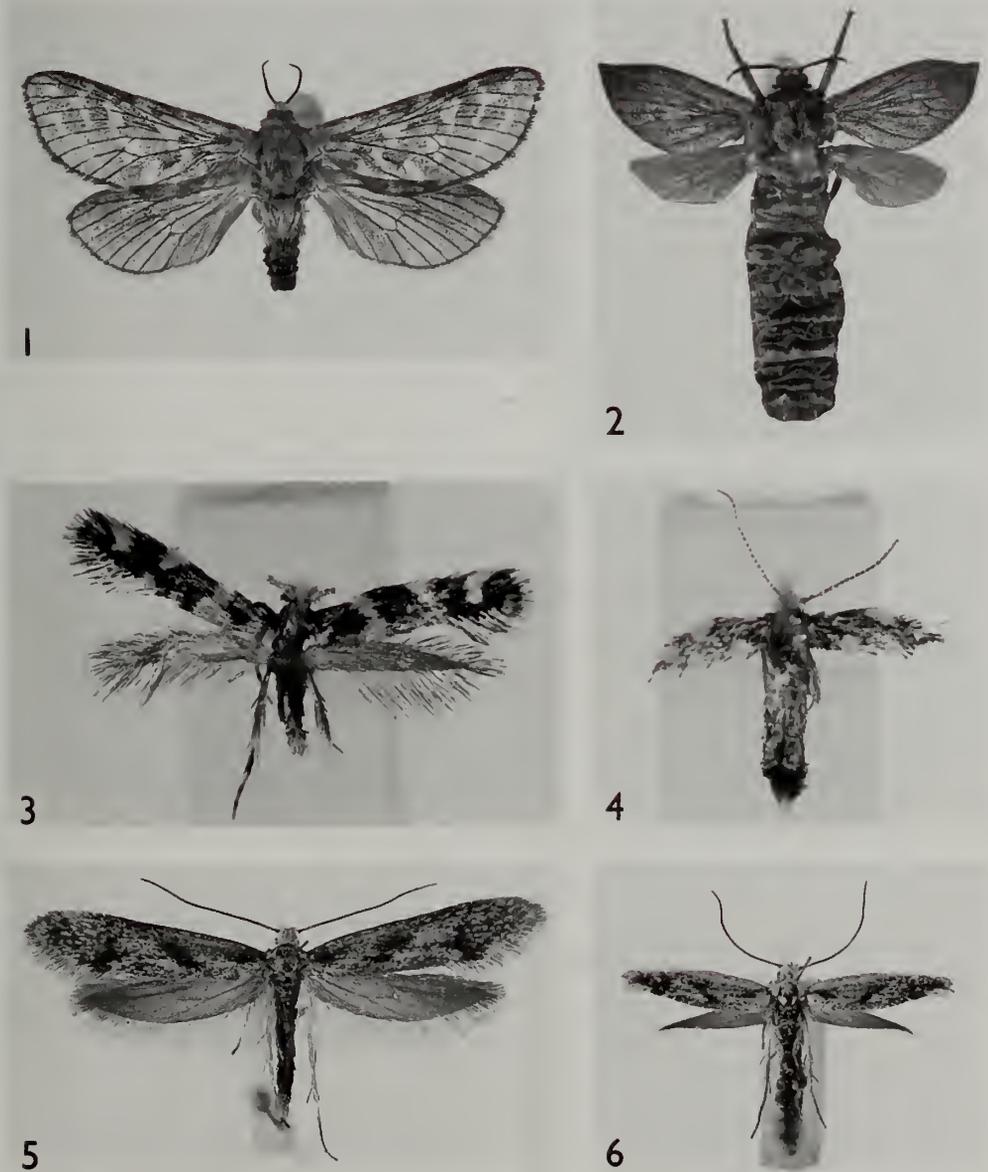
Figs 1–6   1, 2, *Pharmacis pyrenaicus* (Hepialidae), Pyrenees, (1) male, (2) female. 3, 4, *Eudarcia brachyptera* (Tineidae), Italy, (3) male, (4) female. 5, 6, *Kessleria* sp. (Yponomeutidae), Austrian Alps, (5) male, (6) female.

Tineoidea

2. Eriocottidae

In the small family Eriocottidae wing reduction is restricted to the female sex of the Mediterranean to central Asiatic genus *Deuterotinea* Rebel with about 10 nominal species of partly uncertain taxonomic status. The habits of *Deuterotinea* larvae are still unknown but the adults are winter moths (November-March). It can be expected that all species have strongly brachypterous or apterous females although this can only be demonstrated for *D. casanella* (Eversmann) (specimens in BMNH; Zagulajev, 1988: fig. 200), *D. paradoxella* (Staudinger) (Zerny, 1927: 486) and *D. stschetkini* Zagulajev (Zagulajev, 1988: fig. 207). In contrast to all other evidence, Joannis (1917: 260) recorded the adults of *paradoxella* (apparently the males only) as having been collected in June and July.

3. Psychidae

With about 2000 species and an almost world-wide distribution, the Psychidae are the only large family of the Lepidoptera which has adopted flightlessness and wing reduction in the female as a successful family strategy. The loss of locomotion (walking and flying) in the female is so widespread that it must have evolved early in the history of that family. Even the macropterous females of primitive species are often more or less sedentary and a strong tendency towards flightlessness may be a groundplan character of the Psychidae.

The larvae of the Psychidae produce cases which are often clad with plant fragments and other organic or inorganic debris such as lichens, mollusc shells or sand grains. Many species are scavengers or lichen-feeders whilst others are polyphagous on a wide range of green plants. Pupation takes place in the larval case and on ecdysis the pupal exuviae of most species are protruded from the posterior end of the case. With the exception of some primitive species the females are brachypterous or apterous and usually sedentary; their mouthparts and often also the legs and antennae are strongly reduced. When the females emerge from the pupa their egg complement is fully developed, and mating, followed by oviposition, is instantaneous; however, there is also widespread parthenogenesis. The female rarely strays far from the case and inserts its eggs with the aid of a long ovipositor into cracks and crevices nearby or, more frequently, directly into the larval case or pupal exuviae. The ability to deposit the eggs near or into the larval/pupal case immediately after eclosion removes the selective pressure in favour of motility from the female and is a precondition for the reduction of wings and legs. The female's loss of dispersability is successfully compensated by dispersal mechanisms in the larval stage (for a discussion of dispersal in Psychidae see Davis, 1964: 7–8).

According to Saigusa (1962) the single most important factor in the evolution of wing reduction in the Psychidae is the presence of a larval/pupal case. As the females are preadapted to laying eggs into deep cracks with the aid of their long ovipositor the case provides a convenient alternative receptacle for the egg batch. Saigusa identified four stages of reduction of the female's locomotory organs but stated that different degrees of reduction may have evolved independently more than once within the Psychidae. See also Dierl (1973).

(a) The female has fully developed functional wings and legs but the moth is frequently sedentary. It lays its eggs amongst mosses, into crevices in rocks or sometimes into the larval/pupal case.

(b) The female has strongly reduced wings. The legs are developed but are used only for ascending the side of the larval/pupal case. The eggs are laid into the case.

(c) The female has strongly reduced wings and somewhat reduced legs. The moth emerges fully or in part from the pupa and clings to the outer surface of the larval/pupal case near the posterior opening. The pupa is no longer protruded from the case on ecdysis and the eggs are laid into the pupal exuviae.

(d) The female is apterous; its non-functional legs are strongly reduced and lack tarsal claws. The moth remains partially or completely inside the pupa, which is not protruded from the case. A sex attractant is produced by the female from a dorsal hypodermal glandular area (meso- and metathorax, abdominal tergite 1) and is released through a corresponding rupture zone in the pupal skin (Dierl, 1973). The ovipositor is short and the eggs are laid into the pupal exuviae.

4. Tineidae

In the Tineidae wing reduction is rare. Strong reduction of the wings in both sexes occurs in the three species of *Pringleophaga* Enderlein on islands of the sub-Antarctic Kerguelen faunal province (Fig. 59; Crafford *et al.*, 1986: 68, figs 54–88). *Proterodesma turbotti* (Salmon & Bradley) on New Zealand's Antipodes Islands is also strongly brachypterous in both sexes (Salmon & Bradley, 1956: 65, fig. 7) whereas *P. byrsopola* Meyrick is macropterous in New Zealand but shows slight wing reduction on Auckland Island (Dugdale, 1971: 153).

The Asiatic *Pararhodobates syriaca* (Lederer) (Ural and Syria – north-east China) is a winter

moth (October, January-April) with a strongly brachypterous female (Zagulajev, 1975: 162, figs 87, 88). *Tinea allomella* Bradley, with a moderately brachypterous female, is an oreal species in the East African Ruwenzori mountains where it lives at an altitude of about 4000 m amongst the accumulated dead foliage on the trunks of *Senecio* (Compositae) (Bradley, 1965*b*: 118, figs 58, 59).

Eudarcia gallica (Petersen) (Pyrenees) with a case-making lichenivorous larva and brachypterous female (Sauter, 1985: 189, fig. 1) is probably another oreal species whilst the strong brachyptery of the female of *E. brachyptera* (Passerin d'Entréves) (Figs 3, 4; Passerin d'Entrves, 1974: 1, figs 1, 2) from Italy (Liguria) is as yet unexplained by environmental factors. The activity period of the adults, April-May, is a little earlier than that of related species but it is doubtful whether the cold season factor can be invoked. No field observations are available to decide whether the wing reduction in *E. brachyptera* could be the result of a sedentary habit similar to the situation in the Psychidae. All other *Eudarcia*, as far as known, have a similar biology but are macropterous in both sexes.

Yponomeutoidea

5. Yponomeutidae
In the Yponomeutidae wing reduction has evolved in only two unrelated genera. Strong brachyptery is known in both sexes of *Embryonopsis halticella* Eaton (Viette, 1952*a*: 3, fig.), a species inhabiting all the islands of the sub-Antarctic Kerguelen faunal province wherever its larval host-plant, the tussock grass *Poa cookii*, occurs (Crafford *et al.*, 1986: 68, figs 59–61). Slight brachyptery is observed in the females of several closely related oreal species amongst the about 20 otherwise macropterous members of the predominantly Palaearctic genus *Kessleria* Nowicki (Figs 5, 6). The wing-reduced species inhabit higher elevations of European mountain ranges (Pyrenees, Alps, Tatra mountains).

Tinearupa sorenseni Salmon & Bradley and *Campbellana attenuata* Salmon & Bradley, originally placed in the Yponomeutidae, were subsequently transferred to the Oecophoridae and Carposinidae respectively (Dugdale, 1971: 73, 134).

6. Glyphipterigidae
Moderate wing reduction appears to have evolved in the female of *Glyphipterix rugata* Meyrick on New Zealand's South Island; however, little is known about this species. Whilst the wings of the female are slightly shorter than the body, and its hind wings are distinctly narrower than those of related species, the as yet unknown male is probably macropterous. The holotype female from Tisbury (Invercargill) was beaten from the endemic *Weinmannia racemosa* Linnaeus f. (Cunoniaceae).

Gelechioidea

In the Gelechioidea wing reduction is found in most of the currently recognized families except the Coleophoridae (including Batrachedrinae) and the small families Agonoxenidae, Pterolonchidae, Momphidae and Holcopogonidae. All affected species are more or less strongly brachypterous, usually in the female only but occasionally in both sexes, whilst aptery is unknown. The major categories of flightlessness in response to environmental factors are represented by oceanic island species (Oecophoridae, Elachistidae, Gelechiidae), northern hemisphere cold season species (Oecophoridae) and oreal species (Blastobasidae, Symmocidae, Gelechiidae, Lecithoceridae). By far the largest number of brachypterous Gelechioidea is known from the western Palaearctic region including Madeira and the Canary Islands; some species occur in the Nearctic and Neotropical regions, on southern ocean islands, in New Zealand and Hawaii, whilst none have yet been recorded from the Afrotropical and Indo-Australian (except New Zealand) regions.

7. Oecophoridae

Ethmiinae
In the Ethmiinae wing reduction has evolved more than once independently in northern hemisphere cold season species and is restricted to the female sex. A tendency towards flightlessness is observed in the macropterous female of the Palaearctic *Ethmia pyrausta* (Pallas) the adults of which occur in May just before the birch leaves unfold (Nolcken, 1871: 671). Strong wing reduction is recorded in the female of the closely related *E. discrepitella* (Rebel) from south-eastern Russia, the adults of which are active in April to early May. Nothing is known about its biology but the male, like that of *E. pyrausta*, can be expected to fly in the sunshine.

Although in North America there are several spring-flying and autumn-flying Ethmiinae, for example *Ethmia albitogata* Walsingham (January-March), *E. plagiobothrae* Powell (March-April), *E. macelhosiella* Busck (October-November), *E. geranella* Barnes & Busck (October-November) and others, *E. charybdis* Powell, an inhabitant of the Californian San Joaquin Valley and Mojave
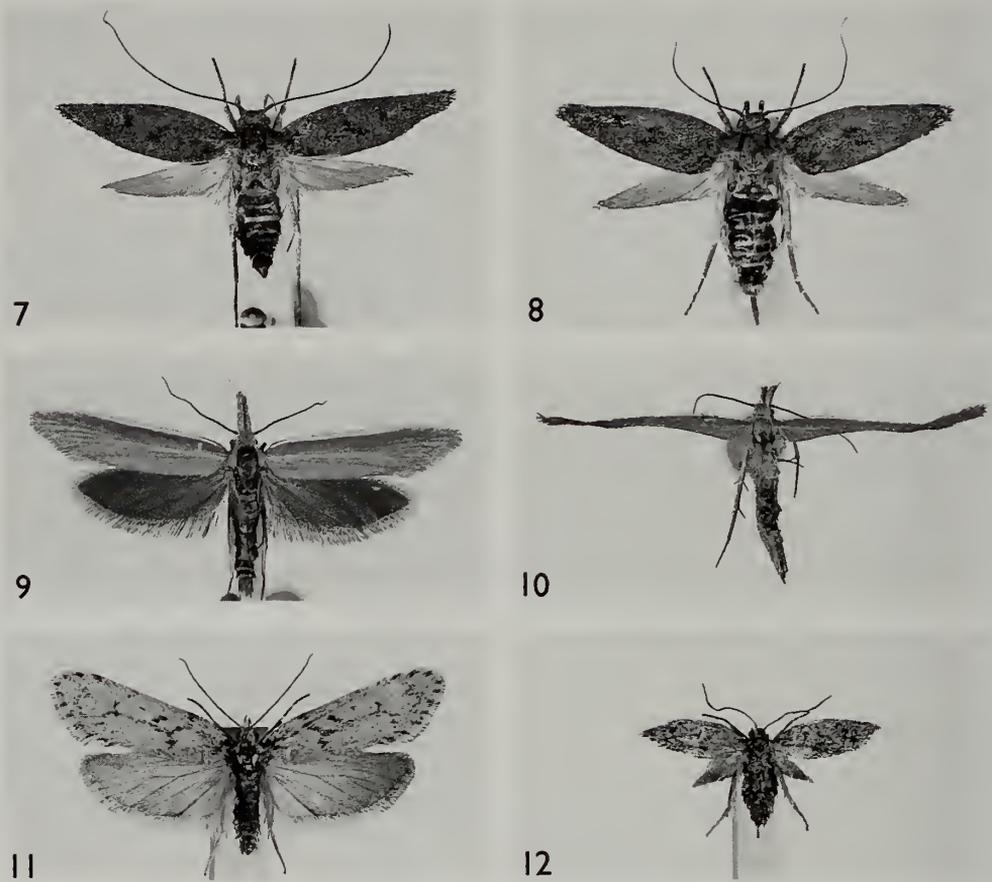
Figs 7–12   7, 8, *Thyrocopa apatela* (Oecophoridae: Xyloryctinae), Hawaiian Islands (Maui), (7) male, (8) female. 9, 10, *Pleurota marginella* (Oecophoridae: Oecophorinae), Austria, (9) male, (10) female. 11, 12, *Diurnea fagella* (Oecophoridae: Chimabachinae), British Isles (England), (11) male, (12) female.

Desert, is the only species with a brachypterous female (Powell, 1971, 1973).

The female of *Dasyethmia hiemalis* Danilevsky from Kazakhstan, a species with diurnal males that fly in January in the sunshine and settle on the snow, is still unknown; however, it seems safe to assume with Danilevsky (1969a, 1969b) that it will prove to be brachypterous.

Xyloryctinae
In the Xyloryctinae wing reduction is known only in the endemic Hawaiian genus *Thyrocopa* Meyrick, where it affects two or three of the about 60 species. *T. apatela* (Walsingham) (Figs 7, 8; Zimmerman, 1978: 937, figs 645, 650, 650–A), is the rare example of an oceanic island species with brachyptery in both sexes in an oreal habitat. It is endemic to East Maui, where it is a member of the aeolian ecosystem in the sparsely vegetated desert-like habitats above 3000 m on the extinct volcano

Haleakala (Howarth, 1979: 14). The larva of *T. apatela* lives in loosely spun sand-clad galleries under small rocks where it feeds on trapped wind-borne organic material, predominantly the dry leaves of *Dubautia menziesii* Gray (Compositae). The brachypterous moths are unable to fly but run well and are capable of making short jumps. The habitat is exposed to strong winds and extreme temperatures. During a visit in late July 1976 there was frost on the ground at 06.00 hrs whereas the daytime temperature in the sun was high and the soil felt hot to the touch (pers. obs.). Brachyptery in both sexes suggests the influence of the wind factor; however, *Thyrocopa mediomaculata* Walsingham, which occurs in the same habitat and has an apparently identical biology, shows at best very slight wing reduction in the female and has a macropterous male which flies (pers. obs.). A related as yet undescribed oreal species on the island of Hawaii is moderately wing-reduced in

both sexes whilst the existence of other flightless forms on windswept lower slopes of the island of Molokai (Perkins, 1913: clxiv) requires confirmation.

Oecophorinae
Wing reduction in both sexes is only recorded in two Southern Ocean island species, *Borkhausenia falklandensis* Bradley in the Falkland Islands (Bradley, 1965a: 122, fig. 1) and *Tinearupa sorenseni* Salmon & Bradley on New Zealand's Campbell Island (Salmon & Bradley, 1956: 66, figs 10, 11) and Auckland Islands (Dugdale, 1971: 135). Wing reduction, restricted to the female sex, is known in at least four of the nine currently recognized species of the endemic New Zealand genus *Atomotricha* Meyrick (see p. 259). There is a progression of wing reduction from the macropterous female of *A. isogama* Meyrick to the strongly brachypterous *A. oeconoma* Meyrick, in which the fore wings are shorter than the abdomen and the vestigial hind wings even lack the frenulum. The adults of the brachypterous species are active in winter to early spring (August–September) and are amongst the few examples of southern hemisphere cold season species. Strong wing reduction is also observed in the female of *Chersadaula ochrogastra* Meyrick (Hudson, 1928: 272, pl. 49, fig. 4), a coastal species with grass root-feeding larvae, on New Zealand's North Island.

The strongly stenopterous female of the Central European *Pleurota marginella* (Denis & Schiffermüller) (= *P. rostrella* (Hübner)) (Figs 9, 10; Hering, 1926: pl. 5, fig. 1; Hackman, 1966: fig. 12, *P. rostrella*) is the only flightless form amongst the 70–80 species of the predominantly Palaearctic genus *Pleurota* Hübner. The fore wings are not reduced in length but are extremely narrow and have lost veins M3 and CuP whilst the hind wings are vestigial without any tubular veins although a double frenulum is still present (Baus, 1936: figs 26, 27, 28, ; 29). The larva of *P. marginella* lives in a silken tube amongst narrow-leaved grasses. The adults occur in mid-summer and the female usually hides deep in the grass; it is active in the sunshine when it can run fast and is capable of jumping in the manner of a small grasshopper (Fischer von Roeslerstamm, 1843: 295). The wing reduction in this case is clearly not the result of familiar environmental factors such as strong winds, the cold season or an oreal habitat. Instead, its evolution may have been favoured by the biology of *P. marginella* as an inhabitant of grassland, which constitutes a more or less permanent, continuous habitat in which the female does not have to resort to flight in search of oviposition sites. Elsewhere in the Gelechioidea wing reduction

in summer-active grassland species is observed in the genus *Megacraspedus* Zeller (Gelechiidae) (see also p. 268).

Chimabachinae
All species of the two closely related Palaearctic genera *Diurnea* Haworth (Figs 11, 12) and *Cheimophila* Hübner are northern hemisphere cold season moths with larvae feeding on deciduous trees; the females are flightless and show various degrees of wing reduction from moderate to strong brachyptery (see for example Saito, 1979: figs 2, 4, 6). The adults of seven species are active in spring (March-May), those of one species in autumn (October-November).

8. Elachistidae
In the Elachistidae, a family of about 350 species with leaf-mining larvae in Gramineae, Cyperaceae and Juncaceae, brachyptery has evolved in both sexes of four species of the large almost worldwide genus *Elachista* Treitschke. All four affected species are inhabitants of sub-Antarctic islands (see p. 259) and there is no evidence of flightlessness or wing reduction in *Elachista* species elsewhere. The recently described *Biselachista brachypterella* Klimesch (Figs 13, 14) with moderately wing-reduced female occurs in the European Alps (Dolomites) where it was found at an altitude of about 1600 m amongst a sedge (*Carex* sp.) growing in open larch woodland. The female is flightless but is capable of jumping (Klimesch, 1990: 145, fig. 2).

9. Blastobasidae
Wing reduction was unknown in the Blastobasidae until Karsholt recently discovered at least two as yet unidentified oreal species with distinctly brachypterous females in the Peruvian Andes at an altitude of 3500 m.

10. Symmocidae
The wing reduction observed in *Ambloma brachyptera* Walsingham (Fig. 17), a species endemic to the Canary Islands (Tenerife), almost certainly affects both sexes although the female is still unknown. The moderately brachypterous male is flightless but can jump. Its habitat, the coastal sand dunes, is exposed to constant strong, storm-force north-easterly winds (Klimesch, 1985: 138, fig. 25). In contrast, the closely related *Ambloma klimeschi* Gozmány, which is also endemic to the Canary Islands (Tenerife, La Gomera) but inhabits localities more sheltered from the wind, has a macropterous male capable of flight (female still unknown) (Klimesch, 1985: 139, fig. 27). Klimesch suggested that *A. klimeschi* may be merely a macropterous morph of *brachyptera*;
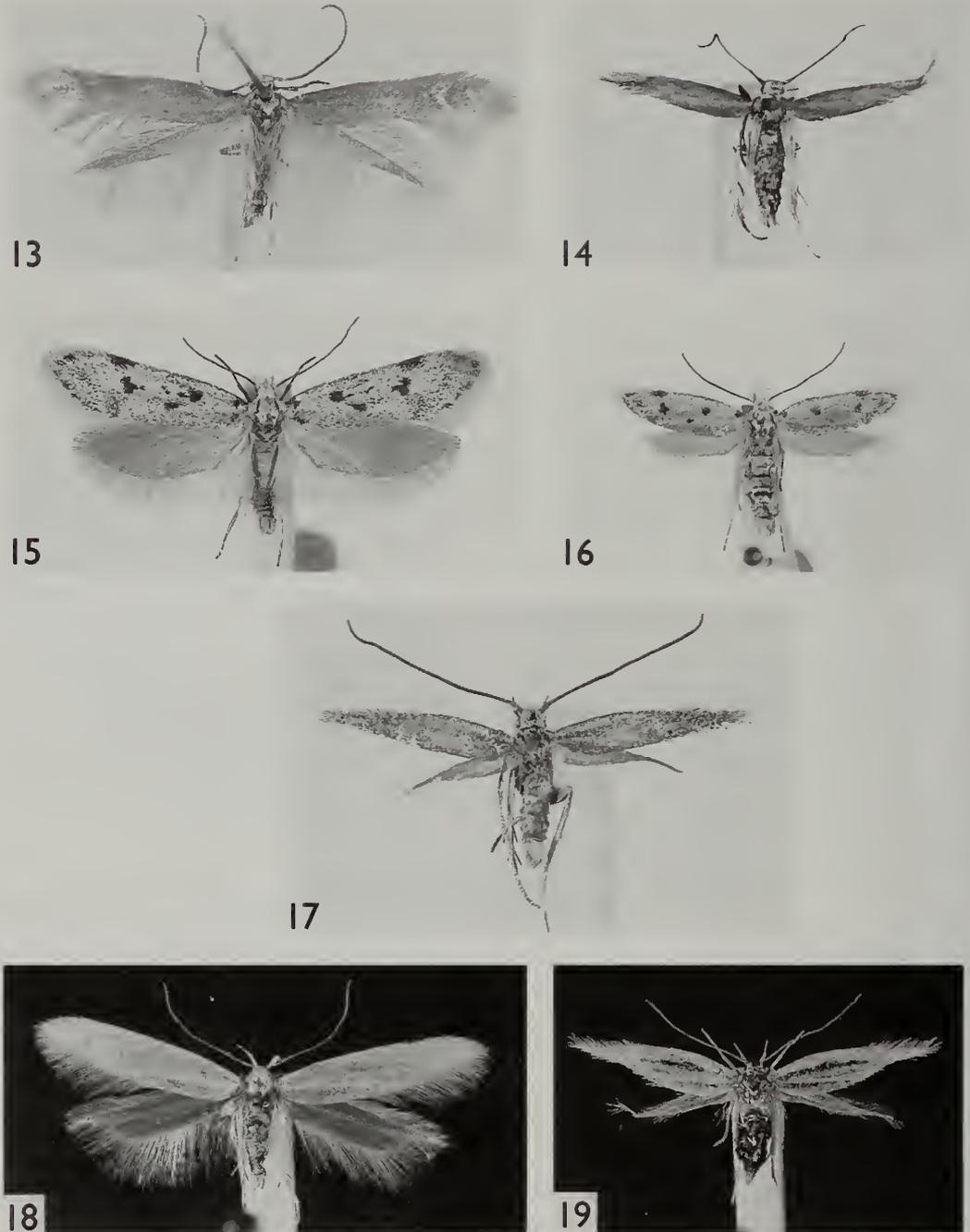
Figs 13–19 13, 14, *Biselachista brachypterella* (Elachistidae), Italian Alps, (13) male, (14) female. 15, 16, *Symmoca signella* (Symmocidae), Austrian Alps, (15) male, (16) female. 17, *Ambloma brachyptera* (Symmocidae), Canary Islands (Gomera), male. 18, 19, *Megacraspedus dolosellus* (Gelechiidae), Italian Alps, (18) male, (19) female.

however, such wing dimorphism is extremely rare in the Lepidoptera and for reasons of intrasexual competition is unlikely to evolve in the male sex.

Wing reduction is also recorded in two oreal species. *Symmoca profanella* Zerny in the Haut Atlas has a strongly brachypterous female (Zerny, 1936: 142, pl. 2, figs 25, 26) whilst that of *S.*

signella (Hübner) in the European Alps, although flightless (Burmann, 1947: 84), is only slightly brachypterous (Figs 15, 16).

11. Cosmopterigidae

In the Cosmopterigidae a weak tendency towards wing reduction can be observed in some European species of the genus *Vulcaniella* Riedl. *Vulcaniella pomposella* (Zeller), *V. grabowiella* (Staudinger) and *V. extremella* (Wocke) are sexually dimorphic in wing shape but only the female of the last can be classed as slightly wing-reduced (Klimesch, 1943: 65, pl. 4, figs 2, 4). The fore wing of the *extremella* female is as long as that of the male but is narrower with a conspicuous constriction near the apex. The hind wing is significantly shorter than the fore wing and its fringe is much reduced. *V. extremella* is known from southern France, eastern Austria,

Yugoslavia and Hungary. Its larva is a leaf-miner in *Salvia* (Labiatae); the moth occurs in June. The extreme wing dimorphism suggests that the female is flightless; however, there are no published observations on its habits.

12. Gelechiidae

In the Gelechiidae flightlessness resulting in wing reduction, usually in the female, has evolved several times independently. Flightlessness in both sexes, with and without brachyptery, has evolved only in a few species of Gelechiinae, tribe Gnorimoschemini. Most Gelechiidae are fully winged and capable of flight but, as they are also agile runners, flying is not their only or even preferred means of locomotion. For example, the adults of many tree-inhabiting species such as *Teleiodes fugacella* (Zeller) and *T. fugitivella*

Figs 20–25   20, 21, *Eulamprotes libertinella* (Gelechiidae), Swiss Alps, (20) male, (21) female. 22, 23, *Kiwaia jeanae* (Gelechiidae) New Zealand (South Island), (22) male, (23) female. 24, 25, *Caryocolum laceratella* (Gelechiidae), Italian Alps, (24) male, (25) female.

(Zeller) on elm, *Gelechia turpella* (Denis & Schiffermüller), *G. rhombelliformis* Staudinger, *Anacampsis populella* (Clerck) and *A. innocuella* (Zeller) on poplar and aspen, and *A. blattariella* (Hübner) on birch, which usually hide in cracks of bark, often prefer to run up or around their host-tree rather than fly away when disturbed. As in many other groups of Lepidoptera, the possession of apparently well developed wings does not indicate that a particular species is a strong flier, and in many Gelechiidae the female is less inclined to fly than the male, for example *Teleiopsis albifemorella* (Hofmann) (Burmann, 1977: 142). There are even a few examples of flightlessness in both sexes of macropterous species (see below). In various species, for example *Eulamprotes wilkella* (L.), some *Chionodes* species, *Acompsia cinerella* (Clerck) and *A. tripunctella* (Denis & Schiffermüller), slight sexual differences in wing shape are observed, with the females having distally narrower fore wings than the males. Sexual wing dimorphism of such kind is seen as representing a trend towards brachyptery (Sattler, 1986: 258), and the existence of distinctly brachypterous species in *Eulamprotes* Bradley and *Acompsia* Hübner further supports this interpretation.

In most instances the brachypterous species are the only examples of wing reduction in large genera of otherwise macropterous species, for example *Eulamprotes* Bradley (1 of 10 species), *Kiwaia* Philpott (3 of 28 species), *Ephysteris* Meyrick (3 of 50+ species), *Caryocolum* Gregor & Povolný (1 of 60+ species), *Acompsia* Hübner (1 of 8 species) and *Stomopteryx* Heinemann (1 of 30+ species). In contrast, about one-third of the 30 or so *Megacraspedus* species show at least some degree of wing reduction whilst all 8 currently recognized *Sattleria* species are strongly brachypterous.

Aristoteliinae
Different degrees of wing reduction can be observed in the females of one-third of the about 30 currently recognized species of the predominantly western Palaearctic genus *Megacraspedus* Zeller (Figs 18, 19). All known species inhabit grassland, where their larvae are probably subterranean grass or grass root feeders. The adults occur in summer, and the males are usually active at dawn and dusk. Some brachypterous species inhabit high elevations, for example *M. culminicola* Le Cerf in Morocco (3200 m) and an unidentified species in Iran (2500 m), but many are found at much lower altitudes.

Daltopora felixi Povolný, an oreal species with brachypterous female (Povolný, 1979: pl. 1, fig. 33), is known only from Mongolia, where it occurs at altitudes of 1450–2500 m. The specimens were collected in the second half of June and most were attracted to light, indicating that *D. felixi* is nocturnal. The biology is unknown but the larvae can be expected to be internal feeders in one or more species of Compositae like those of the genera most closely related to *Daltopora* Povolný.

Progressive wing reduction is observed in the females of the European silver-marked species of *Eulamprotes* Bradley, but only the female of *E. libertinella* (Zeller) (Figs 20, 21), an oreal inhabitant of the European Alps, shows distinct wing reduction and could be described as stenopterous. Its fore wing is particularly narrow in the apical half, whilst the hind wing is vestigial. The females of two lowland species, *E. wilkella* (L.) and *E. superbella* (Zeller), which occur on poor sandy soils, have slightly reduced wings.

Gelechiinae (Gnorimoschemini)
Karsholt & Nielsen (1974) observed flightlessness in both sexes of the macropterous *Gnorimoschema bodillum* Karsholt & Nielsen, an inhabitant of shifting sand dunes on the North Sea coast of Denmark and northern Germany (Schleswig-Holstein). The adults, which occur in June and August, are particularly active on warm sunny days when they run fast over the ground and make jumps of about 10–25 cm. Parallel cases of flightlessness in coastal sand dune habitats are those of *Areniscythris brachypteris* Powell (Scythrididae) in California (see p. 270) and *Ambloma brachyptera* Walsingham (Symmocidae) in the Canary Islands (see p. 265); however, both sexes of these species are distinctly brachypterous. *G. bodillum* appears to be the only flightless species amongst the about 70 members of the Holarctic genus *Gnorimoschema* Busck, except perhaps for the oreal *G. elbursicum* Povolný (Iran, Elburz Mts, 3000 m) known only from a single partly damaged 'apparently brachypterous' ('offenbar brachypteren') female (Povolný, 1984: 264).

Another case of flightlessness in both sexes is that of an as yet undescribed macropterous *Scrobipalpula* species from the Falkland Islands. According to observations by C. Kirke (pers. comm.), who collected a short series of specimens (now in BMNH), the moths are flightless but jump prodigiously. The new species is closely related to Patagonian members of the predominantly New World genus *Scrobipalpula* Povolný.

In the genus *Kiwaia* Philpott, with 25 species endemic to New Zealand and three species in Nepal, wing reduction occurs in several of the New Zealand species; for example the female of *K. plemochoa* (Meyrick) is slightly wing-reduced
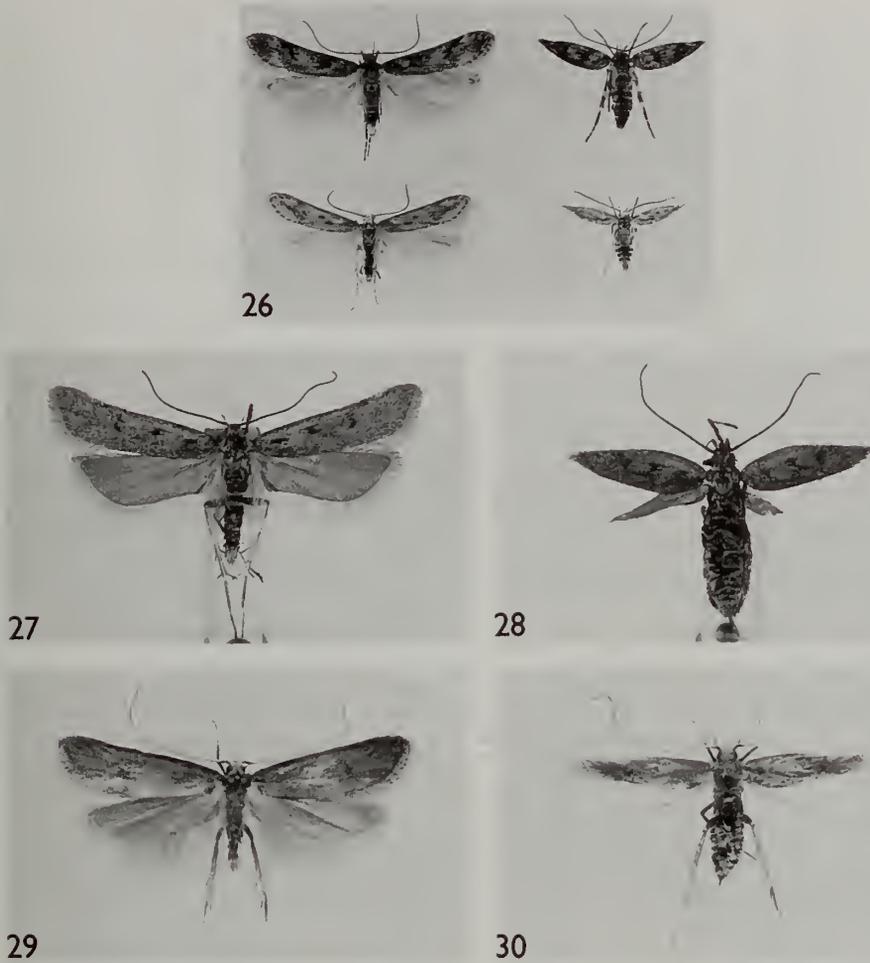
Figs 26–30 26, *Sattleria* species (Gelechiidae), Pyrenees. Males (left) and females (right) of *S. arcuata* (top) and *S. pyrenaica* (bottom). 27, 28, *Acompsia dimorpha* (Gelechiidae), Pyrenees, (27) male, (28) female. 29, 30, *Tegenocharis* species (Lecithoceridae), Nepal, (29) male, (30) female.

whilst that of *K. glaucoterma* (Meyrick) is strongly brachypterous. *K. jeanae* Philpott (Figs 22, 23) is one of only two species of Gelechiidae with distinct brachyptery in both sexes and at the same time the only fully brachypterous Lepidoptera species on the mainland of New Zealand. Its habitat, Birdlings Flat near Christchurch, South Island, is a windswept coastal stormbeach on the long narrow peninsula that separates Lake Ellesmere from the ocean. Moths are found from above EHWS, where they may be exposed to occasional blasts of heavy spray, to the back of the first dune-line. The ground is largely rounded shingle and sand with scattered mat-plants, mostly *Raoulia* (Compositae), where shelter is afforded by the loosely packed margins of *Raoulia* mats and interstices in the shingle (Dugdale, pers. comm.).

Both sexes of *K. jeanae* are able to run very fast and make jumps of up to 15 cm (Sattler, 1988: 232).

In the Old World genus *Ephysteris* Meyrick brachyptery is known in three of the about 50 currently recognized species. *E. kasyi* Povolný was described from a single female collected at an altitude of 3000 m on the Dasht-i-Newar plateau in Afghanistan. According to an illustration of the wings that accompanies the original description (Povolný, 1968: 7, pl. 20, fig. 4) the female is moderately brachypterous; the unknown male is probably macropterous. *E. curtipennis* (Zerny), a species with macropterous male and distinctly brachypterous female, is endemic to the Haut Atlas in Morocco, where it occurs at an altitude of about 3200 m. In contrast, an as yet undescribed

species, closely related to and sometimes mis-identified as *E. curtipennis*, is endemic to the Atlantic island of Madeira and is brachypterous in both sexes (Sattler, 1988: 232). A short series of this species collected in grassland at an altitude of about 1400 m (Uffen, pers. comm.), is now in BMNH.

Moderate wing reduction of the female sex is observed in only one of the more than 60 species of *Caryocolum* Gregor & Povolný. *C. laceratella* (Zeller) (Figs 24, 25), which inhabits sparsely vegetated alpine scree, is only found in the south-eastern European Alps (Julijske Alpe). The slightly brachypterous females are flightless but, like those of many other flightless oreal species, are able to run and jump (Huemer & Sattler, 1989: 256, figs 1, 2 (♂, ♀).

All known species of *Sattleria* Povolný, which inhabit the alpine zone of certain European mountain ranges, have strongly brachypterous females capable of running and jumping (Figs 26, 54, 55; Pitkin & Sattler, 1991).

Anacampsinae

Stompteryx mongolica Povolný, the only of the 30+ species of the Old World genus *Stomopteryx* Heinemann with wing reduction, is widespread and common in Mongolia, where the adults occur in June-August at altitudes of 600–2200 m. The biology is still unknown and, whilst the macropterous males are frequently attracted to light, the strongly brachypterous females are rarely observed.

The Palaearctic, predominantly European, genus *Acompsia* Hübner comprises eight species, most of which show slight sexual wing dimorphism. The female of *A. dimorpha* Petry (Figs 27, 28), an endemic of the central Pyrenees, is distinctly brachypterous, whereas other oreal species such as *A. tripunctella* (Denis & Schiffermüller) and *A. maculosella* (Herrich-Schäffer) are macropterous and apparently capable of flight in both sexes.

13. Lecithoceridae
In the Old World family Lecithoceridae wing reduction is known in the females of two unrelated genera. Brachyptery occurs in three of the seven currently recognized species of the western Palae-arctic genus *Ceuthomadarus* Mann whilst the female of one species is macropterous and those of three species are still unknown (Gozmány, 1978: 52–60, pl. 1). Most species inhabit mountainous areas although only *C. funebrella* (Chrétien) and *C. naumanni* Gozmány appear to be restricted to higher altitudes (2000–2700 m). The adults of all species are summer-active but the larval habits are unknown.

An as yet unidentified *Tegenocharis* species (Figs 29, 30) with macropterous male and strongly brachypterous female was discovered in 1983 in Nepal at an altitude of about 2500 m, where the adults were collected by members of the former Lepidoptera Section (BMNH) in late May in primary montane oak forest.

14. Scythrididae
Scythrididae are inhabitants of low-growing vege-tation. The adults of all species are summer-active; they are often diurnal and visit flowers. Many Scythrididae are reluctant fliers; they can run and, when disturbed, individuals sometimes jump rather than fly to safety, for example *S. inspersella* (Hübner) (Sattler, 1981: 16). As many species occur in mountainous regions at high altitudes it is surprising that none of them are brachypterous. Indeed, the only scythridid with significant wing reduction is a coastal species with strong brachyptery in both sexes. *Areniscythris brachypteris* Powell is endemic to the coastal Santa Maria sand dune system in San Luis Obispo County, California, where its larva lives in silken tunnels just beneath the surface of the sand and feeds on the partially buried green stems and leaves of a variety of plants without showing host-plant specialization. The brachypterous adults are capable of jumping 10–15 cm into the air and are then blown by the continuous strong wind over the sand like fragments of plant material. It is interest-ing to note that the moths produce small pits in the sand in which to shelter against the wind, a behaviour not observed in other species (Powell, 1976b). *A. brachypteris* is the only continental Lepidoptera species with brachyptery in both sexes; all other fully brachypterous species inhabit oceanic islands.

Tortricoidea

15. Tortricidae
In the Tortricidae wing reduction is rare but is known in several species of Tortricinae and one species of Olethreutinae (see p. 260). The only species with brachypterous male and female, *Sorensenata agilitata* Salmon & Bradley (Fig. 31), is an inhabitant of *Poa litorosa* grassland on New Zealand's sub-Antarctic Campbell Island. The adults were only observed in September–October amongst grass, where they jumped with great agility from stem to stem (Salmon & Bradley, 1956: 73, fig. 42).

The European *Exapate congelatella* (Clerck) (Figs 33, 34) and *E. duratella* (Heyden) are northern hemisphere cold season species (October-November) with strongly brachypterous females.

Figs 31–36 31, *Sorensenata agilitata* (Torticidae), New Zealand (Campbell Island), male. 32, *Pollanisus calliceros* (Zygaenidae: Procridinae), Australia (New South Wales), female. 33, 34, *Exapate congelatella* (Tortricidae), British Isles, (33) male (England), (34) female (Scotland). 35, 36, *Sphaleroptera alpicolana* (Tortricidae), Austrian Alps, (35) male, (36) female.

By contrast, *Tortricodes alternella* (Denis & Schiffermüller), a European cold season species with an adult activity period in February-March, is macropterous in both sexes and capable of flight. Flightlessness with only slight wing reduction is recorded in the heavy-bodied female of the western North American *Synnoma lynosyrana* Walsingham (Tortricinae, Sparganothini), the adults of which are active in October-November (Powell, 1976a). Whilst sexual dimorphism is not unusual in Sparganothini the females of most species are able to fly, except for example the macropterous female of *Synalocha gutierreziae* Powell (Powell, 1985: 65).

Although Tortricidae are well represented in the faunas of many mountain ranges in most parts of the world, only two oreal species with brachypterous females are known, *Sphaleroptera alpicolana* (Frölich) (Figs 35, 36) in the European Alps and Pyrenees and *Olethreutes orestera* Bradley in the East African Ruwenzori mountains.

A tendency towards wing reduction is also observed in the females of *Oxypteron* Staudinger, a predominantly Mediterranean genus of about 10 species, but it is unknown whether any of them are flightless. The females of several species are macropterous but those of *O. impar* Staudinger

(southeastern Europe, Turkey) and *O. exiguana* (de la Harpe) (Sicily, North Africa) are slightly brachypterous. Whilst some *Oxypteron* are cold season species, for example *O. homsana* (Amsel) (Syria, Jordan: November–December; female unknown, possibly brachypterous) and perhaps *O. impar* (September–October), that cannot be said for *O. exiguana* (August–September).

Zygaenoidea

16. Heterogynidae
The systematic status of the small family Heterogynidae, which comprises two genera with an uncertain number of species, is not yet clear and its current placement in the Zygaenoidea is tentative. The females of the Mediterranean genus *Heterogynis* Rambur are apterous (Freina & Witt, 1990: pl. 10) and have strongly reduced mouthparts and legs. According to observations on *H. penella* (Hübner) (Daniel & Dierl, 1966) the female stays on the cocoon after emergence from the pupa, because its head and legs remain firmly attached to the pupal skin. After mating, the female returns into the cocoon and re-enters the pupal exuviae where it lays its eggs. As in the Psychidae, the loss of wings and reduction of legs in the female can be interpreted as the direct result of sedentary habit. The females of the South African genus *Janseola* Hopp are unknown.

17. Zygaenidae
The only example of wing reduction in the Zygaenidae, a family of about 1000–1500 species worldwide, is the micropterous female of the Australian *Pollanisus calliceros* Turner (Procridinae) (Fig. 32), a species recorded from mountaineous areas of about 600–1500m in New South Wales and Tasmania. Only a single female is known to date and was described as having simple antennae, a broad abdomen with grey anal tuft, small but normal thorax and legs and very small rudimentary wings (Turner, 1926: 443–444); no information on its habits is available. As far as known the females of all other *Pollanisus* species are macropterous and can fly.

18. Somabrachyidae
The systematic status and placement of the small family Somabrachyidae in the Zygaenoidea are also uncertain. *Somabrachys* Kirby, the only included genus, is of Mediterranean distribution (North Africa – Syria) and comprises between 1 and 20 species depending on author (Freina & Witt, 1990: 48–50, pl. 6, figs 54–91). The apterous females superficially resemble those of *Orgyia antiqua* (L.) (Lymantriidae) but, in contrast to the latter, have well developed legs and are able to

run fast (Seitz, 1912: 336, pl. 50 d). The macropterous males are nocturnal and are attracted to light. With an adult activity period in September – November all known *Somabrachys* are cold season species.

Copromorphoidea

19. Carposinidae
The small family Carposinidae is mostly tropical with the majority of its about 200 species occurring in the Indo-Australian region. Wing reduction is known only in *Campbellana attenuata* Salmon & Bradley, an inhabitant of New Zealand's sub-Antarctic Campbell Island with strong brachyptery in both sexes (Salmon & Bradley, 1956: 68, fig. 38). The biology is unknown but the adults live amongst the tussock and are able to jump like small grasshoppers. *C. attenuata* was originally described in the Yponomeutidae but was subsequently transferred to the Carposinidae (Dugdale, 1971: 73).

Pyraloidea

20. Pyralidae
In the Pyralidae, with an estimated 25,000 species possibly the largest Lepidoptera family, examples of wing reduction are known in the subfamilies Pyralinae, Crambinae, Acentropinae, Pyraustinae and Scopariinae. There are two oceanic island species (Scopariinae, Pyraustinae) with brachyptery in both sexes, several oreal species (Crambinae, Pyraustinae) with more or less brachypterous females and an aquatic species (Acentropinae) with wing dimorphism in the female (a macropterous and a brachypterous form). However, there are apparently no wing-reduced cold season Pyralidae.

Pyralinae
Wing reduction is known in several of the dozen species of the Palaearctic genus *Synaphe* Hübner. The females of some species, for example *S. punctalis* (Fabricius), *S. amuralis* (Hampson), *S. bombycalis* (Denis & Schiffermüller) (Figs 37, 38) and *S. moldavica* (Esper), have narrower wings and proportionately longer abdomens than the males, but extreme brachyptery is only developed in *S. oculatalis* (Ragonot) from Northwest Africa (Zerny, 1936: 121, pl.2, fig. 12 (♀)). The reasons for this trend towards brachyptery in *Synaphe* are still unclear, because the females are not noticeably heavy-bodied and none of the species is restricted to the cold season or confined to oreal habitats. The adults of *S. oculatalis* occur in late August – early October, too early to qualify
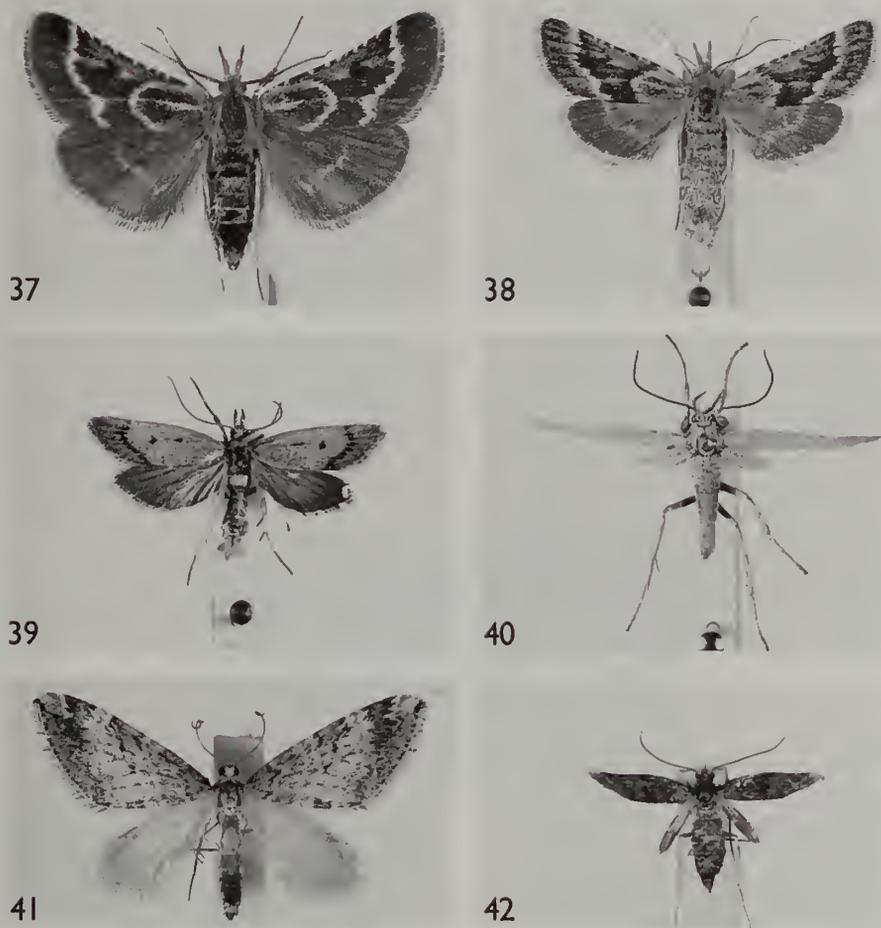
Figs 37–42 37, 38, *Synaphe bombycalis provincialis* (Pyralidae: Pyralinae), Spain, (37) male, (38) female. 39, *Udea hageni* (Pyralidae: Pyraustinae), Tristan da Cunha, male. 40, *Exsilirarcha graminea* (Pyralidae: Scopariinae), New Zealand (Campbell Island) male. 41, 42, *Apleria* sp. (Geometridae: Larentiinae), Chile (Magallanes), (41) male, (42) female.

clearly as cold season species, and inhabit lowland localities, although they reach altitudes of about 2000 m in the Moyen Atlas.

Crambinae

A tendency towards sexual dimorphism of the wing shape is noticed in several Palaearctic Crambinae, in which the females sometimes have slightly narrower, more pointed fore wings than the males but are still capable of flight, for example *Agriphila poliella* (Treitschke) (Bleszynski, 1965: pl. 14, figs 161–1 (♂), 161–2 (♀)). Stronger wing reduction coupled with flightlessness is recorded in the southern European oreal *Catoptria digitella* (Herrich-Schäffer) (Bleszynski, 1965: pl. 18, figs 215–1 (♂), 215–2 (♀)), *C. biformella*

(Rebel) (Bleszynski, 1965: pl. 20, figs 234–1 (♂), 234–2 (♀)) and *C. majorella* (Drenowski) (Bleszynski, 1965: pl. 20, figs 235–1 (♂), 235–2 (♀)). Slight wing reduction is also noted in the female of *Fernandocrambus falklandicellus* (Hampson) in the Falkland Islands, but field observations have shown that it is still capable of flight (Kirke, pers. comm.).

Amongst the New Zealand Crambinae a tendency towards wing reduction is observed in several of the about 50 species of the endemic genus *Orocrambus* Purdie. For example, the female of *O. lectus* (Philpott), an inhabitant of subalpine to alpine regions on South Island, is distinguished from the male by an acutely pointed fore wing and slightly reduced hind wing (Hudson,

1939: pl. 56, fig. 17 (♀); Gaskin, 1975: fig. 53 (♂)) and may be flightless. According to Gaskin (1975: 308), the unknown female of *O. crenaeus* (Meyrick), a species of alpine grassland on South Island, may be brachypterous; however, strong wing reduction is only observed in the indisputably flightless female of *O. lindsayi* Gaskin, an endemic of Mount Ida on South Island. Whilst the as yet unknown male of *lindsayi* is almost certainly macropterous, the female has narrow, lanceolate fore wings and similarly shaped but much shorter hind wings (Gaskin, 1975: figs 22d, 55). Although currently retained in a separate genus, *Kupea electilis* Philpott probably is merely another *Orocrambus* species with some degree of wing reduction. The loss of vein M2 in both fore and hind wing of the male may be interpreted as a first step towards wing reduction whilst the unknown female is suspected of being brachypterous (Gaskin, 1975: 345, figs 22f, 82). Flightlessness and associated wing reduction would not surprise in *K. electilis* because it shares its stormy coastal habitat Birdlings Flat with at least one other Lepidoptera species that is strongly brachypterous in both sexes (*Kiwaia jeanae* Philpott, Gelechiidae, see p. 269).

Acentropinae
Acentria ephemerella (Denis & Schiffermüller) (= *Acentropus niveus* (Olivier)), distributed in the western Palaearctic and Nearctic regions, is the only known aquatic moth with brachyptery. Whilst the male is always fully winged and capable of flight, in the dimorphic female a macropterous and a brachypterous form are known. The larva of *A. ephemerella* lives submerged on various water plants and, whilst the macropterous males and females leave the water, the brachypterous females remain permanently under water, where they crawl about plants or swim with the aid of their meso- and metathoracic legs which are equipped with a fringe of long hairs. The adults are nocturnal – the macropterous males and females are attracted to light – and the brachypterous female swims to the surface where is raises the apex of its abdomen out of the water to attract males, one of which eventually lands on the female's back and effects the copula. Brachyptery in this case is undoubtedly an adaptation to life under water, where fully developed wings would be disadvantageous. However, the mechanism for the female wing dimorphism is not yet fully understood. The suggestion that a brachypterous generation may alternate with a macropterous one was not confirmed by the observations of Berg (1941), who believed that environmental factors such as higher water temperatures in summer were responsible for the development or macropterous females.

Pyraustinae
Slight wing reduction in the female is recorded for *Nomophila heterospila* (Meyrick), a species found in the South American Andes at an altitude of about 3000–5000 m (Munroe, 1973: 199, figs 39, 41 (♂), 40, 42 (♀). It is not known whether the reduction is an indication of flightlessness; however, a comparison with analogous cases of sexual wing dimorphism in some other Lepidoptera, for example certain Gelechiidae, suggests that the female of *N. heterospila* is still capable of flight. Some wing reduction is also recorded in *Udea hageni* Viette (Fig. 39) on Tristan da Cunha in the South Atlantic. The males are flightless and stay on the ground (Viette, 1952b: 3, 18); the unknown female is almost certainly brachypterous.

Scopariinae
Both sexes of *Exsilirarcha graminea* Salmon & Bradley, an inhabitant of New Zealand's sub-Antarctic Campbell Island and Auckland Islands, are strongly reduced (Fig. 40). The adults were observed in September in large numbers amongst the tussock grass *Poa litorosa*; they walk and are capable of jumping (Salmon & Bradley, 1956: 73–77, figs 24–30). Female brachyptery is known in *Protyparcha scaphodes* Meyrick, on the Auckland Islands. Both species were previously considered to be Crambinae but are now included in the Scopariinae (Dugdale, 1988: 159).

Geometroidea

21. Geometridae
With about 20,000 species the Geometridae are one of the largest Lepidoptera families and, at the same time, also the family with by far the largest number of species with wing reduction (disregarding the Psychidae). Within the Geometridae brachyptery has evolved many times independently and is recorded in the subfamilies Oenochrominae, Larentiinae (tribes Xanthorhoini and Operopterini) and Ennominae (tribes Semiothisini, Bistonini and Gnophini). Although in this family flightlessness and wing reduction are usually restricted to the female sex, there appears to be a slight tendency towards reduction in the males of some species endemic to New Zealand's sub-Antarctic islands. For example in *Asaphodes oxyptera* (Hudson) and *A. campbellensis* (Dugdale) (Larentiinae), both species with brachypterous females, the wings of the males are distinctly narrower than those of related *Asaphodes* species in mainland New Zealand. Reduction in the size

of the hind wings, as it is observed in the males of many Larentiinae with normal macropterous females, for example *Tatosoma* Butler, *Tympanota* Warren and *Sauris* Guenée (Dugdale, 1980), is disregarded here because it does not impair the ability to fly and is unrelated to the phenomenon of flightlessness. In the Geometridae all stages of wing reduction, from weak brachyptery to microptery and aptery, have been observed. For example in the alpine *Elophos zelleraria* (Freyer) or the arcto-alpine *Pygmaena fusca* (Thunberg) wing reduction is usually slight and females may still be able to fly at least short distances, whilst flight is almost certainly impossible for the females of Japanese cold season *Protalcis* species with wings only about half the size of those of the males (Inoue, 1982: pl. 98, figs 12–15). Greater reduction can be seen in the females of *Alsophila*

Hübner, *Operophtera* Hübner (Fig. 56), *Larerannis* Wehrli and others, in which the wings are usually shorter than the body. Various species referred to as apterous in the literature, for example *Erannis* species (Fig. 57) and *Chondrosoma fiduciarium* Anker (Fig. 43), are in fact micropterous and still possess wing vestiges although these are often concealed in the dense thoracic hair cover where they can only be found with careful examination. True aptery is rare but is confirmed for *Cheimoptena pennigera* Danilevsky (Danilevsky, 1969a: 183, fig. 10). A rare example of stenoptery is the female of the central Asiatic *Spartopteryx kindermannaria* (Staudinger) (Figs 44, 45; Wehrli, 1941: 466, pl. 41 b).

As far as known, in the Geometridae all wing-reduced females have fully developed legs and are motile; however, whilst they are able to walk, they

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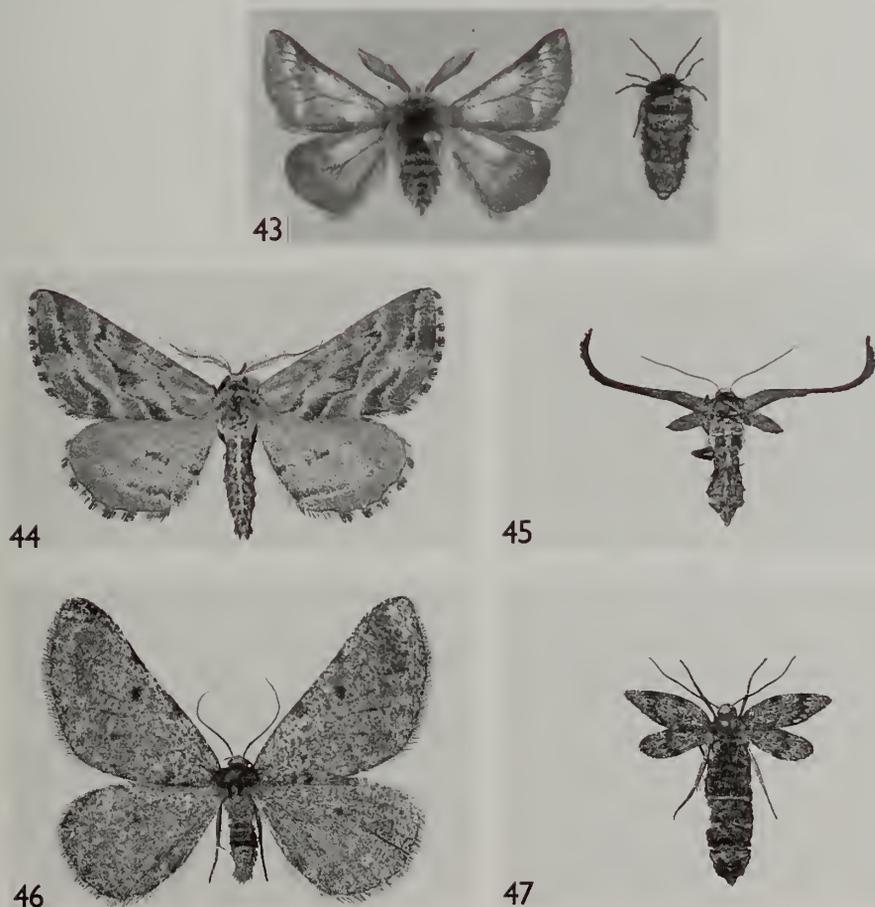
Figs 43–47   43, *Chondrosoma fiduciarium* (Geometridae: Ennominae), Austria; male (left), female (right). 44, 45, *Spartopteryx kindermannaria* (Geometridae: Ennominae), Siberia, (44) male, (45) female. 46, 47, *Elophos caelibaria* (Geometridae: Ennominae), Austrian Alps, (46) male, (47) female.

do not usually run fast and appear to be unable to jump. Most of the Geometridae with wing-reduced females are northern hemisphere cold season species, for example *Alsophila* Hübner, *Alsophiloides* Inoue, *Inurois* Butler (Oenochrominae), *Operophtera* Hübner (Larentiinae), *Apocheima* Hübner, *Lycia* Hübner, *Cheimoptena* Danilevsky, *Chondrosoma* Anker, *Agriopis* Hübner, *Erannis* Hübner, *Pachyligia* Butler, *Descoreba* Butler and others (Ennominae). A southern hemisphere cold season species with strongly brachypterous female is *Zermizinga indocilisaria* Walker (Ennominae) in New Zealand. Some cold season species are diurnal, for example *Lycia zonaria* (Denis & Schiffermüller), *Cheimoptena pennigera* Danilevsky and *Chondrosoma fiduciarium* Anker, and their males usually fly under sunny conditions when they are able to absorb solar radiation to raise their thoracic temperature high enough to allow the flight musculature to operate (see p. 253). However, most species are nocturnal and their males are adapted to flying at low thoracic temperatures (see p. 253).

The large number of brachypterous cold season species, which represent at least three independent evolutionary lineages within the Geometridae, indicates the potential in that family to respond with wing reduction to appropriate environmental conditions. It is therefore surprising that the incidence of brachyptery is rather low amongst oreal species although the Geometridae are extremely well represented in the highland faunas of the world. In the Palaearctic region a more or less pronounced trend towards flightlessness is observed in the females of alpine Ennominae, particularly in the tribe Gnophini, but a significant degree of wing reduction has only evolved in several of the about 10 species of the genus *Elophos* Boisduval. Whilst the female of *E. zelleraria* (Freyer) is distinctly smaller than the male, but can still be described as macropterous, those of most other species are more strongly brachypterous, for example *E. caelibaria* (Herrich-Schäffer) (Figs 46, 47) and *E. zirbitzensis* (Pieszczek) in the European Alps (Forster & Wohlfahrt, 1980: pl. 24, figs 40–43; pl. 25, figs 1–8) as well as *E. iveni* (Erschoff) (Wehrli, 1953: 621) and *E. banghaasi* (Wehrli) (Wehrli, 1922: 27, pl. 2, figs 41, 56) in Central Asia.

In the European oreotundral *Pygmaena fusca* (Thunberg) the female has noticeably narrower wings than the male (Forster & Wohlfahrt, 1980, pl. 25, figs 44 (♂), 52 (♀)) and their length, according to Hackman (1966: 2), varies considerably; however, whilst many authors considered the female as flightless or nearly so, Wehrli (1953: 640) disputed this and described it as a skilful flier.

Slight wing reduction is also found in the female of *Sciadia tenebraria* (Esper) in the European mountains (Pyrenees, Alps, Appenin), but no observations on its ability to fly are available.

In East Africa several *Xanthorhoe* species (Larentiinae) with strongly brachypterous females, e.g. the nocturnal *X. alluaudi* (Prout) and the diurnal *X. barnsi* (Prout) and *X. wellsi* (Prout), inhabit the ericaceous zone and alpine zone of the Ruwenzori mountains (Fletcher, 1958: 77, figs 12–18).

In New Zealand wing reduction in oreal species is found in an unidentified species of Oenochrominae (McQuillan, 1986: 263) and in the large genus *Asaphodes* Meyrick (Larentiinae). For example the female of *A. nephelias* (Meyrick) differs from the male by narrower, more pointed fore wings but is still able to fly (Dugdale, pers. comm.) whilst the brachypterous female of *A. dionysias* (Meyrick) is flightless. Moderate wing reduction is observed in the female of *Aponotoreas villosa* (Philpott) (Hudson, 1928: 123, pl, 15, figs 23 (♂), 24 (♀)).

In South America, the subcontinent most poorly explored for wing-reduced forms, an as yet undescribed species of *Apleria* Warren (Larentiinae) (Figs 41, 42) with strongly brachypterous female was discovered in southern Chile, Munoz Gomero Peninsula (Magallanes). According to Perry (pers. comm.) it occurs at an altitude of about 500 m in low vegetation near and above the treeline of *Nothofagus antarctica* forest, where a series of males and females, now preserved in BMNH, was collected in the daytime in March 1973; some adults were also observed above the treeline at about 1300 m.

A case of strong female brachyptery unexplained by seasonal factors or the biotope is that of the Holarctic *Itame loricaria* (Eversmann) (Ennominae, Semiothisini), a summer-active moth with birch-feeding larva. As far as known, no other *Itame* species is wing-reduced or flightless.

Bombycoidea

22. Lasiocampidae

The family Lasiocampidae, with representation on all continents, comprises about 1000 species the adults of which are usually short-lived and, with reduced mouthparts, non-feeding. Although they are mostly heavy-bodied and the sluggish females fly little, particularly whilst still carrying their full egg complement, wing reduction is rare in this family and is only recorded in two genera in the western Palaearctic region and one monotypic genus in southern Africa. In each case the reduction is confined to the female sex and there are no

examples of wing reduction or diminished ability to fly in the male. The females of all affected species have vestigial wings and thus must be classed as micropterous, although they were sometimes incorrectly referred to as wingless; no example of a lesser degree of wing reduction is known. Reduction of the wings in Lasiocampidae is probably a consequence of the more or less sedentary habit of the gravid female with its heavy abdomen.

As in the Palaearctic region the adult activity periods of many Lasiocampidae extend into the autumn and sometimes winter, it could be argued that wing reduction is a response to adult life in the cold season. However, the adult activity of such species usually commences in summer (July or August) so that only part of the population would be exposed to autumn or winter conditions. By contrast, true winter species such as *Trichiura ilicis* (Rambur) (Iberian Peninsula, North Africa; December-April) and *Stoermeria regraguii* (Lucas) (Morocco; December-January) have macropterous females. Moreover, all known micropterous species are confined to southern Europe and North Africa, whilst the cold season Lasiocampidae occurring in the harsher climate of central and northern Europe are without exception macropterous, for example *Trichiura* Stephens, *Poecilocampa* Stephens and *Eriogaster* Germar.

Microptery in the female is observed in all taxa of the Mediterranean genus *Chondrostega* Lederer (Freina & Witt, 1987: 330, pl. 25, figs 1–11); however, the total number of species, which is still unknown because the taxonomic status of most of the currently recognized 15 species is uncertain, may not exceed three or four. The North African *Lasiocampa staudingeri* Baker (Freina & Witt, 1987: 362, pl. 28, figs 39–41) which has an adult activity period in August-January, is the only *Lasiocampa* species with wing reduction. Related species with similarly late flight periods, for example *L. serrula* (Guenée) (southern Spain, North Africa; September-November) and *L. eversmanni* (Eversmann) (southern Russia; August-October), have macropterous females (Freina & Witt, 1987: 359, 360, pl. 29, figs 6–15).

The only non-Palaearctic lasiocampid with wing-reduced female, *Mesocelis montana* (Stoll) (Pinhey, 1975: 119, pl. 22, figs 500a (♂), 500b (♀), is found in southern Africa, where the adults are active in summer (November). With a small head, very small eyes, much reduced antennae, mouthparts and legs, and vestigial wings, the heavy-bodied female resembles those of some Lymantriidae. After emerging from the pupa the female remains within the cocoon, where it lays about 30–100 eggs. During oviposition the dense cover of body hair is rubbed off and fills the cocoon as loose fluff which may have irritating properties and acts to protect the eggs from predators (Hesse, 1935). Although both sexes normally occur, Taylor (1950, 1954) observed a parthenogenetic population, a sample of which he reared in captivity for at least eight generations. The moths reproduced vigorously and produced all-female offspring.

Noctuoidea

23. Lymantriidae

The family Lymantriidae has an almost worldwide distribution and comprises about 2500 species. Their usually summer-active adults are non-feeding – those of most species have reduced mouthparts – and many species are apparently protected from predators by distasteful substances in conjunction with aposematic coloration. The larvae are mostly foliage feeders on a wide variety of broad-leaved and coniferous trees and shrubs; many species are polyphagous whilst others are more restricted in their diet although few are monophagous.

In many species the females are heavy-bodied; they are reluctant fliers and some are practically flightless although still in possession of fully developed wings, for example the Arctic *Gynaephora rossii* (Curtis) and *G. groenlandica* (Wocke) or *Lymantria dispar* (L.) (Ferguson, 1978: 20, 21, 94). Wing reduction, restricted to the female sex, has evolved in several independent lineages and can be interpreted as a consequence of the females' reduced motility and sedentary habit. In most cases the wing-reduced females are micropterous or even apterous, with small thorax, more or less reduced legs and a large egg-filled abdomen; however, brachyptery is also known. After emerging from the pupa micropterous and apterous females usually stay on the pupal cocoon onto which they lay their eggs after mating with the frequently diurnal males.

The genus *Orgyia* Ochsenheimer (including *Teia* Walker and *Hemerocampa* Dyar, which are sometimes treated as separate genera) occurs on all continents and comprises about 45 species. Whilst a few of them have macropterous females, e.g. the African *O. basalis* (Walker) (Pinhey, 1975: 179, pl. 47, figs 863 a-c), or are brachypterous, e.g. the African *O. hopkinsi* Collenette, most Palaearctic, African, Indo-Australian and American species are micropterous, e.g. *O. antiqua* (L.) (Fig. 60), and some even apterous, e.g. *O. dubia* (Tauscher) (Kozhanchikov, 1950: fig. 2) and *O. ericae* (Germar) (Heitmann, 1934: 180). For further examples of wing reduction in *Orgyia* see

Ferguson (1978: pls. 7, 8) and Freina & Witt (1987: pl. 15). A rare case of wing dimorphism is recorded in the Japanese *O. thyellina* Butler; the females of the first generation are macropterous (Inoue, 1982: pl. 148, figs 9 (♂), 10 (♀)), those of the second generation to about one-third macropterous and two-thirds strongly brachypterous or micropterous and the third generation almost totally micropterous (Cretschmar, 1928: 298). Hackman (1966: 4, fig. 2), misinterpreting an illustration depicting a female with partly removed wings (Kozhanchikov, 1950: fig. 1), erroneously recorded *Gynaephora lugens* Kozhanchikov (junior synonym of *G. rossii* (Curtis)) as brachypterous.

Moderate brachyptery, without loss of wing veins, is observed in the female of *Penthophera morio* (L.) (Eggers & Gohrbandt, 1938: 267, fig. 2; Freina & Witt, 1987: 206, pl. 15, figs 3–6), an inhabitant of open places in south-eastern Europe, where its larva feeds on a variety of grasses.

Brachyptery and microptery have evolved in the females of several Indo-Australian species of *Lymantria* Hübner, an Old World genus of about 150 species, the adults of which frequently are aposematically coloured. The females of some species are flightless but nevertheless macropterous, and retention of the non-functional wings may in this case be advantageous because it enhances the effect of the aposematic coloration. In contrast, those of several Indo-Australian species are brachypterous, for example *L. obfuscata* Walker and *L. turneri* Swinhoe, whilst others such as *L. detersa* Walker, *L. incerta* Walker and *L. ampla* (Walker) are micropterous.

As far as known the females of all eight species of *Bracharoa* Hampson, a genus restricted to sub-Saharan Africa, are strongly wing-reduced, probably apterous. The female of *B. dregei* (Herrich-Schäffer) 'apparently deposits her eggs within the cocoon' (Taylor, 1949: 84, pl. 1, figs 18, 18A (♂, ♀)); however, it is not clear from this statement whether the female remains inside the cocoon after emerging from the pupa or sits on the outside and merely lays its eggs into it.

Further examples of wing reduction are the African *Aroa melanoleuca* Hampson (♀ micropterous or apterous) (Pinhey, 1975: 176, pl. 44, figs 841a (♂), 841 b (♀)), Asiatic *Lachana ladakensis* Moore (♀ micropterous or apterous), *Laelia heterogyna* Hampson (♀ brachypterous), *Dasorgyia pumila* Staudinger (♀ slightly brachypterous) and *D. selenophora* Staudinger (♀ micropterous or apterous) and the Australian *Iropoca rotundata* (Walker) (♀ micropterous) (Common, 1990: 428, figs 43.5, 43.6). The apterous females of an as yet unidentified species (male still unknown) probably belonging to the Lymantriidae were discovered in

May and October 1989 at an altitude of 3000 m in the South African Drakensberge sitting in the sun (Scholtz in litt.).

24. Arctiidae
The family Arctiidae, here taken to include the Ctenuchinae and Thyretinae which are sometimes considered separate families, is distributed on all continents and comprises about 10,000 species. The mostly summer-active adults are often aposematic; they are usually non-feeding, with reduced mouthparts, and many species are heavy-bodied. In the females there is a widespread tendency towards flightlessness, and various degrees of brachyptery and microptery have evolved in several independent lineages. Strong reduction of the hind wings is observed in the males of certain South American Ctenuchinae but does not impair their ability to fly; in the most extreme case, *Diptilon culex* Draudt (Draudt, 1915: 120, pl. 19 e), the hind wings of the male are reduced to tiny appendages which are hidden in the thoracic scale cover. The larvae of many Arctiidae are polyphagous, mostly on herbaceous plants.

Wing reduction in the females of Arctiidae may generally be interpreted as a consequence of their low motility and sedentary habit, although in several cold season *Ocnogyna* species and a few oreal species some response to environmental factors may additionally be involved.

In the Lithosiinae a high degree of flightlessness is recorded in the females of the European genus *Setina* Schrank (= *Endrosa* Hübner); however, wing reduction is at best slight (Freina & Witt, 1987: pls 3, 4). According to observations on this genus by Burmann (1957) in the European Alps, both sexes emerge from the pupae in the early hours of the morning, usually before 10.00 hrs. The diurnal males, which fly in the sunshine, commence their courtship flight soon after sunrise and mate with the freshly emerged females, which at that time still sit on or near their pupal cocoons. Mating sometimes takes place before the female has fully expanded its wings. Egg-laying begins soon after the copula has separated, and the first batch of eggs is often deposited not far from the pupal site. After having laid most of its eggs the female may fly short distances, usually in late afternoon, thus ensuring some dispersal of its egg complement. Strong wing reduction is known in *Xanthodule* Butler, an endemic Australian genus with two species. After emerging from the pupa the female stays on the outside of its cocoon where it mates and deposits its eggs in the manner of *Orgyia* species (Common, 1990: 437, pl. 31.4). According to McQuillan (1986: 271) the female of the Tasmanian *Thermeola tasmanica* Hampson is

Figs 48–53 48, 49, *Ocnogyna parasita* (Arctiidae: Arctiinae), Hungary, (48) male, (49) female. 50, 51, *Cymbalophora haroldi* (Arctiidae: Arctiinae), Algeria, (50) male, (51) female. 52, 53, *Syntomis mestralii* (Arctiidae: Ctenuchinae), (52) male (Lebanon), (53) female (Israel).

also flightless; however, it is not stated whether it has reduced wings.

The largest number of wing-reduced Arctiidae is found in the subfamily Arctiinae, particularly amongst north-west African species. In the western Palaearctic genus *Coscinia* Schrank appreciable wing reduction is known in the North African *C. libyssa* (Püngeler), which at the same time shows some variation in the degree of brachyptery, with the female of the oreal subspecies *C. libyssa liouvillei* Le Cerf in the Atlas mountains being more strongly reduced than that of the nominate subspecies at low elevations (Freina & Witt, 1987: 112, pl. 5, figs 44–49). Varying degrees of wing reduction affect all females of the about 10 predominantly south-western Palaearctic cold season species of the genus *Ocnogyna* Lederer, from moderate reduction in some forms of *O. zoraida* (Graslin) through distinct brachyptery in *O. parasita* (Hübner) (Figs 48, 49) to microptery

in *O. baetica* (Rambur) and possibly aptery in *O. pudens* (Lucas) (Freina & Witt, 1987: pl. 5, figs 50–66, pl. 6, figs 1–28; Seitz, 1910: 76, pl. 14; Draudt, 1931b: 72, pl. 6). Strong brachyptery is also known in the female of *Tancrea pardalina* Püngeler from Turkestan (Püngeler, 1899: 95, pl.8, figs 1a (♂), 1b (♀); Seitz, 1910: 75, pl. 14 b (♂), 16 a (♀)). There must be some doubt that an Algerian specimen, now preserved in BMNH, with narrow fore wings and short, curiously curved hind wings represents the normal female of *Maurica breveti powelli* (Oberthür) (Oberthür, 1911: pl. 78, fig. 711; Freina & Witt, 1987: pl. 6, fig. 40) because the female of the nominate subspecies *M. breveti breveti* (Oberthür) is macropterous.

Whilst the females of the North African *Cymbalophora haroldi* (Oberthür) (Figs 50, 51; Freina & Witt, 1987: pl. 8, figs 9–13) and Mediterranean *C. rivularis* (Ménétriés) (Freina & Witt, 1987: pl. 8, figs 1–6) are respectively brachypterous and

micropterous, those of other *Cymbalophora* species are macropterous. Moderate brachyptery is observed in the female of *Spilosoma bretaudiaui* (Oberthür) from Tibet and Nepal (Seitz, 1910: 97, pl. 17 h (♂, ♀)) whilst those of all other species in that genus are macropterous. Outside the Palaearctic region microptery is observed in the females of three species of *Metacrias* Meyrick, a genus endemic to New Zealand. *M. erichrysa* Meyrick and *M. huttoni* (Butler) are restricted to alpine habitats but *M. strategica* Hudson appears to be more widespread. The males are diurnal and the females remain within their cocoons for mating and ovipositing (Gibbs, 1962: 153). Female microptery and a similar biology are also known in the closely related Australian genus *Phaos* Walker, which has oreal species in the Australian Alps and Tasmania (McQuillan, 1986: 270).

In South America strong wing reduction occurs in several of the about 75 species of *Paracles* Walker; for example the densely hairy females of the Argentinian *P. deserticola* Berg (Seitz, 1920: 321, pl. 41 d (♂, ♀)), *P. brittoni* Rothschild and *P. insipida* Rothschild are micropterous, that of the Chilean *P. rudis* Butler strongly brachypterous. Another species with micropterous female, the oreal *P. imitatrix* Rothschild in the Peruvian Andes (about 5000 m), may not be congeneric with the preceding ones.

In the Ctenuchinae some wing reduction can be observed in the females of the large Old World genus *Syntomis* Ochsenheimer. *Syntomis* species are summer-active, diurnal, aposematic moths with often sluggish females. Brachyptery is recorded in the middle-eastern *S. mestralii* Bugnion (Figs 52, 53; Seitz, 1910: 38, pl. 9 b (♂), 9 d (♀)), *S. antiochena* Lederer (Seitz, 1910: 38, pl. 9 d (♂, ♀)) and *S. libanotica* Bang-Haas (Draudt, 1931a: 57, pl. 5 e (♂, ♀)). Outside the Palaearctic region brachyptery occurs in the female of the South African *Epitoxis amazoula* Boisduval. Wing reduction is also known in the South American genus *Eurota* Walker, where the female of the Argentinian *E. spegazzinii* Jörgensen is strongly brachypterous (Draudt, 1915: 98, pl. 16 c (♂), pl. 26 , (♀), and is recorded in the female of the closely related *E. strigiventris* Guerin from Brazil, Argentina and Bolivia (Draudt, 1915: 98).

In the small subfamily Thyretinae, strong brachyptery in the female of the South African *Automolis meteus* (Stoll) (Pinhey, 1975: 144, pl. 36, figs 647a, 647b) is the only known case of wing reduction. Other species have macropterous females.

25. Noctuidae

With about 20,000 species the cosmopolitan Noctuidae are one of the largest Lepidoptera families.

As adults, Noctuidae are relatively long-lived, mostly nocturnal moths with well developed mouthparts; the majority of species feeds on a wide variety of liquid plant substances such as nectar, sap from injured trees, decaying fruit etc. Although many species are relatively heavy-bodied, most of them are enduring fliers with rapid wing beat and excellent manoeuvrability.

Wing reduction has evolved independently in several lineages, and examples are known in the subfamilies Acronictinae, Cuculliinae and Hadeninae but mostly in the Noctuinae. Whilst in the noctuoid families Lymantriidae and Arctiidae wing reduction is confined to the female sex of the affected species and is primarily, if not exclusively, the consequence of sedentary habit, in the Noctuidae it is a response to environmental factors and in some instances affects both sexes. In contrast to the Lymantriidae and Arctiidac the wing-reduced Noctuidae are motile and able to run fast, for example *Agrotis fatidica* (Hübner) (Vorbrodt, 1928: 54; Bergmann, 1931: 30), but there is no indication that any of them are capable of jumping.

Wing reduction in both sexes or only in the female is recorded in several species on southern ocean islands. On the South Atlantic island of Tristan da Cunha *Dimorphinoctua pilifera* (Walker) (Noctuinae) has a brachypterous female but macropterous male (Viette, 1952b: 6, pl. 2), whilst both sexes of *D. cunhaensis* Viette (Viette, 1952b: 9, pl. 1) are micropterous. Slight wing reduction is also known in the female of *Neoleucania exoul* (Walker) (Hadeninae) whilst its male is macropterous and flies well (Viette, 1952b: 14, pl. 3). Microptery, almost certainly in both sexes, is recorded in *Dimorphinoctua goughensis* Fletcher (Fig. 58) (female unknown) (Fletcher, 1963: 17) and *Peridroma goughi* Fletcher (female unknown) (Fletcher, 1963: 18) on South Atlantic Gough Island and *Agrotis patricei* (Viette) (Noctuinae) (Viette, 1959: 25, fig. 5 ♀) on Amsterdam Island in the South Indian Ocean.

An example of brachyptery in the female of an oreal species in Africa is *Saltia acrapex* Tams (Hadeninae) occuring at an altitude of about 4800 m on Kilimanjaro (Tams, 1952: 870, figs 3, 4). The as yet unknown female of the closely related *S. edwardsi* Tams, occurring at an altitude of about 4000 m on Mt. Elgon in Kenya (Tams, 1952: 873, fig. 13, ♂), may also be brachypterous.

In the northern hemisphere wing reduction is observed in the females of certain tundral, oreo-tundral or oreal Noctuinae. Strong brachyptery is known in *Xestia* (*Schoyenia*) *alaskae* (Grote), north-western Nearctic (Lafontaine *et al.*, 1983: 341, figs 5–7) and *X.* (*S*) *aequeva* (Benjamin),

Figs 54–60 54, *Sattleria basistrigella* (Gelechiidae), Swiss Alps, male. 55, *Sattleria basistrigella* (Gelechiidae), Swiss Alps, female. 56, *Operophtera brumata* (Geometridae: Larentiinae), British Isles (England), mating pair. 57, *Erannis defoliaria* (Geometridae: Ennominae), British Isles (England), female. 58, *Dimorphinoctua goughensis* (Noctuidae: Noctuinae), Gough Island, male. 59, *Pringleophaga marioni* (Tineidae), Prince Edward Islands (Marion Island), male. 60, *Orgyia antiqua* (Lymantriidae), British Isles (England), female.

north-western Nearctic (Lafontaine *et al.*, 1983: 345, figs 8–10), whilst *X. (S.) brachiptera* (Kononenko), northern Palaearctic (Lafontaine *et al.*, 1983: 347, figs 11, 27, 28) and *X. (S.) liquidaria* (Eversmann), northern Palaearctic – northwestern Nearctic (Lafontaine *et al.*, 1983: 363, figs 23, 24) are moderately brachypterous and other related species macropterous. Another northern tundral species with moderately brachypterous female is *Xestia (Anomogyna) laetabilis* (Zetterstedt), Scandinavia – Labrador (Nordström & Wahlgren [1937]: 105, pl. 18, fig. 9, (♂, ♀)).

Moderate to distinct brachyptery has also evolved in the females of several species of the

large genus *Agrotis* Ochsenheimer, including the arcto-alpine *A. fatidica* (Hübner) (Bergmann, 1931: 25, pl. 2; Mentzer & Moberg, 1987: 35, figs 1–4) with its close relative *A. luehri* Mentzer & Moberg from Norway (Mentzer & Moberg, 1987: 40, figs 5–7) and the central Asiatic *A. robusta* Eversmann (Mentzer & Moberg, 1987: 37, fig. 11 (♂)) and *A. trifurcula* Staudinger (Mentzer & Moberg, 1987: 39, figs 9, 10).

According to Dierl & Reichholf (1977: 29) further unspecified noctuine genera with many species, all of them with wing-reduced females and most inhabiting the alpine zone, occur in the high mountain ranges of Asia. However, in spite of an extensive literature search few records were found, e.g. the Tibetan *Perissandria argillacea* (Alpheraki) (Bang-Haas, 1922: 34, pl. 4, fig. 8, as *agama* Staudinger) and *Estimata herrichschaefferi* (Alpheraki) from Siberia and Mongolia. The assumption that the females of all *Estimata* species are wing-reduced (Dierl, 1983: 141) is contentious because that sex is known only in *herrichschaefferi*.

At least two examples of female brachyptery are known in autumn-flying (September-October) central Turkish species of the genus *Victrix* Staudinger (Acronictinae): *V. karsiana lithoxys* Varga & Ronkay (Varga, pers. comm.) and *V. gracilis* (Wagner) (Hacker & Lödl, 1989: 77, pl. 2, figs 1, 2 (♂, ♀)).

Microptery observed in the female of the Mediterranean to western Asiatic *Ulochlaena hirta* (Hübner) (Cuculliinae) (Draudt, 1938: 132, pl. 16 1 (♂,♀)) is interpreted as a result of the cold season effect because the main adult activity period falls into the months October-November (Hacker, 1989: 162). However, this explanation is not entirely satisfactory as there are records of the adults occurring from August onwards. Moreover, *hirta* is restricted to altitudes below 1500 m and inhabits only the warmest spots.

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