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BRACHYPTERY AND APTERY IN LEPIDOPTERA

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ABSTRACT.– The conditions of wing reduction (brachyptery) and loss of wings (aptery), and modifications thereof, are reviewed across all known families of Lepidoptera where this has been observed in either males or females, or both sexes. Brachyptery or aptery is known in 35 families of Lepidoptera, including families or species where a kind of brachyptery is only evident as extreme wing reduction of the hind wings. Examples from most families known to have brachyptery of some form are illustrated among 147 figures.

KEY WORDS: Alucitidae, Anthelidae, Arctiidae, Blastobasidae, Brachodidae, Carposinidae, Cosmopterigidae, Cossidae, Ctenuchinae, Elachistidae, Epiplemidae, Eriocottidae, Gelechiidae, genetics, Geometridae, Glyphipterigidae, Gracillariidae, Hepialidae, Heterogynidae, Himantopteridae, Lasiocampidae, Lecithoceridae, Limacodidae, Lycaenidae, Lymantriidae, Lyonetiidae, Noctuidae, Notodontidae, Oecophoridae, Oxychirotidae, Papilionidae, Psychidae, Pterophoridae, Pyralidae, Scythrididae, Sesiidae, Somabrachyidae, Sphingidae, Syntominae, Thyretidae, Thyrididae, Tineidae, Tortricidae, Yponomeutidae, Zygaenidae.

Brachyptery (wing reduction) or aptery (loss of wings) is an unusual phenomenon in adults among several orders of insects (La Greca, 1954). In Lepidoptera, brachyptery has been reviewed most recently by Hackman (1966), Dierl and Reichhoff (1977), and by Huemer and Sattler (1989). Earlier comprehensive papers on brachyptery in Lepidoptera were by Chapman (1913, 1913a, 1917), Hudson (1912), Jordan (1884), Knatz (1891), and Porritt (1913). Lepidoptera with some degree of wing reduction or complete loss of wings in one or both sexes have been recorded now in 35 families (see Table 1):

Hepialidae, Tineidae, Eriocottidae, Psychidae, Oecophoridae, Lecithoceridae, Elachistidae, Gelechiidae, Blastobasidae, Cosmopterigidae, Scythrididae, Carposinidae, Glyphipterigidae, Yponomeutidae, Thyrididae, Pyralidae, Heterogynidae, Zygaenidae, Himantopteridae, Somabrachyidae, Cossidae, Limacodidae, Tortricidae, Papilionidae, Lycaenidae, Epiplemidae, Geometridae, Anthelidae, Lasiocampidae, Sphingidae, Notodontidae, Thyretidae, Lymantriidae, Arctiidae, and Noctuidae.

Among most of these families, brachyptery is very rare (e.g., Hepialidae, Pyralidae, Tortricidae, and Noctuidae), but in a few families, notably Psychidae, Heterogynidae, Somabrachyidae, and Lymantriidae, it is very common for most species to have brachypterous females, many being apterous (Bourgogne, 1958; Buszko and Sliwinski, 1980; Daniel and Dierl, 1966; Powell, 1911; Zilli and Racheli, 1989). In some cases, complete brachyptery is not evident, but the hindwings have extreme reduction in size (e.g., some species of Lecithoceridae, Cosmopterigidae, Himantopteridae, Cossidae, Limacodidae, Geometridae, Sphingidae, Notodontidae, Thyretidae and the arctiid subfamilies Ctenuchinae and Syntominae). Not included in this definition of brachyptery are species having extremely narrow wings (stenopterous) as in many microlepidoptera, particularly in such families as Gracillariidae, Lyonetiidae, Cosmopterigidae, and Sesiidae, or such wing modifications as in Alucitidae, Oxychirotidae, and most Pterophoridae. Other families excluded from the definition of brachyptery include such families as Brachodidae, where the enlarged abdomens of the mostly sessile females (Heppner, 1983) of some European species give the appearance of a kind of wing reduction, yet where the ratio of female wings to male wings is not very much different from 1:1.

Female *Orgyia* sp. (Lymantriidae) on cocoon (Gainesville, FL). © J. Heppner

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Fig. 1. HEPIALIDAE: *Pharmacis pyrenaicus* (Donzel) ♀, Spain.

Table 1 lists the known brachypterous and apterous species from a search of the literature and museum collections, yet some species may have been missed and many more will undoubtedly be added as additional searches are made of alpine and xeric (eremic) regions where such species are most apt to be found. There also are other species known to be brachypterous from such places as the high elevations of the Rocky Mountains of North America, but which are not yet described (Hodges, in. litt.). Butterfly species, other than four Papilionidae and one Lycaenidae with relatively extreme hindwing reduction, or any of the most primitive moth families (four species of Hepialidae being the only known exceptions), do not exhibit any brachyptery, as opposed to mutations (Fig. 141-144) or rare eclosion accidents (Bowden, 1963; Shapiro, 1983). Hindwing reduction included in Table 1 refers only to an extreme form, with a fore- to hindwing ratio of near 3:1 or more (a few cases are included where there is hindwing reduction on the borderline of these criteria, notably in Zygaenidae, Papilionidae, Lycaenidae, and Sphingidae).

Hindwing reduction is common among Syntominae and the Ctenuchinae (Arctiidae), for example. One of the most extreme cases is a Brazilian species, *Diptilon culex* Draudt, where the reduced hind wings are so small that they are hidden among the thoracic scales at the wing bases (Draudt, 1915); other *Diptilon* species (Fig. 123-126) also show some hindwing reduction. In Tineidae there is at least one extreme example, the species *Meessia brachyptera* Passarin d'Entrèves, where the forewings of the female are only slightly reduced but the hindwings are minute (Fig. 2). Other families with examples can be noted in Table 1. The development of wing reduction only in the hindwings is curious and appears without apparent reason in Lepidoptera other than possibly being sexually derived, since among several groups the females have more developed hindwings and only the males have markedly reduced hindwings. Cases of reduced forewings are known in some families (e.g., Dismorphiinae in Pieridae), but this really is narrowing of the forewings, or enlargement of the hindwings, and not a kind of brachyptery as considered here.

Brachyptery usually occurs only in the female but it has been recorded in both sexes in a few cases, primarily in moths from isolated oceanic islands: the Kerguelen Is. (Viette, 1948) and Heard Id. (Common, 1970) of the south Indian Ocean; the Antipodes Is. (Salmon and Bradley, 1956), Auckland Islands (Dugdale, 1971), and Campbell Id. (Dugdale, 1964; Viette, 1954) near New Zealand; and the Falkland Is. (Bradley, 1965) of the south Atlantic Ocean. Families from these island faunas of brachypterous moths include Tineidae, Oecophoridae, Elachistidae, Yponomeutidae, Tortricidae, and Pyralidae. The only known species with brachypterous wings in both sexes from a continental area, although from coastal sand dunes, is a species of Scythrididae, *Areniscythris brachypteris* Powell (Fig. 26), from California (Powell, 1976). Another undescribed sand dune scythrid appears to reside in coastal dunes of western Florida. Both scythrid species are unusual in the construction of larval sand tubes of silk at the base of their host plant. Hackman (1966) referred to a Gelechiidae species from Morocco, *Ephysteris curtipennis* (Zerny), as another continental species where both sexes are brachypterous, but although the male does have extremely narrowed wings (stenopterous), Povolný (1968) noted that the males of this species can fly.

Brachyptery on both fore- and hindwings, or even complete wing loss, is most common in females. This condition is normal in the families of Lymantriidae, Somabrachyidae, and Psychidae. Likewise, it is a regular occurrence among many primitive Tineoidea. Typically, the females are relatively immobile in these groups, often sequestered within the larval and pupal case, as in the example of the Psychidae or bagworms. All are terrestrial except for one case of brachyptery among the few known aquatic moths in the family Pyralidae: *Acentria ephemerella* (Denis and Schiffermüller) [formerly *Acentropus nivea* (Olivier)] (Fig. 43). In the case of this aquatic moth, the female is dimorphic, with some females of a population fully winged and others almost apterous (Berg, 1941).

Female wing reduction in Lepidoptera is rarely polymorphic. The dimorphic example of the aquatic moth, *Acentria ephemerella* (Pyralidae), has already been noted. Another form of facultative wing reduction occurs in a few species having seasonal forms, one generation having fully winged females and another generation having brachypterous or apterous females; this wing reduction is usual among some species with autumn or winter generations in temperate climates (Kimura and Masaki, 1977; Sachrov, 1914). Wing reduction polyphenism of this kind is prevalent in some Lymantriidae, e.g., *Orgyia thyellina* Butler (Cretschmar, 1928). In *Thaumetopoea* species (Notodontidae) females usually are winged but can be brachypterous on occasion (Loritz, 1952). Wing reduction in geographical variation is rare: an example is the arctic geometrid *Psychophora sabinii* Curtis, where the females have some wing reduction on the Pribilof Is., Alaska, but elsewhere are fully winged (Downes, 1964, 1965). The same occurs with the arctic arctiid, *Pararctia subnebulosa* (Dyar) (Sotavalta, 1965). Another case of geographic brachyptery occurs in the geometrid *Lycia hirtaria* (Clerck), females being

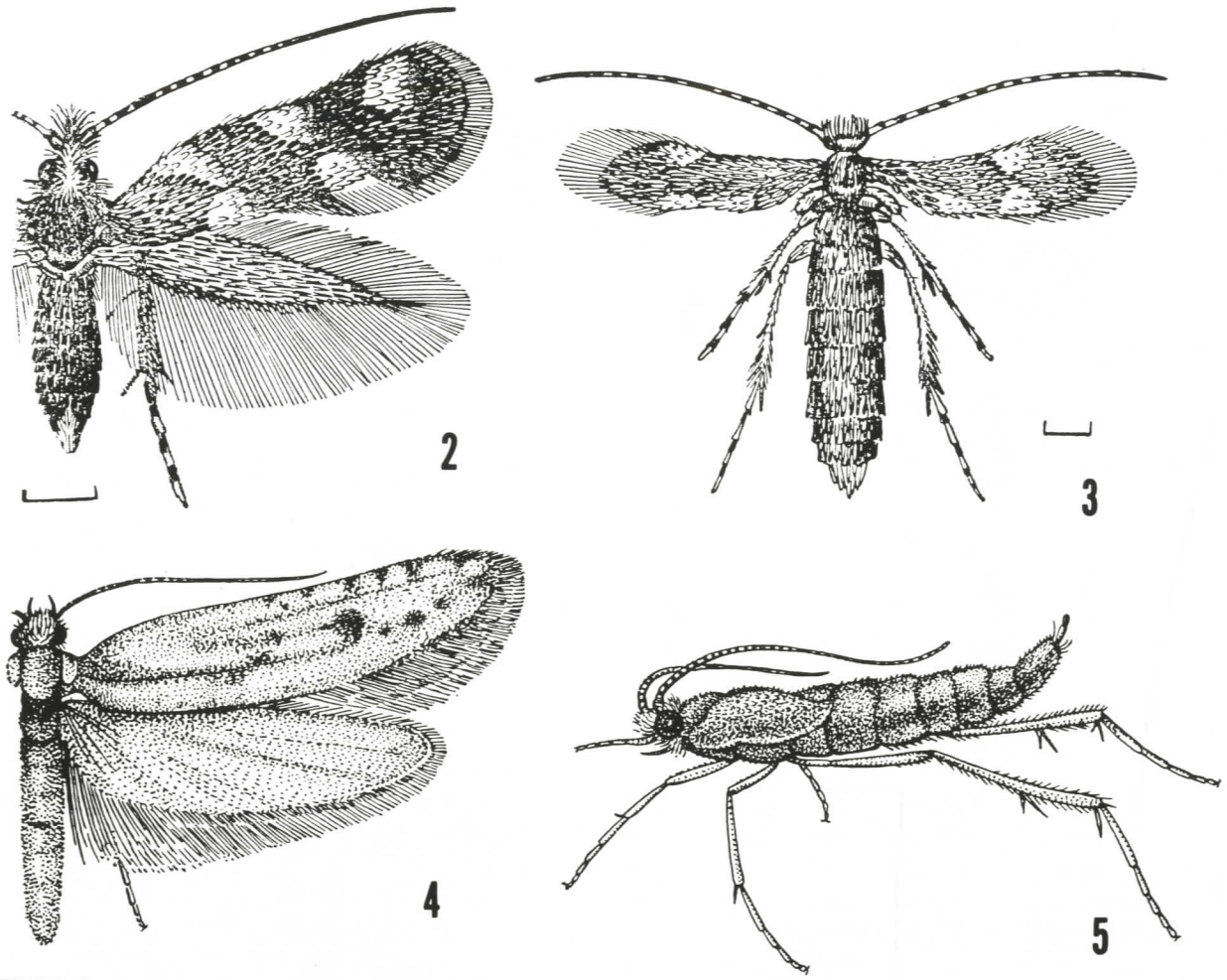


Fig. 2-5. TINEIDAE: 2. *Meessia brachyptera*,Passerin d'Entrèves ♂, USSR; 3. same ♀, USSR; 4. *Pararhodobates syriacus* (Lederer) ♂, USSR; 5. same ♀, USSR [Fig. 2-3 after Zagulajev (1979); 4-5 after Zagulajev (1981)].

brachypterous in southern Russian populations (Nordman, 1946), but this also involves genetic factors of wing reduction induced by hybridization (Hackman, 1966). Hackmann (1966) also noted the varying reduction of female wings of the arctiid *Cymbalophora rivularis* (Ménétries) in different mountain regions of central Asia.

Obligatory brachyptery, usually apterousness in most cases, is particularly prevalent among Lymantriidae, Somabrachyidae, and Psychidae. Only female wing reduction is known in these families. The females disperse pheromones to attract fully winged males. In the Psychidae the females do not leave the larval case and pupal chamber, and the responding male copulates with the female remaining in the case. Females of these bagworm species are often virtually larviform in appearance (Bourgogne, 1958). Interestingly, in such families as Brachodidae and Sesiidae, which also rely on sex pheromones to attract males, the often sedentary females do not have any known cases of significant wing reduction from their normal and usually narrow wings (Heppner, 1983; Heppner and Duckworth, 1981).

Gene dispersal in brachypterous species usually is via the winged male, inasmuch as the usually sedentary females do not have a wide geographic range for oviposition sites. Hackman (1966) noted that among most known brachypterous species, dispersal is eased either by the presence of a common widespread host plant or by the species being polyphagous. A few instances are known of male-female dispersal in copula (e.g., *Operophtera* spp. geometrids), but this is not known to occur regularly even in any one species (Fournier, 1984; Hackman, 1966; Kozhanchikov, 1950). Among Psychidae, eggs often are laid within the larval-female case. The few examples of brachyptery in both sexes involve species adapted to relatively special habitats, as for example, sand dunes. The brachypterous California scythrid, *Areniscythris brachypteris*, is adapted to rapid running and hopping movements over the sand dunes, possibly with passive wind dispersal (Powell, 1976). The illustrations of brachypterous Tineidae and Eriocottidae, showing long female legs (Fig. 4, 8, 11), also indicate a possibly similar behavior for movement in searching for oviposition sites.

The origin of wing reduction is uncertain and has prompted considerable speculation. Several early workers attempted to discern some correlations between tympanal organs and brachyptery, or between the haustellum and brachyptery (Baus, 1937; Gorbandt, 1938, 1940, 1940a; Heitmann, 1934; Naumann, 1937), but this proved unfounded. Undoubtedly it is a genetic phenomenon, possibly originally evolved in each case through haphazard adaptive mutations followed by ecological or biological adaptive

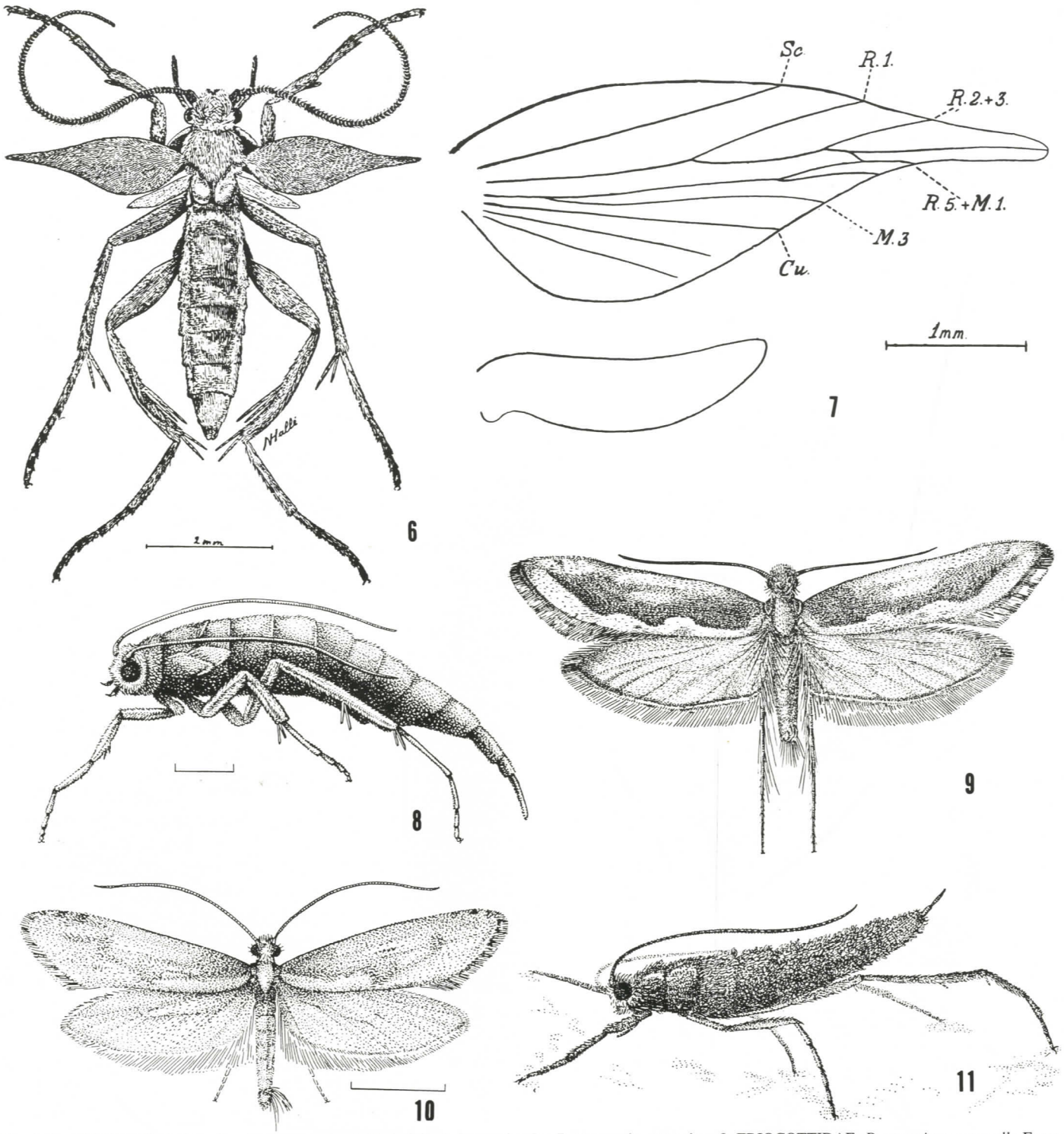


Fig. 6-11. TINEIDAE: 6. *Pringleophaga kerguelensis* Enderlein ♂, Kerguelen Is.; 7. same, wing venation; 8. ERIOCOTTIDAE: *Deuterotinea casanella* Eversmann ♀, USSR; 9. same ♂, USSR; 10. *Deuterotinea stschetkini* Zagulajev ♂, USSR; 11. same ♀, USSR [Fig. 6-7 after Viette (1948); 8-9 after Zagulajev (1988); 10-11 after Zagulajev (1981)].

maintenance in some species (Dierl and Reichholf, 1977; Downes, 1965; Knatz, 1891; Saigusa, 1962). Mutations have often been recorded of malformed pharate adults where wing pads did not inflate properly or genetic mutations produced brachypterous adults (Bowden, 1963; Shapiro, 1983; Lemche, 1933; Nüesch, 1947; Seppänen, 1958). These isolated accidents invariably resulted in death and non-procreation in the individuals involved, thus being nonadaptive. Cases of normal brachyptery or apterousness, however, are more numerous among insects at high elevations (Mani, 1968) and in xeric regions (Downes, 1964, 1965; Hackman, 1966). In Lepidoptera, among families with only sporadic brachyptery, this may be correlated with conservation of energy in cold environments, either arctic or high altitude, or for desert adaptation in eremic areas (Hackman, 1966). Cases

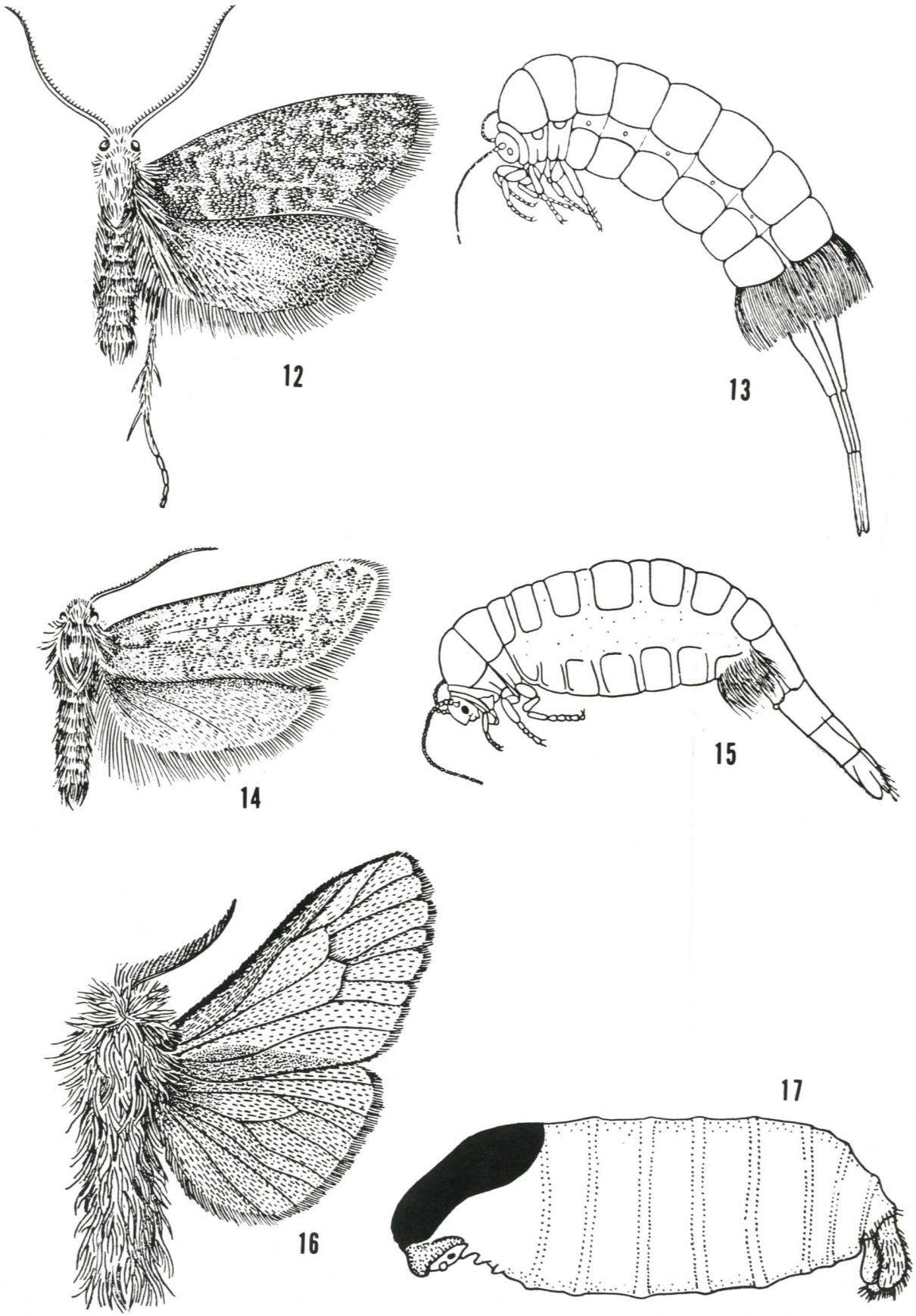


Fig. 12-17. PSYCHIDAE: 12. *Taleporia tubulosa* (Retzius) ♂. USSR; 13. same ♀, USSR; 14. *Solenobia cembrella* (Linnaeus) ♂, USSR; 15. *Solenobia lichenella* (Linnaeus) ♀, USSR; 16. *Oiketicoides senex* Staudinger ♂, USSR; 17. same ♀, USSR [Fig. 12, 14-17 after Zagulajev (1978); 13 after Kozhanchikov (1956)].

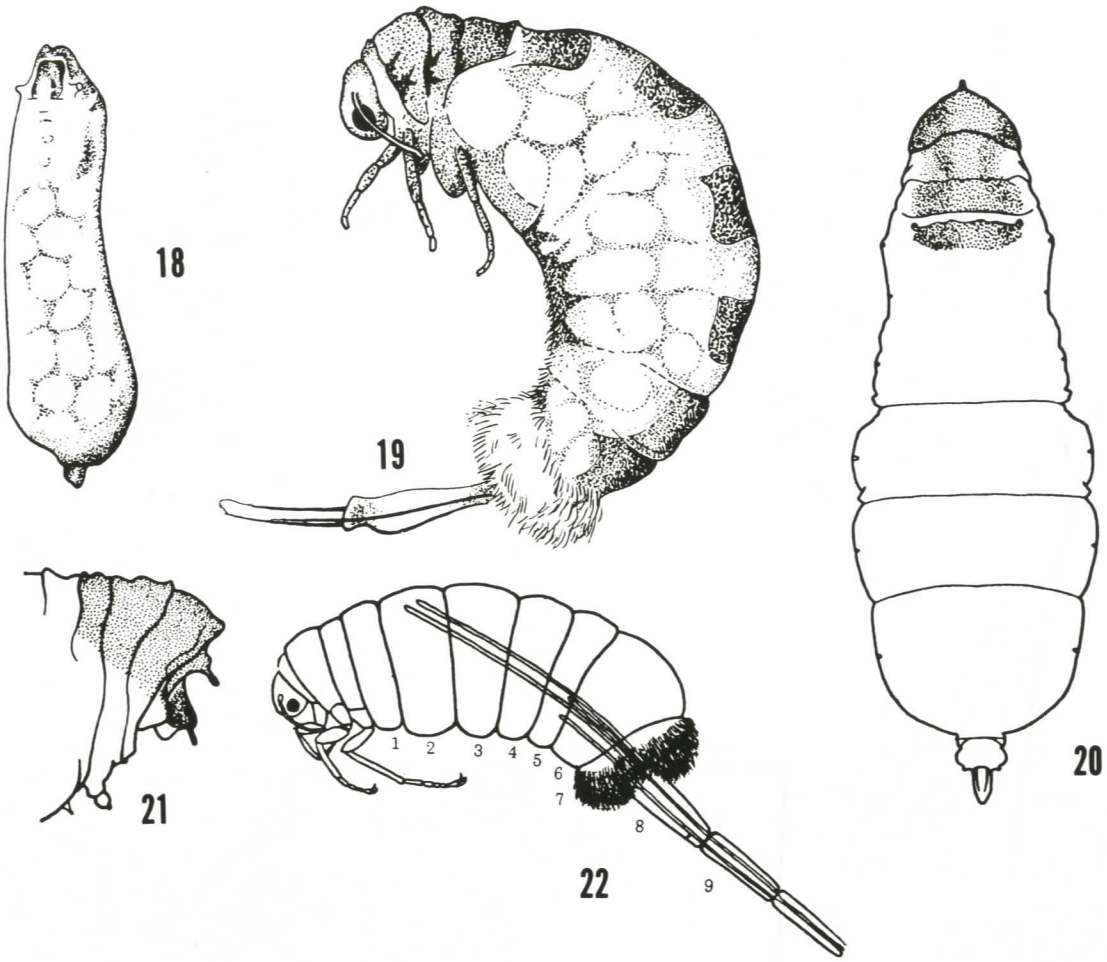
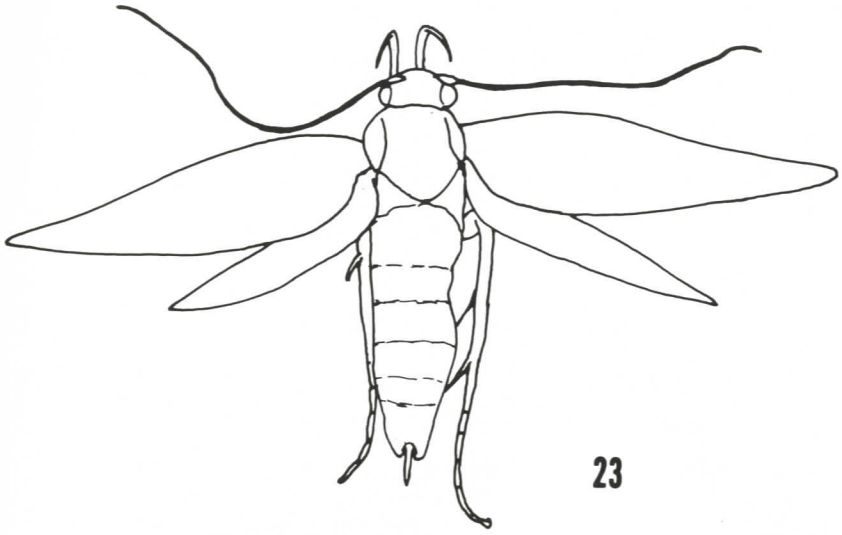


Fig. 18-22. PSYCHIDAE: 18. *Acanthopsyche nipae* Bourgogne ♀, France; 19. *Psyche crassiorella* Bruand ♀, France; 20. *Eumeta rougeoti* Bourgogne ♀ (dorsal view) Nigeria; 21. *Eumeta cervina* (Druce) ♀ (head and thorax profile) Nigeria; 22. *Fumea casta* (Pallas) ♀, USSR [Fig. 18-19 after Bourgogne (1958); 20-21 after Entwistle (1963); 22 after Kozhanchikov (1956)].

of brachyptery among island dwellers and coastal areas, however, may have developed wing reduction due to other environmental parameters, notably thermoregulation or wind adaptation (Powell, 1976). Brachyptery among the aquatic Pyralidae undoubtedly is due to some adaptive advantage under water, possibly easier movement for oviposition, although there may be some offsetting factor in the reduction in underwater air retention beneath normal folded wings as is prevalent in some other Nymphulinae pyralids which also dive underwater to oviposit (Berg, 1941).

In Lepidoptera, part of the probable evolutionary development of wing reduction in females involves two modes of brachypterous females (Hackman, 1966): 1) the case where females have developed enlarged abdomens with many eggs prior to oviposition, making flight difficult; and 2) the case where females have a normal abdominal size and are mobile, thus capable of rapid flight when desired. The Psychidae females and some Lymantriidae are examples of the former type and such moths as the scythrid, *Areniscythris*, are typical of the latter type. A development towards brachyptery may be evident in species like the European arctiid *Artimelia hemigena* (Grasl.) (Fig. 109-110) or the noctuid *Agrotis fatidica* (Hübner) (Fig. 132-133): these species are listed in Table 1 as brachypterous, but the females have only somewhat reduced wings. Given this range of brachypterous females, considerable speculation has been made as to the development of brachyptery in Lepidoptera. Theories have been proposed by Naumann (1937), Eggers (1939), and Downes (1964). Their main points pertain to a development of brachyptery in response to decreased mobility due to abdominal enlargement from excessive egg numbers, with adaptive mutations progressing to brachypterous or apterous forms. A number of species worldwide exhibit enlarged abdomens in the female, resulting in reduced flight or little apparent flight: e.g., females of the Great Basin tortricid, *Synnoma lynosyrana* Walsingham, have an enlarged abdomen prior to egg laying and do not readily fly (Powell, pers. comm.). Among Brachodidae, the Palearctic genus *Brachodes* has females that are relatively sedentary prior to copulation and only fly for egg laying (Heppner, 1983; Heppner and Duckworth, 1981).

As noted previously, in various habitats (cold regions, high altitudes, eremic regions, and coastal areas) there appear to be adaptive benefits to brachyptery. Hackman (1966) notes, however, that the evolution of extreme wing reduction in some of the almost larviform females of Lymantriidae (Fig. 102-108) and Psychidae (Fig. 18-22) is not easily explained. The more mobile type of brachypterous female is also not explained by the Naumann-Eggers-Downes theory, as Hackman (1966) calls it,



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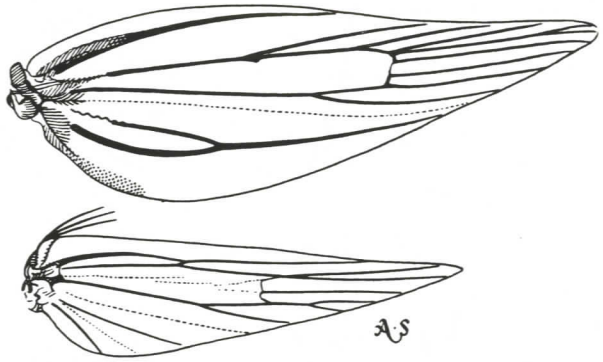

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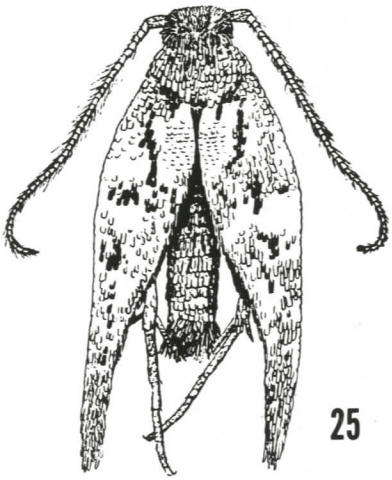

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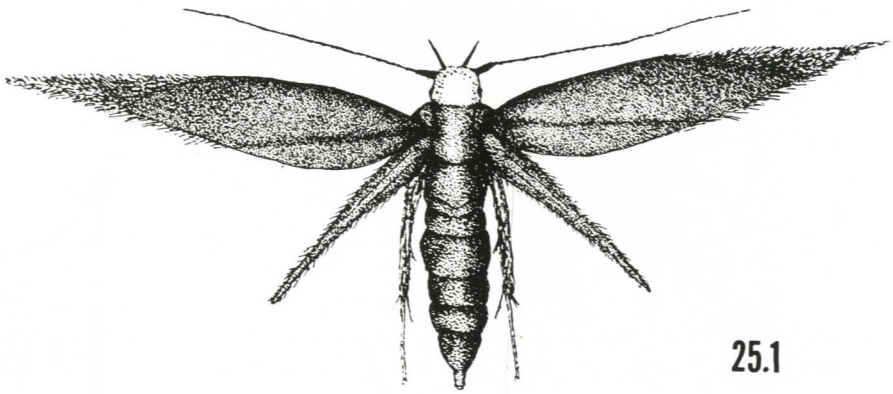

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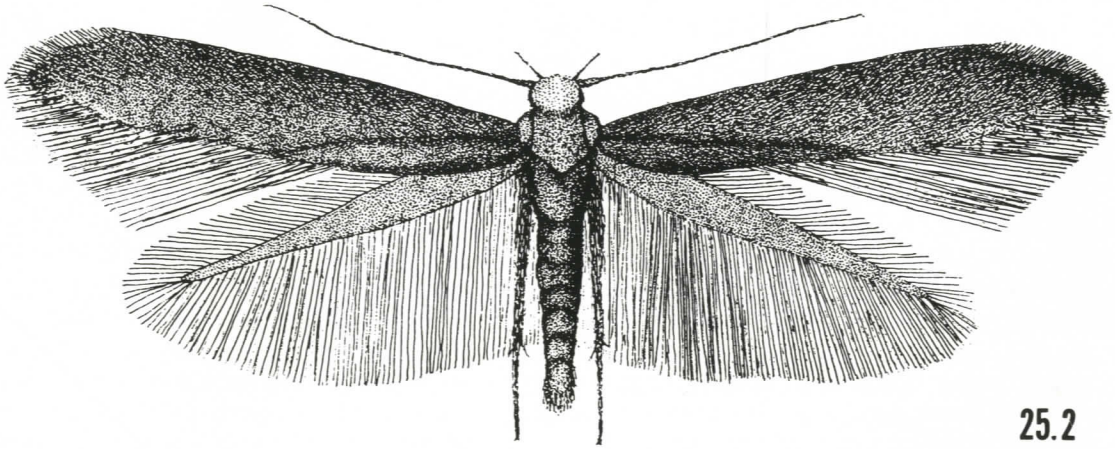
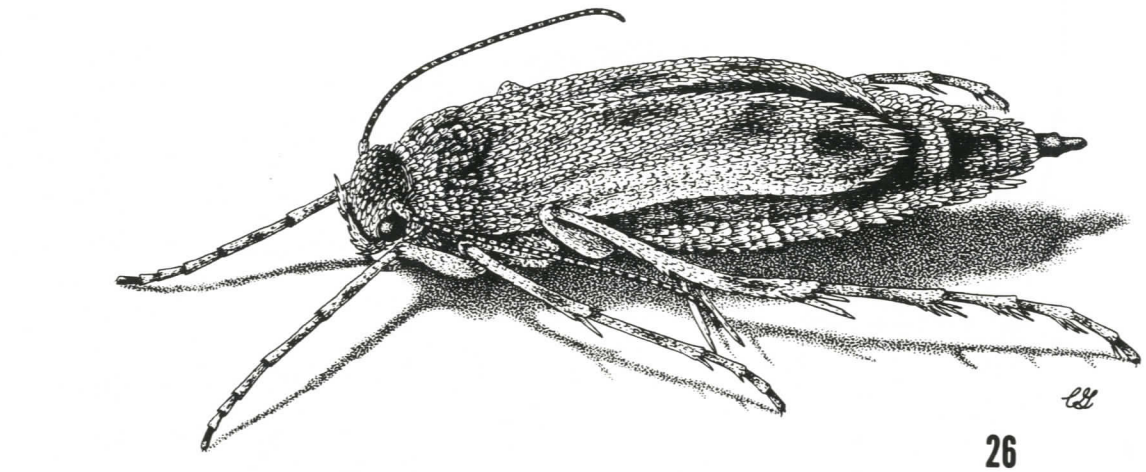
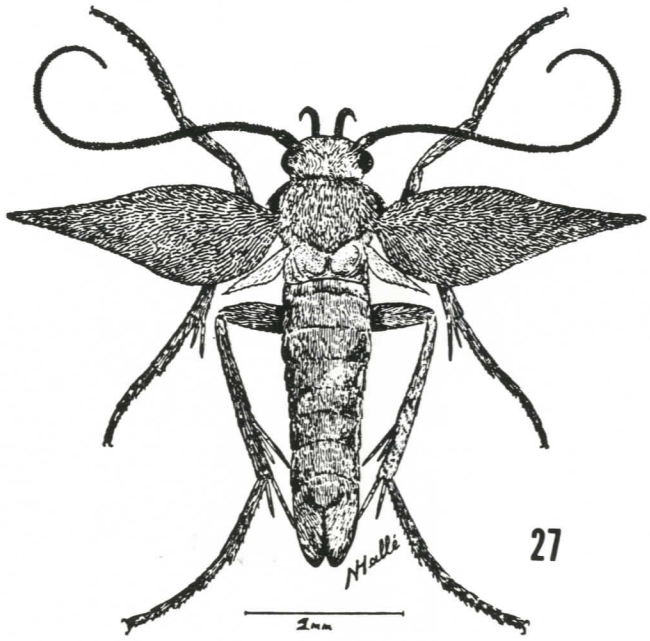


25.2

Fig. 23-25.2. OECOPHORIDAE: 23. *Thyrocopa apatela* (Walsingham) ♀, Hawaii; 24. same, wing venation; 25. *Borkhausenia falklandensis* Bradley ♂, Falkland Is.; ELACHISTIDAE: 25.1. *Biselachista brachypterella* Klimesch ♀, Italy; 25.2. same, ♂. [Fig. 23-24 after Zimmerman (1978) [23 drawn from photo]; 25 after Bradley (1965); 25.1-25.2 after Klimesch (1990)].





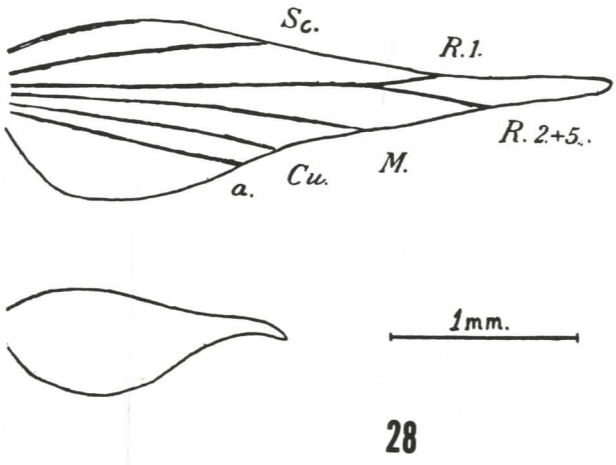


Fig. 26-28. SCYTHRIDIDAE: 26. *Areniscythris brachypteris* Powell ♀, USA (California); YPONOMEUTIDAE: 27. *Embryonopsis halticella* Eaton ♂, Marion Is.; 28. same, wing venation [Fig. 26 after Powell (1976); 27 after Viette (1948); 28 after Common (1970)].

since three types of these mobile forms are evident: 1) arboricolous cold-season species; 2) terricolous species; and 3) aquatic species (in this last case, only *Acentria ephemerella* is known). Additional theories of the evolution of brachyptery in these forms involve environmental adaptations (e.g., thermoregulation, protection from high wind, cold stupor, etc.), whereby sedentary females remain on or near host plants (Chapman, 1913; Hudson, 1912; Wood, 1913). Additionally, there is predator evasion as a probable adaptive advantage for many brachypterous species (e.g., *Sattleria dzieduszycskii* (Nowicki)) which hide in low alpine plants (Hackman, 1966). Wing reduction in the aquatic species is likewise not easily explained by the above theories, although environmental adaptation for oviposition would seem to be the cause, but this unique case is more complex due to the dimorphic female, which may be fully winged or brachypterous within the same population and generation.

Species listed in Table 1 are brachypterous to fully apterous (usually only females) in one or both sexes (M or F), or have an extreme degree of hindwing reduction (*). Examples listed having only hindwing reduction usually are included only if this condition is extreme (fore- to hindwing ratio of 3:1 or more) but a few borderline cases are included where some hindwing reduction is evident (especially, Zygaenidae, Papilionidae, Lycaenidae, and Sphingidae). The range of each taxon is noted to the far right of each name. A few species are facultatively brachypterous, where only some individuals develop this condition, and this is noted after the name; facultative here also includes cases where a species has brachyptery only in parts of its range (e.g., *Psychophora sabinii*, in Geometridae). Names listed in Table 1 are considered valid herein, but various researchers may list some of them as synonyms (e.g., *Phigalia* in Geometridae is used as a valid genus for Nearctic species, yet it is listed as a synonym of *Apocheima* by many European workers).

Faunal literature has been searched for all known references to brachypterous Lepidoptera (Bradley, 1958, 1965; Burmann, 1951, 1954, 1956, 1957, 1958, 1973, 1977; Chapman, 1913a; Chauvin and Vernon, 1981; Common, 1970; Comstock, 1940; Cotty and Dethier, 1981; Diakonoff, 1973, 1983; Draudt, 1915; Dugdale,

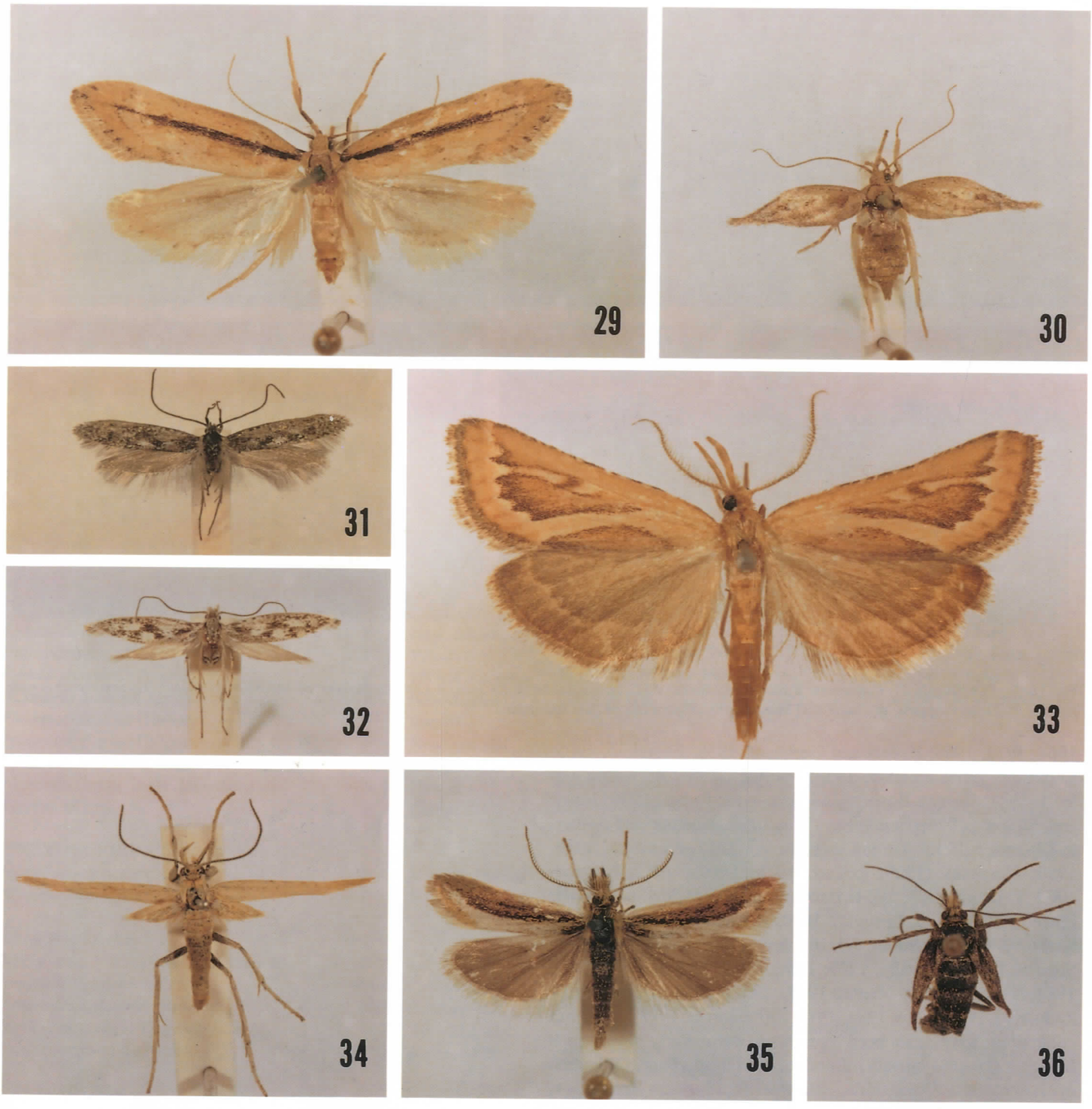


Fig. 29-36. OECOPHORIDAE: 29. *Atomotricha versuta* Meyrick ♂ (27mm), New Zealand; 30. same ♀ (17mm), New Zealand; YPONOMEUTIDAE: 31. *Kessleria pyrenaea* Friese ♂ (15mm), France; 32. same ♀ (9mm), France; PYRALIDAE: 33. *Cledeobia oculatalis* (Ragonot) ♂ (31mm), Algeria [♀ is brachypterous (not illustrated)]; 34. *Exsilirarcha graminea* Salmon & Bradley ♂ (19.5mm), Antipodes Is.; 35. *Protyparcha scaphodes* Meyrick ♂ (19mm), New Zealand; 36. same ♀ (9mm length), New Zealand [all BMNH specimens].

Fig. 37-40. COSSIDAE: 37. *Callocossus hyalinipennis* Strand ♂ (32.5mm), Tanzania; 38. same ♀ (30mm), Malawi; SOMABRACHYIDAE: 39. *Somabrachys codet* Austaut ♂ (21mm), Algeria; 40. same ♀ (13mm length), Algeria [all BMNH specimens].

1964, 1971, 1988; Eggers and Gorbandt, 1938; Enderlein, 1905; Entwistle, 1963; Fletcher, 1958; Fournier, 1984; de Freina and Witt, 1987; Gomez-Bustillo and Fernandez-Rubio, 1976; Hafez and El-Said, 1970; Heinänen, 1936, 1950; Huemer and Sattler, 1989; Inoue, 1956; Kimura and Masaki, 1977; Klimesch, 1943, 1990; Kusnesov, 1929; LeCerf, 1928; Loritz, 1952; Munroe, 1964; Philpott, 1923, 1931; Povolný, 1968; H. Powell, 1911; J. Powell, 1973, 1976; Prittwitz, 1870; Rindge, 1974, 1975, 1980; Sachrov, 1914; Salmon and Bradley, 1956; Snodgrass, 1925; Soenen, 1967; Sotavalta, 1965; Tams, 1952; Theim, 1950; Tuck, 1984; Turner, 1960; Viette, 1948, 1952, 1954; Wood, 1913; Zagulajev, 1978, 1979, 1981, 1988; Zimmerman, 1978). Museum collections have also been consulted, particularly the British Museum (Natural History), London, the Florida State Collection of Arthropods, Gainesville, and the Smithsonian Institution, Washington, DC.

Table. 1. **BRACHYPTEROUS LEPIDOPTERA OF THE WORLD**

HEPIALIDAE		
Aoraia senex (Hudson)	F	New Zealand
Pharmacis anselminae (Teobaldelli)	F	Alps
Pharmacis bertrandi (Le Cerf)	F	Alps
Pharmacis pyrenaicus (Donzel)	F	Spain
TINEIDAE		
Meessia brachyptera Passarin d'Entrèves	F	USSR
Pararhodobates syriacus (Lederer)	F	Syria/USSR
Pringleophaga crozetensis Enderlein	M/F	Crozet Is.
Pringleophaga kerguelensis Enderlein	M/F	Kerguelen Is.
Proterodesma turbotti (Salmon & Bradley)	M/F	Antipodes Is.
Tinea allomella Bradley	F	Uganda
?*Tinea amphitrite* Meyrick	F	Uganda
ERIOCOTTIDAE		
Deuterotinea casanella Eversmann	F	USSR
Deuterotinea stschetkini Zagulayev	F	USSR
PSYCHIDAE		
(all species except Penestoglossinae)	F	world
OECOPHORIDAE		
Atomotricha spp.	F	New Zealand
Borkhausenia falklandensis Bradley	M/F	Falkland Is.
Cheimophila spp.	F	Palearctic
Chersadaula ochrogastra Meyrick	F	New Zealand
Diurnea spp.	F	Palearctic
Ethmia charybdis Powell	F	USA (California)
Oxythecta austrina Meyrick	F	New Zealand
Pleurota rostrella (Hübner)	F	Europe
Proteodes clarkei Philpott	F	New Zealand
Tinearupa sorenseni Salmon & Bradley	M/F	Campbell Id.
Thyrocopa apatella (Walsingham)	M/F	Hawaii
Xenomicta spp.	F	Europe
LECITHOCERIDAE		
**Ceuthomadarus* spp.	F	Morocco/Europe
**Lecithocera brachyptila* Diakonoff	F	New Guinea
ELACHISTIDAE		
Biselachista brachypterella (Klimesch)	F	Italy
Irenicodes galatheae (Viette)	M/F	Campbell Id.
Irenicodes holdgatei (Bradley)	M/F	Falkland Is.
Irenicodes hookeri Dugdale	M/F	Auckland Is.
Irenicodes pumila Dugdale	M/F	Auckland Is.
GELECHIIDAE		
Acompsia dimorpha Petry	F	Spain/France
Caryocolum laceratella (Zeller)	F	Alps
Ephysteris curtipennis (Zerny)	F	Morocco
Ephysteris sp.	M/F	Madeira
Eulamprotes libertinella (Zeller)	F	Alps
Gelechia dzieduszynskii Burmann	F	Austria
Gnorimoschema spp.	F	Europe
Ilseopsis spp.	F	Palearctic
Kiwaia jeanae Philpott	M/F	New Zealand
**Megacraspedus* spp.	F	Europe
Opacopsis spp.	F	Europe
Paraschema detectendum Povolný	F	Bolivia
Sattleria spp.	F	Alps
BLASTOBASIDAE		
Symmoca profanella Zerny	F	Morocco
Symmoca signella (Hübner)	F	Alps
Symmoca umbrinella Zerny	F	Morocco
COSMOPTERIGIDAE		
**Stagmatophora extremella* Klimesch	F	Europe
SCYTHRIDIDAE		
Areniscythris brachypteris Powell	M/F	USA (California)
?*Areniscythris* sp.	M/F	USA (Florida)
Scythris sp.	F	New Zealand
CARPOSINIDAE		
Campbellana atennuata Salmon & Bradley	M/F	Campbell Id.
GLYPHIPTERIGIDAE		
Glyphipterix rugata Meyrick	F	New Zealand
Glyphipterix xestobela Meyrick	F	New Zealand
YPONOMEUTIDAE		
Embryonopsis halticella Eaton	M/F	Marion Id.
Kessleria pyrenaea Friese	F	France
Kessleria zimmermannii (Nowicki)	F	Poland
THYRIDIDAE		
**Glanycus foochowensis* Chu & Wang	M	China
**Glanycus insolitus* Walker	M	se. Asia
**Glanycus tricolor* Moore	M	India
**Meskea* spp.	M/F	Neotropics
PYRALIDAE		
Acentria ephemerella (D. & S.) [facultative]	F	Europe
Cledeobia oculatalis Ragonot	F	Morocco
Exsilirarcha graminea Salmon & Bradley	M/F	Campbell Id.
Protyparcha scaphodes Meyrick	F	New Zealand
Pseudoschoenobius opalescalis (Hulst)[1]	F	USA (California)
HETEROGYNIDAE		
Heterogynis penella Hübner	F	Europe
Heterogynis spp.	F	Europe
Janseola titaea Druce	F	South Africa
ZYGAENIDAE[2]		
**Harrisina americana* (Guérin-Méneville)	M/F	e. USA
**Pampa* spp.	M/F	Brazil
**Pryeria sinica* Moore	M/F	China/Japan
**Stylura cirama* (Druce)	M	Guatemala
**Thyrassia penangae* Moore	M	se. Asia
**Triprocris flavipuncta* Tarmann	M/F	Brazil
HIMANTOPTERIDAE		
**Doratopteryx* spp.	M/F	Africa
**Himantopterus fuscinervis* Wesm	M/F	se. Asia
**Pseudothymara staudingeri* Rogh	M/F	Sierra Leone
**Semioptila* spp.	M/F	Africa
**Thymara* spp.	M/F	India
SOMABRACHYIDAE		
Somabrachys spp.	F	N. Africa

COSSIDAE

**Callocossus hyalinipennis* Strand	M	Malawi
**Eulophonotus myrmeleon* Felder	M	South Africa
**Eulophonotus obesus* Karsch	M	Ghana
**Pyraphlecta melissodes* Tams	M/F	Uganda
**Zeuzera nigra* Moore	M	India
**Zeuzerops hyalinipennis* Strand	M	Africa

LIMACODIDAE

**Cheromettia* spp.	M	se. Asia
**Doratifera nagodina* Hering	M	New Guinea
**Phobetron pithecium* (Smith)	M	USA
**Pseudopsyche dembowskii* Oberthür	M/F	USSR/Korea
**Sibine auromacula* Schaus	M	Venezuela

TORTRICIDAE

**Allodemis stegopa* DIakonoff	M	Sumatra
**Archilobesia drymoptila* (Meyrick)	M	Australia
**Borneogena antigrapha* Diakonoff	F	Borneo/Sumatra
Euledereria alpicolana (Frölich)	F	Europe
Exapate congelatella (Clerck)	F	Europe
Exapate duratella Heydenreich	F	Alps
Olethreutes orestera Bradley	F	Uganda
Oxypteron impar Staudinger	F	USSR
Sorensenata agilitata Salmon & Bradley	M/F	Campbell Id.
**Theorica lamyra* (Meyrick)	M	New Guinea
**Xenolepis dolichoschiza* Diakonoff	M	Indonesia

PAPILIONIDAE

**Parides hahneli* Staudinger	M/F	Brazil
**Parides tiopas* Godart	M/F	Guyana
**Ornithoptera meridionalis* Rothschild	M	New Guinea
**Ornithoptera paradisea* Staudinger	M	New Guinea

LYCAENIDAE

**Syrmatia dorilas* (Cramer)	M	Brazil

EPIPLEMIDAE

**Aphyodes pilosa* Warren	M	Peru
**Nyctibadistes informis* Warren	M	Peru
**Nyctibadistes nigrata* Warren	M	Peru

GEOMETRIDAE

Agriopis spp. [some spp.]	F	Europe
Alsophila spp.	F	world
Amorphogynia spp.	F	Europe
Animomyia spp.	F	USA
Apocheima spp.	F	Old World
Asaphodes spp.	F	New Zealand
Asaphodes oxptera (Hudson)	M/F	Auckland Is.
Biclavigera spp.	F	South Africa
**Brabira apatopleura* Prout	M	Fiji
**Cheimoptena pennigera* Danilevsky	M/F	USSR
Chondrosoma fiduciaria Anker	F	Europe
**Dypteris abortivaria* Herrich-Schäffer	M/F	USA
**Dystypoptila hebes* Prout	M	Sulawesi
Egea spp.	F	USSR
Elophos spp.	F	Europe
Erannis spp.	F	world
**Erateina* spp. [some spp.]	M/F	South America
**Eupithecia* spp. [some spp.]	M	world
**Hydrelia sylvata* (D. & S.)	F	Europe
**Idaea furciferata* Packard	M	USA
Inurois spp.	F	Japan
Itame loricaria (Linnaeus)	F	Europe
Ithysia pravata Hübner	F	Europe
Larerannis spp.	F	Palearctic
Lignyoptera fumidaria (Hübner)	F	Europe
Lignyoptera thaumastaria Rebel	F	Europe
Lycia spp.	F	Europe/Nearctic
Lycia hirtaria (Clerck) [facultative]	F	Palearctic
Malacodea regularia Tengström	F	Finland
Microbiston spp.	F	USSR
Napocheima robiniae Chu	F	China
Nyssiodes spp.	F	USSR
Operophtera spp.	F	world
Pachyerannis obliquaria (Motschulsky)	F	e. Asia
Paleacrita spp.	F	Nearctic
Palaeonysia trisecta Warren	F	Europe
Phigalia spp.	F	Nearctic
Phigaliohybernia fulvinfula Inoue	F	Japan
Phthorarcha spp.	F	USSR
Protalcis concinnata (Wileman)	F	Japan
Psychophora sabinii Curtis [facultative]	F	Pribilof Is.
Pygmaena fusca (Thunberg)	F	Europe
**Remodes remodesaria* (Walker)	M	Sri Lanka
**Remodes triseriata* Moore	M	Sri Lanka
**Rheumaptera hastata* (Linnaeus) [facultative]	F	Europe
**Sauris* spp. [some spp.]	M	se. Asia/Fiji
**Sauris interrupta* Moore	M/F	se. Asia
Sciadia tenebraria (Esper)	F	Europe
Sebastosema bubonaria Warren	F	Japan
Somatolophia cuyama Comstock	F	USA (California)
Spartopteryx spp.	F	USSR
Sucra jujuba Chu	F	China
**Tatosoma tipulata* (Walker)	M	New Zealand
Theria spp.	F	Europe
Xanthorrhoe spp. [some spp.]	F	Africa
Yala pyricola Chu	F	China
Zamacra spp.	F	Europe
Zermizinga indocilisaria Walker	F	New Zealand

ANTHELIDAE

Pterolocera amplicornis Walker	F	Australia
Pterolocera capnospila Turner	F	Australia

LASIOCAMPIDAE

Artace itatiaya Schaus	F	Brazil
**Borocera* spp. [some spp.]	M	Madagascar
Chondrostega spp.	F	Europe
**Gonometa fulvida* (Distant)	M	South Africa
**Gonometa postica* Walker	M	South Africa
Laruma heterogenea Walker	F	Venezuela
Lasiocampa staudingeri Baker	F	Algeria
**Melopla abhorrens* Lajonquière	M	Madagascar
**Mesocelis montana* (Stoll)	F	South Africa
**Nadiasa polydora* (Druce)	M	c. Africa
**Nadiasa uniformis* (Aurivillius)	M	South Africa
**Neoborocera esteban* (Dognin)	M	Ecuador
**Paradoxopla cardinalis* Holloway	M	Borneo
**Phoenicladocera parvinota* (Hering)	M	Madagascar
**Streblota panda* (Hübner)	M	Spain/n. Africa
**Suana concolor* Walker	M	China
**Suana divisa* (Moore)	M	India
**Ticera castanea* Swinhoe	M	China

SPHINGIDAE[3]

**Cephonodes* spp.	M/F	Asia/Australia
**Euproserpinus euterpe* H. Edwards	M/F	USA (California)
**Hemaris* spp.	M/F	world
**Oxyambulyx japonica* Rothschild	M/F	east Asia
**Protambulyx* spp. [some spp.]	M/F	South America
**Sataspes* spp.	M/F	se. Asia

NOTODONTIDAE

**Lirimiris arpi* Draudt	M	Brazil
**Lirimiris auriflua* Draudt	M	Brazil
**Thaumetopoea* spp. [facultative]	F	Europe

THYRETIDAE

Automolis meteus (Stoll)	F	South Africa
**Balacra* spp.	F	Europe
**Paramelisa* spp. [some spp.]	M/F	c. Africa
**Pseudapicinoma angolensis* Kiriakoff	M/F	Angola
**Pseudapicinoma vitrina* Oberthür	M/F	Cameroon
**Pseudodiptera musiforme* Kaye	M/F	Zaire

LYMANTRIIDAE

Aroa melanoleuca Hampson	F	Africa
Bracharoa spp.	F	Africa
Dasyorgyia spp.	F	Asia
Gynaephora alpherakii (Grum-Grschimailo)	F	China
Gynaephora lugens	F	Europe
Herecampa spp.	F	Asia
Lachana ladakensis Moore	F	Tibet
Orgyia spp. [most spp.]	F	world
Penthophera morio (Linnaeus)	F	Europe
**Perina nuda* (Fabricius)	M	se. Asia
Teia anartoides Walker	F	Australia
Teia spp.	F	N. Africa

ARCTIIDAE

**Amata* spp. [some species]	F	Europe
Amata antiochena (Lederer)	F	Turkey
Amata libanotica (Bang-Haas)	F	Lebanon
Amata mestralii (Bugn.)	F	Lebanon
**Amata rubicunda* (Mabille)	M/F	Uganda
Amata taurica (Hampson)	F	Turkey
**Amaxia* spp. [some spp.]	M	C. & S. Amer.
**Araeomolis canalis* Schaus	M	Panama
Arctia rivularis Ménétries	F	USSR
Artimelia hemigena (Grasl.)	F	Europe
**Auriculoceryx* spp.	M/F	se. Asia
**Caeneressa* spp. [some spp.]	M/F	se. Asia
**Ceryx* spp.	M/F	Africa/Asia
Coscinia liouvillei Le Cerf	F	Morocco
Coscinia romeii Sagarra	F	Spain
**Crocomela colorata* (Walker)	M	Colombia
Cymbalophora haroldi Oberthür	F	Algeria
Cymbalophora rivularis (Ménétries)	F	USSR
**Diptilon* spp. [some spp.]	F	Neotropical
**Dubianaclia* spp. [some spp.]	M	Madagascar
**Ecpantheria* spp. [some spp.]	M	S. America
Endrosa spp. [some spp.]	F	Europe
**Eressa* spp.	M/F	se. Asia
**Eurota* spp.	F	South America
Gonerda breteaudeaui Oberthür	F	Sikkim
**Himeracrtia* spp.	M	South America
**Hyperandra diminuta* Dognin	M	Brazil
**Idalus aleteria* (Schaus)	M	South America
**Isanthrene* spp. [some spp.]	M	South America
**Lithosia cereola* Hübner	F	Europe
**Machaeraptenus crocopera* (Schaus)	M	Guyana
**Maculonaclia* spp.	M/F	Madagascar
Mallocephala spp.	F	Chile
Maurica breveti powelli (Oberthür)	F	Algeria
Metacrias spp.	F	New Zealand
**Neaxia bella* Schaus	M	French Guiana
Ocnogyna spp.	F	Europe
**Ordishia* spp.	M	South America
**Ormetica* spp. [some spp.]	M	South America
**Pararctia subnebulosa* (Dyar) [facultative]	F	USA (Alaska)
**Phaemolis bacchans* (Schaus)	M	French Guiana
**Phaemolis beata* (Dognin)	M	French Guiana
**Pseudomya sanguiceps* Hampson	M	Panama
**Pseudonaclia puella* (Boisduval)	M/F	Africa
**Pseudosphenoptera nephelophora* Hampson	M	Brazil
Setina spp. [some spp.]	F	Europe
**Stictonaclia* spp.	M/F	Madagascar
**Sutonocrea fassli* (Dognin)	M	Colombia
**Sutonocrea lobifer* (Herrich-Schäffer)	M	South America
**Tenuinaclia* spp. [some spp.]	M/F	Madagascar
**Thyrosticta* spp. [some spp.]	M/F	Madagascar
**Toulgoetinaclia obliquipuncta* Rothschild	M/F	Madagascar
**Trichaeta pterophorina* (Mabille)	M	Africa
**Trichaetoides* spp. [some spp.]	M/F	se. Asia
**Tritonaclia stephania* Oberthür	M	Madagascar
**Syntomidopsis variegata* (Walker)	M	Jamaica
**Viviennea moma* Schaus	M	South America

NOCTUIDAE

Agrotis fatidica (Hübner)	F	Europe
Agrotis poliochroa (Hampson)	F	Sikkim
**Bocula xanthostola* Hampson	M	se. Asia
**Chandica* spp.	M/F	se. Asia
Dimorphinoctua cunhaensis Viette	M/F	Cunha Is.
Dimorphinoctua goughensis Fletcher	M/F	Gough Id.
Epipsiliamorpha alaskae Grote	F	Pribilof Is.
Eriopygodes imbecilla (Fabricius)[4]	F	Europe
Pachnobia okakensis Packard	F	Canada
Pachnobia scropulana Morrison	F	Canada
Peridroma goughi Fletcher	M/F	Gough Id.
Perissandria spp.	F	Tibet
Saltia acrophyla Tams	F	Tanzania
Saltia edwardsi Tams	F	Kenya
**Tyana falcata* (Walker)	M	se. Asia
Ulochlaena hirta (Hübner)	F	Eurasia
Ulochlaena superba Alpheraky	F	Europe

(* = extreme hindwing reduction only; F = female; M = male)

1. *Pseudoschoenobius opalescalis*: brachypterous females in winter on Mojave Desert sand dunes, California (Powell, pers. comm.).
2. Zygaenidae are on the borderline of the criteria of hindwing reduction used for including taxa in this listing; likewise for Papilionidae and Lycaenidae.
3. Sphingidae listed have fore- and hindwing ratios of only somewhat better than a 2:1 ratio, thus are on the borderlin of the criteria for listing herein.
4. Noctuidae: *Eriopygodes imbecilla* has only slight brachyptery in the female.

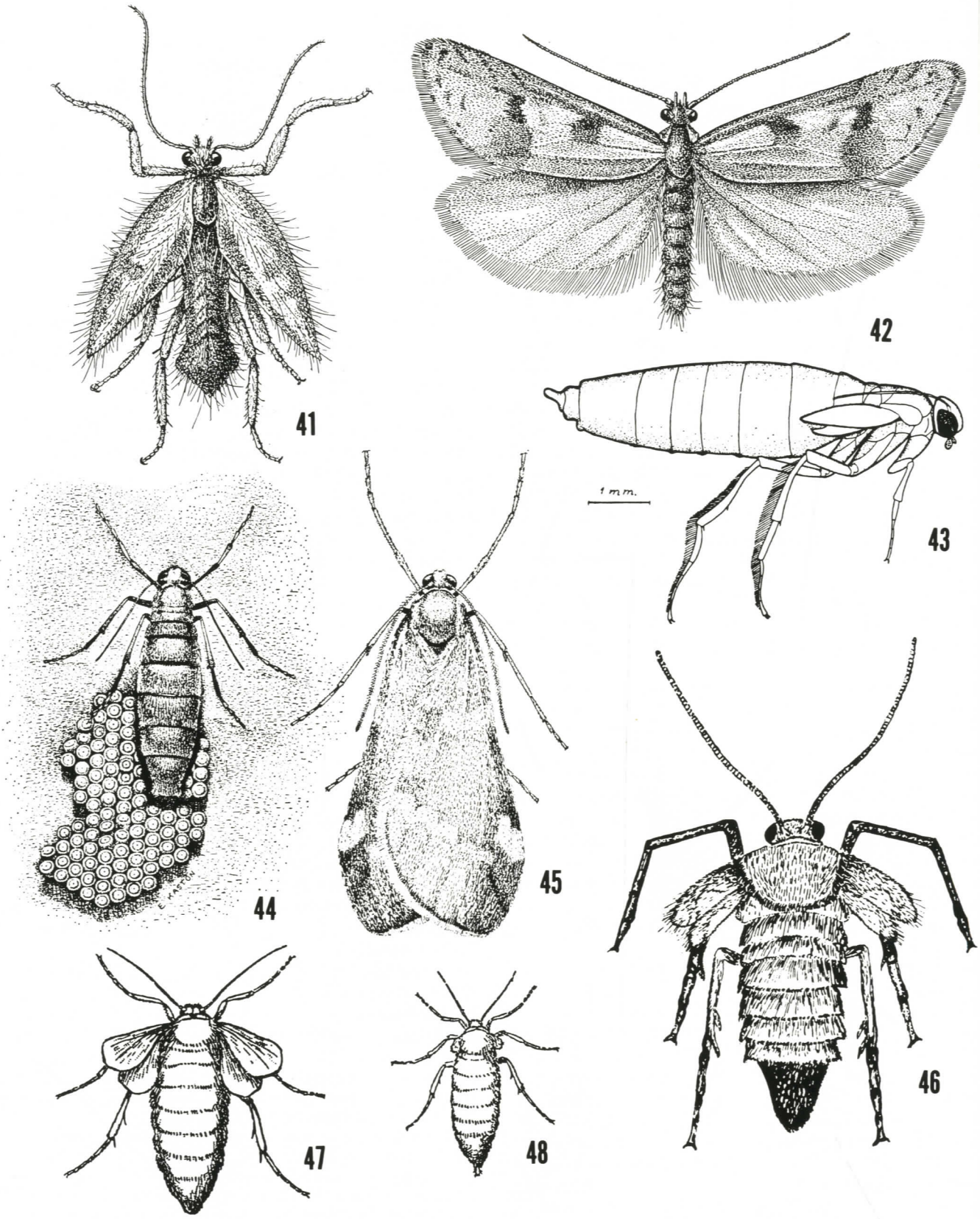


Fig. 41-48. TORTRICIDAE: 41. *Exapate congelatella* (Clerck) ♀, USSR; 42. same ♂, USSR; PYRALIDAE: 43. *Acentria ephemerella* (Denis & Schiffermüller) ♀, Europe; GEOMETRIDAE: 44. *Alsophila pometaria* (Harris) ♀, USA; 45. same ♂, USA; 46. *Operophtera brumata* (Linnaeus) ♀, Europe; 47. *Operophtera* sp. ♀, USA; 48. *Operophtera bruceata* (Hulst) ♀, USA [Fig. 41-42 after Zagulajev (1978); 43 after Berg (1941); 44-45 after Turner (1960); 46 after Soenen (1967); 47-48 after Snodgrass (1924)].

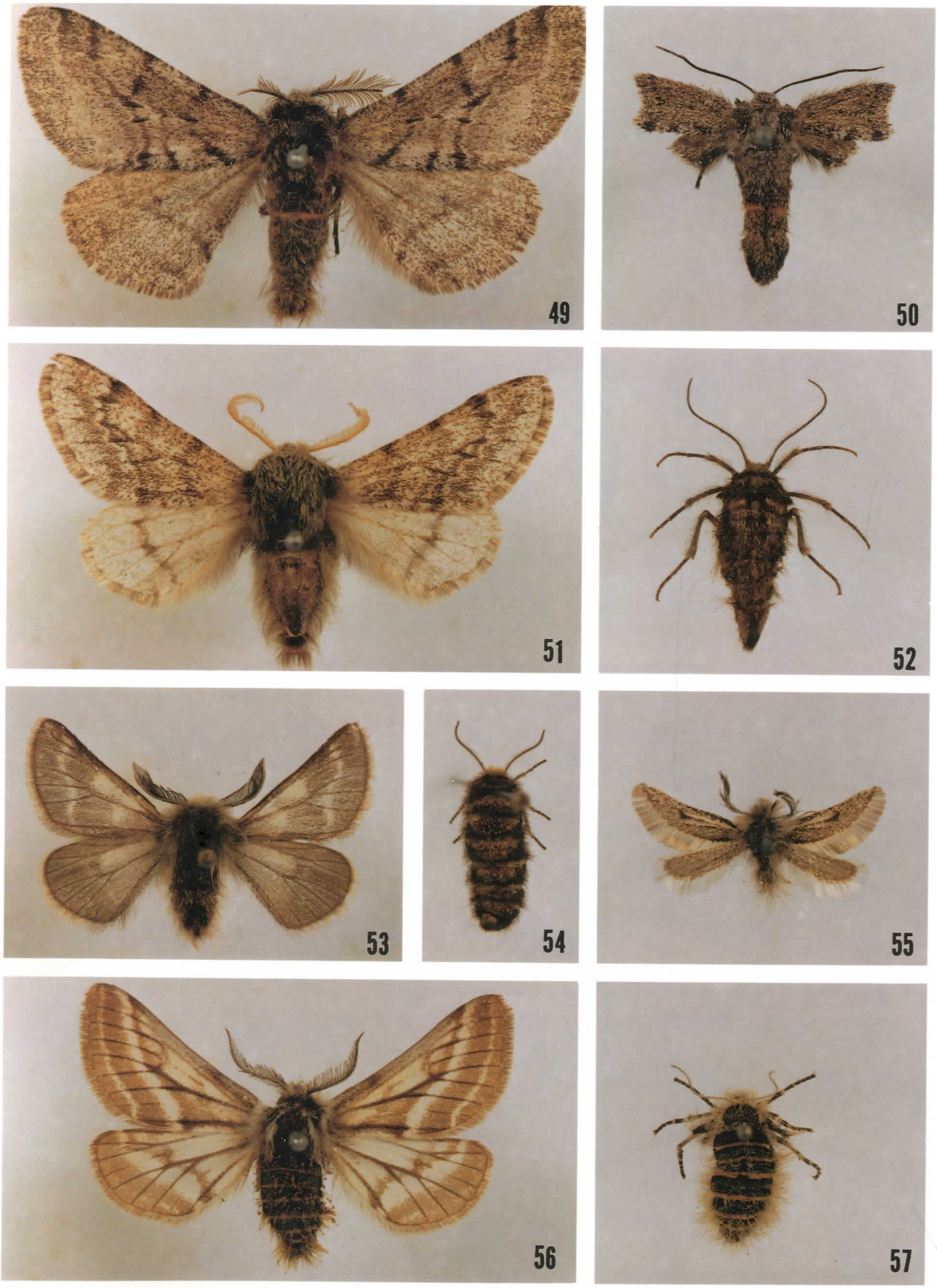


Fig. 49-57. GEOMETRIDAE: 49. *Amorphogynia necessaria* Zeller ♂ (39.5mm), N. Africa; 50. same ♀ (17.5mm), N. Africa; 51. *Apocheima hispidaria* (Denis & Schiffermüller) ♂ (34mm), Hungary; 52. same ♀ (12.5mm length), England; 53. *Chondrosoma fiduciaria* Ankar ♂ (23mm), Austria; 54. same ♀ (11mm length), Austria; 55. *Cheimoptena pennigera* Danilevsky ♂ (17mm), USSR (Turkmenia); 56. *Nyssia zonaria* (Denis & Schiffermüller) ♂ (29mm), Denmark; 57. same ♀ (11 length), England [all BMNH specimens].

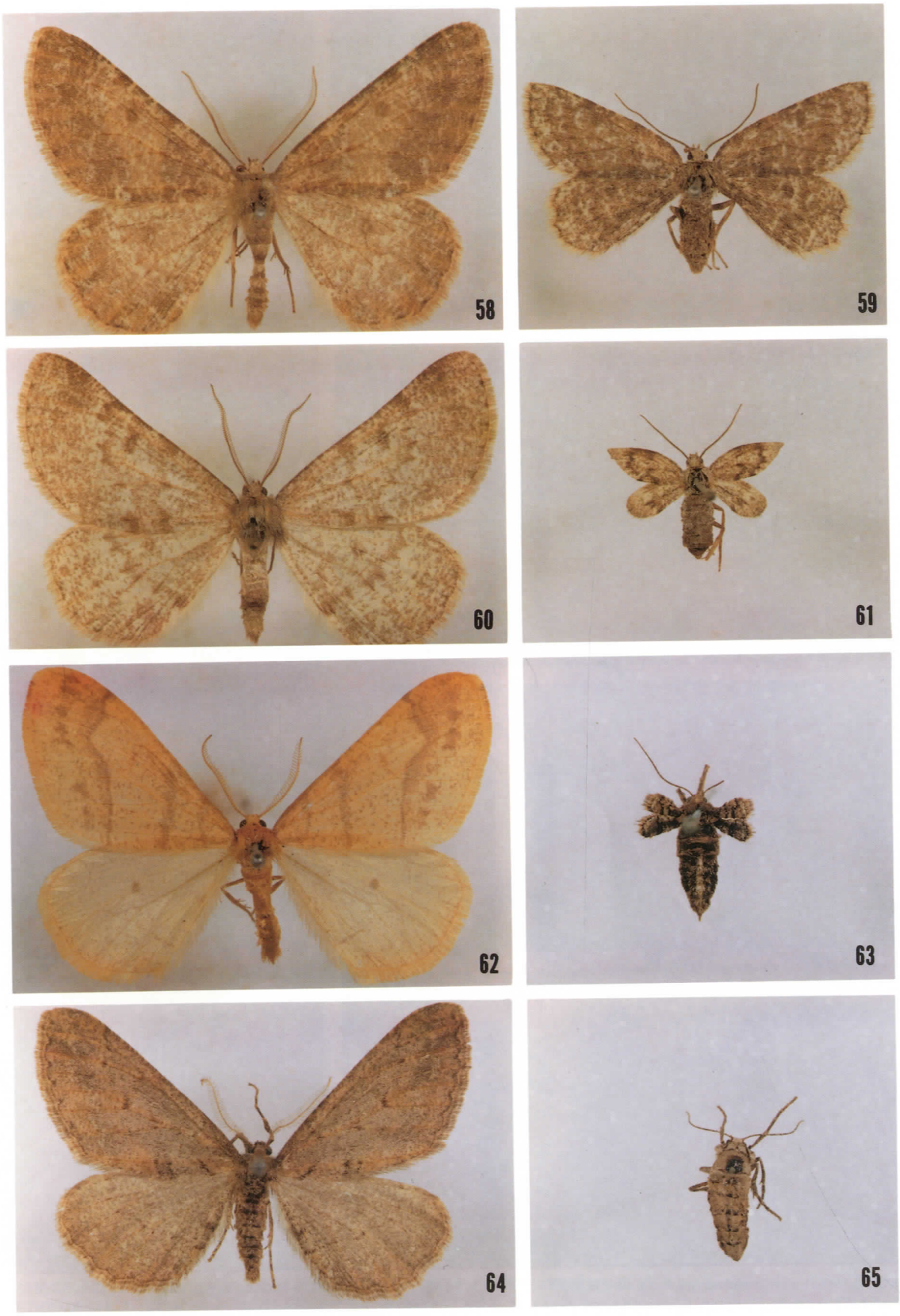


Fig. 58-65. GEOMETRIDAE: 58. *Elophos andereggaria* (Harpe) ♂ (39mm), Germany; 59. same ♀ (26mm), Germany; 60. *Elophos operaria* (Hübner) ♂ (39mm Europe; 61. same ♀ (15mm), Austria; 62. *Argiopis aurantiaria* Hübner ♂ (36mm), Germany; 63. same ♀ (9mm length), France; 64. *Argiopis bajaria* (Denis & Schiffermüller) ♂ (33mm), Yugoslavia; 65. same ♀ (10mm length), Germany [all BMNH specimens].

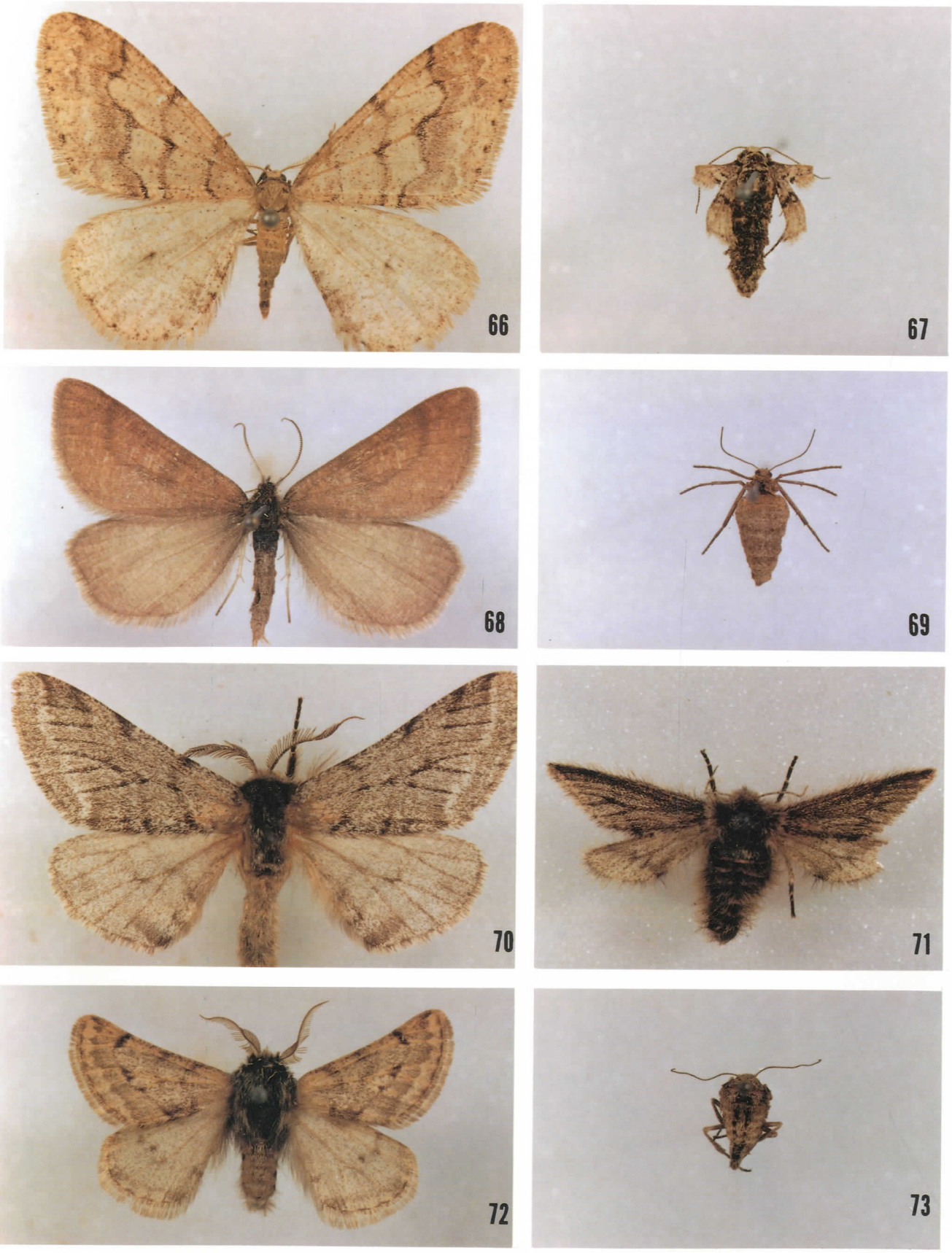


Fig. 66-73. GEOMETRIDAE: 66. *Larerannis miracula* Prout ♂ (36mm), Japan; 67. same ♀ (9mm), Japan; 68. *Ligynoptera fumidaria* (Hübner) ♂ (31mm), England; 69. same ♀ (8.5mm length), Austria; 70. *Lycia ursaria* Walker ♂ (41mm), Canada (Manitoba); 71. same ♀ (28mm), Canada; 72. *Microbiston phaeothorax* Wehrli ♂ (27mm), USSR (Dagestan); 73. same ♀ (7mm length), USSR (Dagestan) [all BMNH specimens].

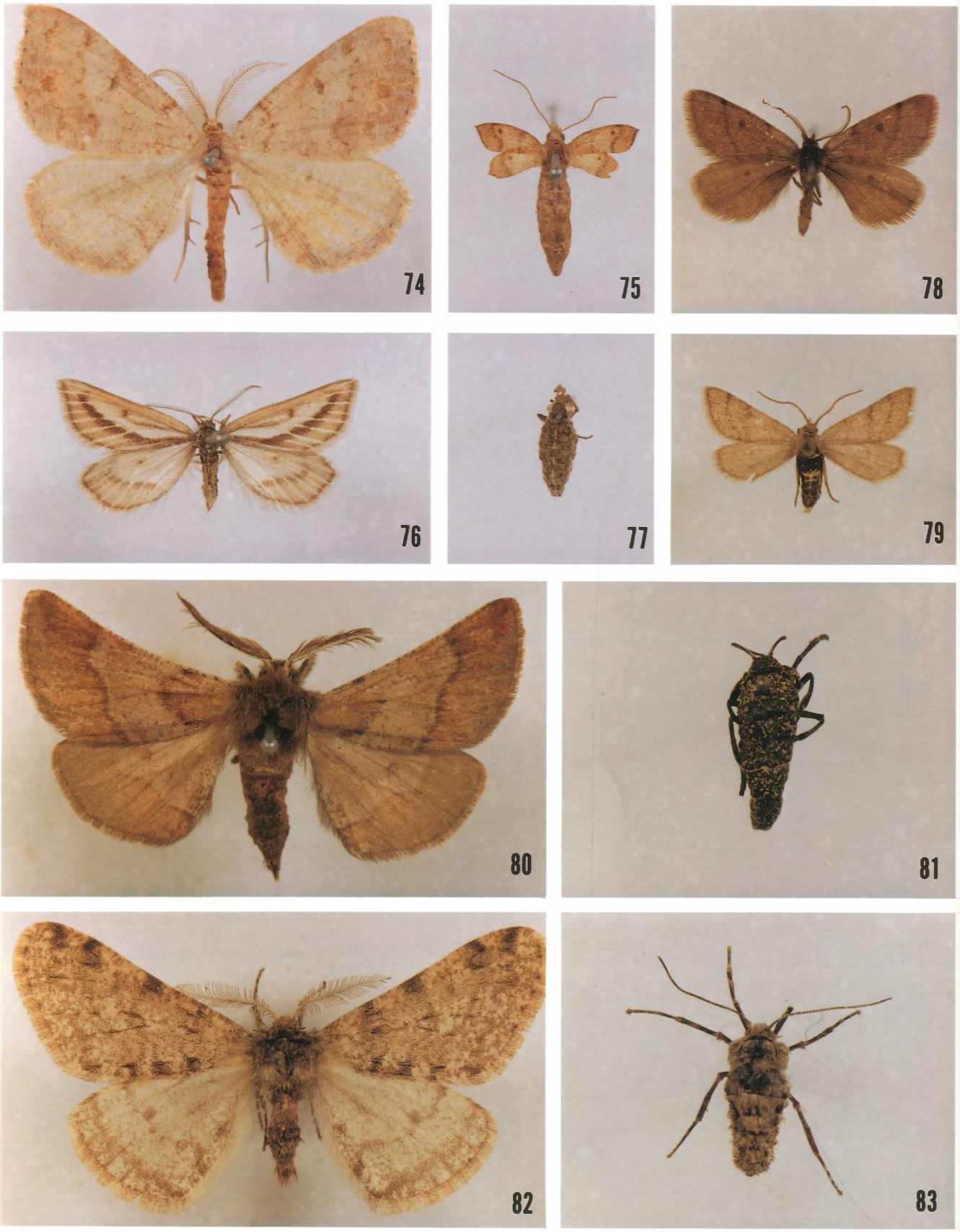


Fig. 74-83. GEOMETRIDAE: 74. *Itame loricaria* (Linnaeus) ♂ (28mm), Finland; 75. same ♀ (12mm), Finland; 76. *Ithysia pravata* Hübner ♂ (21mm), [Europe]; 77. same ♀ (8mm length), USSR (c. Russia); 78. *Pygmaena fusca* (Thunberg) ♂ (17mm), France; 79. same ♀ (15mm), Switzerland); 80. *Palaeonyssia trisecta* Warren ♂ (34.5mm), South Africa; 81. same ♀ (13.5mm length), South Africa; 82. *Apocheima pilosaria* (Denis & Schiffermüller) ♂ (45.5mm), England; 83. same ♀ (12mm length), Germany [all BMNH specimens].

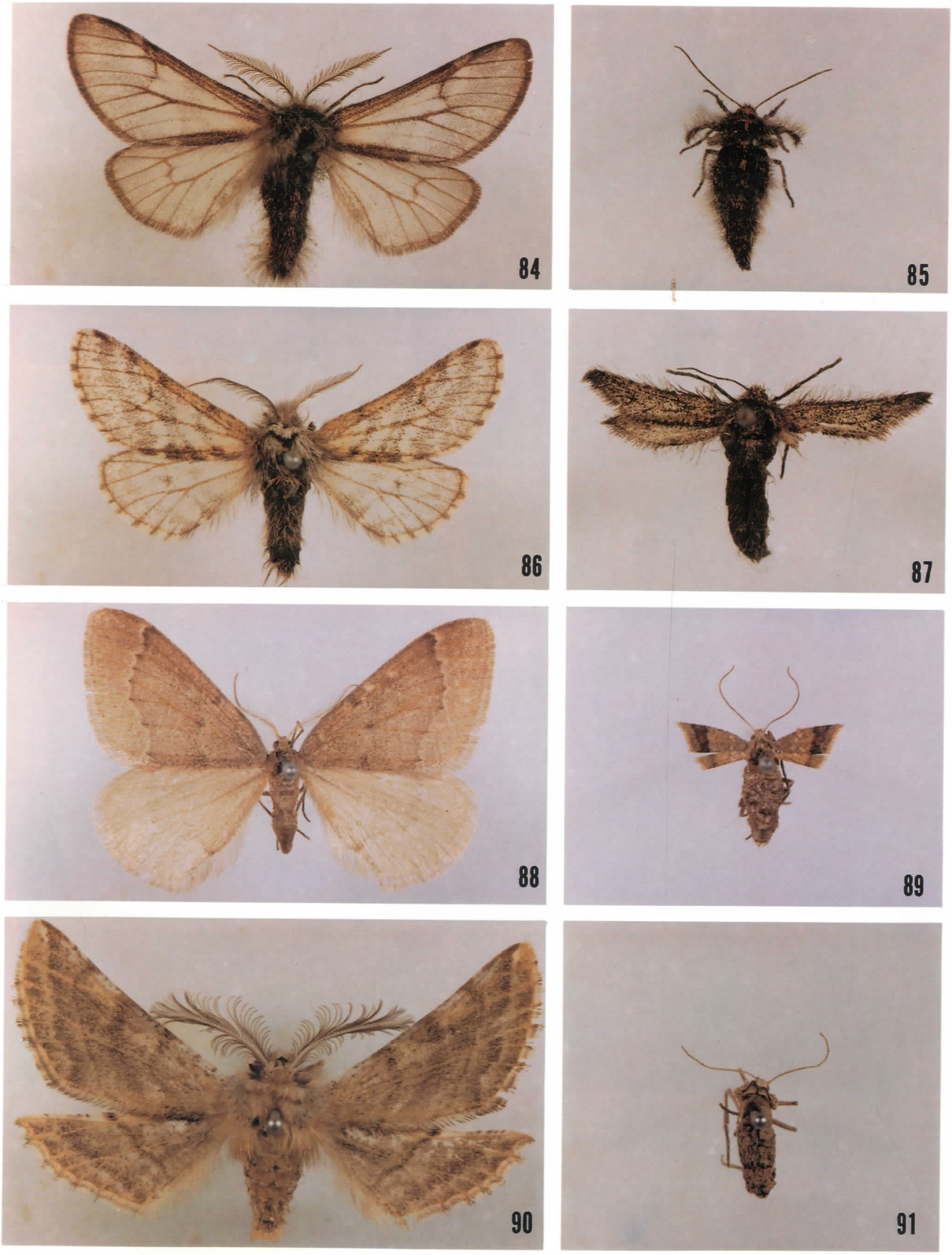


Fig. 84-91. GEOMETRIDAE: 84. *Lycia lapponaria* (Boisduval) ♂ (32mm), [Europe]; 85. same ♀ (12mm length), [Europe]; 86. *Lycia pomonaria* (Hübner) ♂ (30mm), Germany; 87. same ♀ (24mm), England; 88. *Theria rupicapraria* (Denis & Schiffermüller) ♂ (29mm), Germany; 89. same ♀ (12mm), Germany; 90. *Zamacra flabellaria* Heeger ♂ (37mm), Cyprus; 91. same ♀ (9mm length), Turkey [all BMNH specimens].

Fig. 92-95. GEOMETRIDAE: 92. *Zermizinga indocilisaria* Walker ♂ (28mm), New Zealand; 93. same ♀ (14mm), New Zealand; ANTHELIDAE: 94. *Pterolocer capnospila* Turner ♂ (34mm), Australia (WA); 95. same ♀ (28mm length), Australia (WA) [all BMNH specimens].

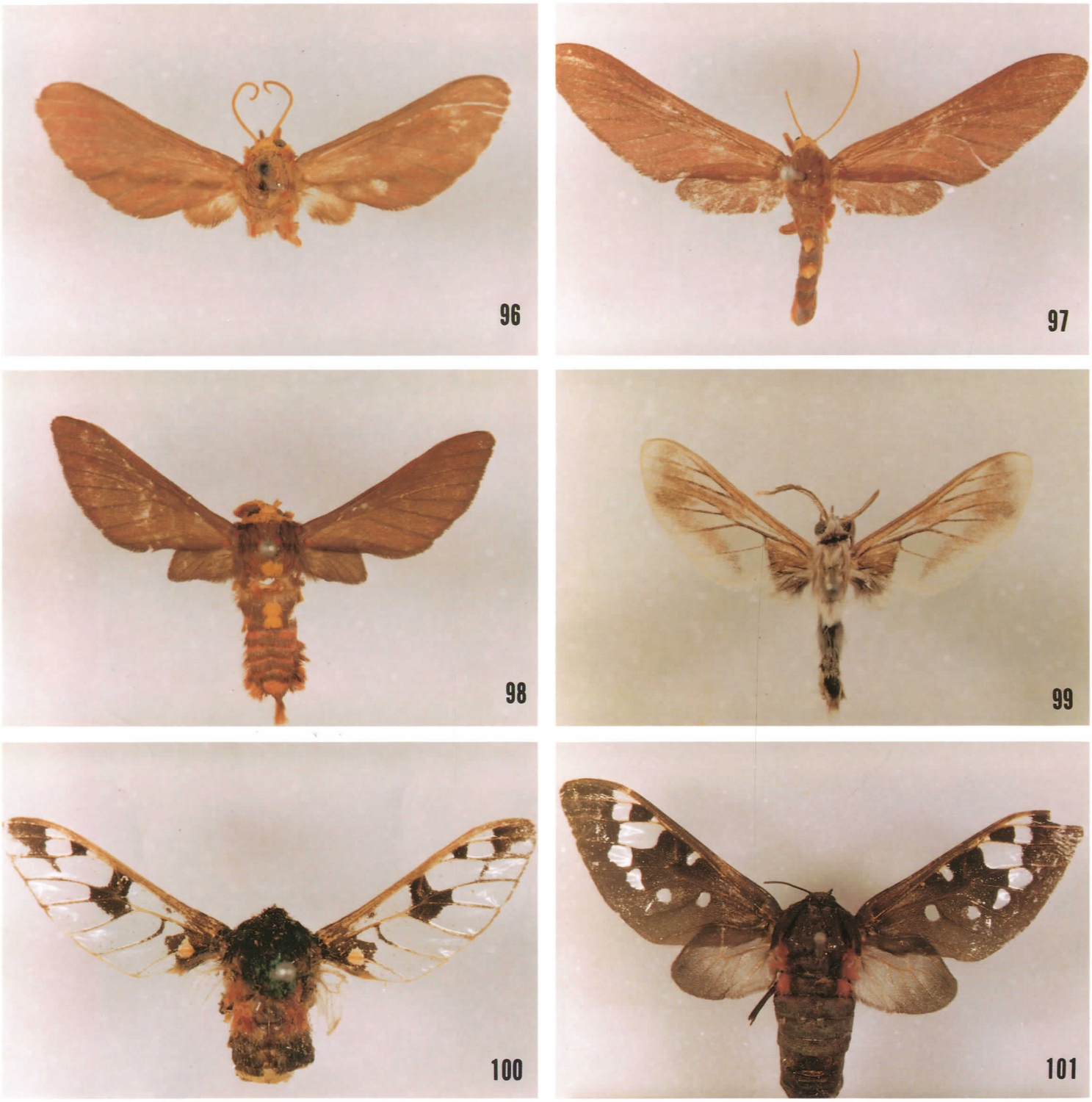
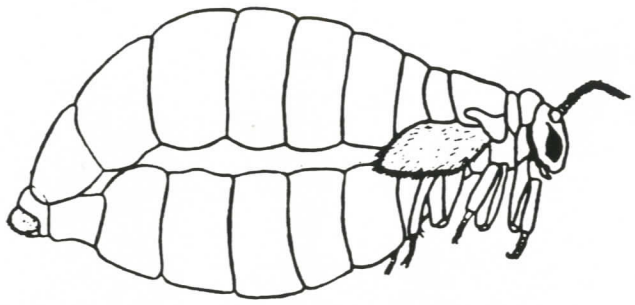


Fig. 96-101. THYRETIDAE: 96. *Balacra affinis* Rothschild ♂ (33mm), Congo; 97. same ♀ (39mm), Cameroon; 98. *Balacra daphaena* Hampson ♂ (31.5mm), South Africa; 99. *Pseudapicinoma angolensis* Kiriakoff ♂ (28mm), Angola; 100. *Balacra diaphana* Kiriakoff ♂ (38mm), Uganda; 101. same ♀ (53mm), Uganda [all BMNH specimens].



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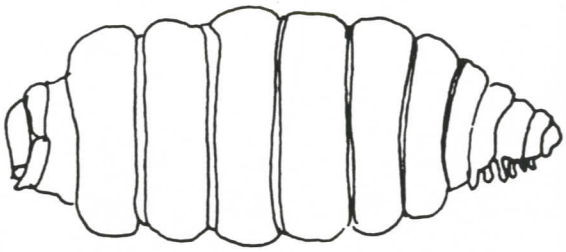

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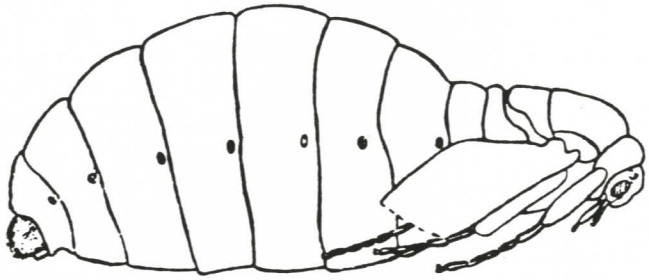

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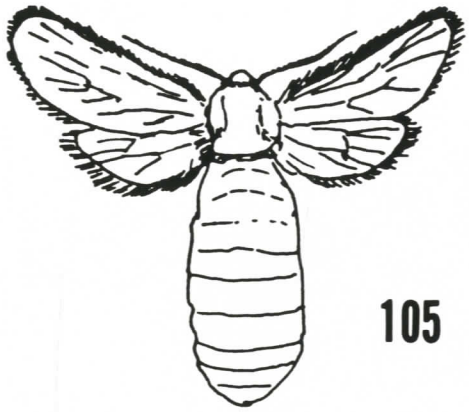

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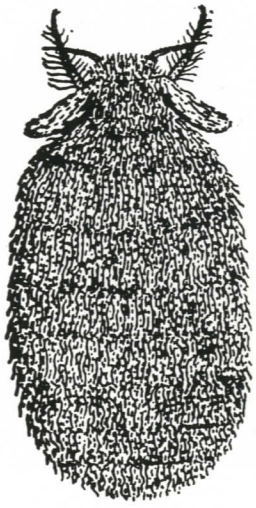

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Fig. 102-108. LYMANTRIIDAE: 102. *Orgyia recens* (Hübner) ♀, USSR [lateral view]; 103. *Teia dubia* (Tauscher), USSR [lateral view]; 104. *Gynaephora luge* ♀, USSR [lateral view]; 105. *Penthophera morio* (Linnaeus) ♀, USSR [dorsal view]; 106. *Orgyia recens* (Hübner) ♀, Poland [dorsal view]; 107. *Orgyia ericae* (Germ ♀, Poland [dorsal view]; 108. *Orgyia antiqua* (Linnaeus) ♀, Poland [dorsal view] [Fig. 102-105 after Kozhanchikov, 1956; 106-108 after Buszko and Sliwinski, 198

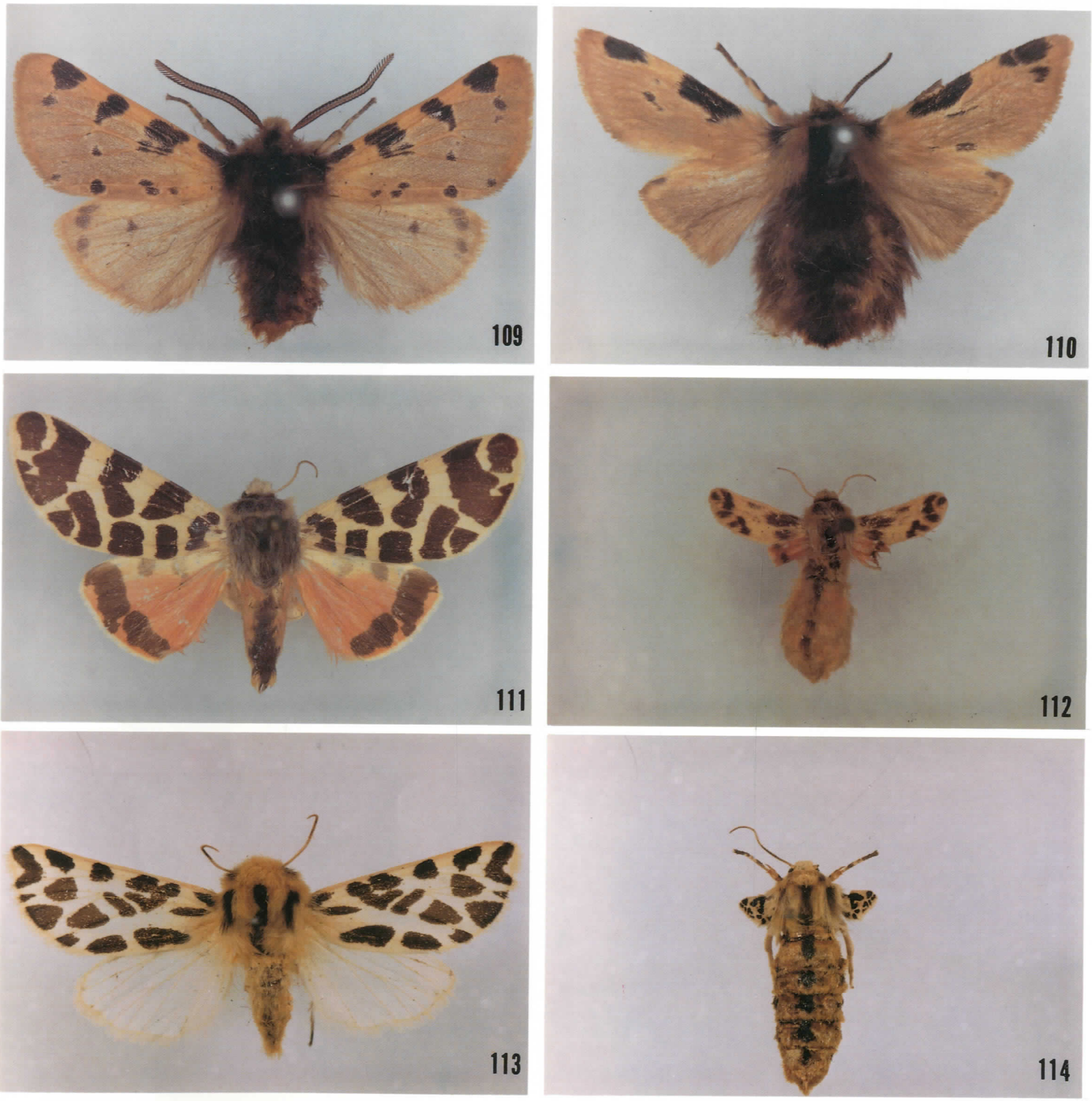

Fig. 109-114. ARCTIIDAE: 109. *Artimelia hemigena* (Grasl.) ♂ (29mm), [Europe]; 110. same ♀ (23mm), [Europe]; 111. *Cymbalophora haroldi* Oberthür ♂ (31mm), Algeria; 112. same ♀ (20mm), Algeria; 113. *Cymbalophora rivularis* (Ménétries) ♂ (37mm), Italy; 114. same ♀ (17mm), USSR [all BMNH specimens].


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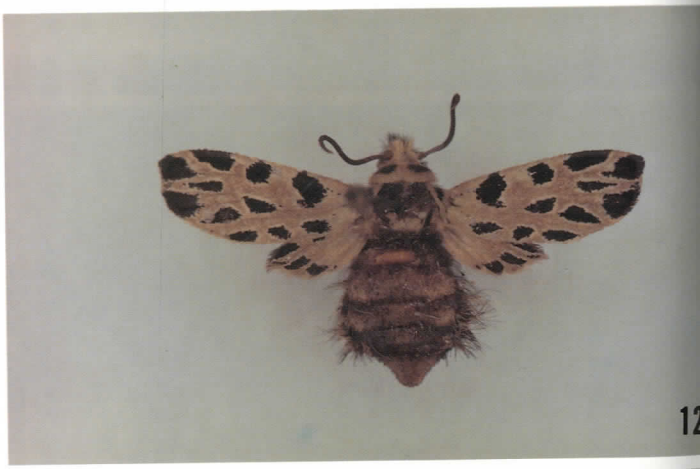
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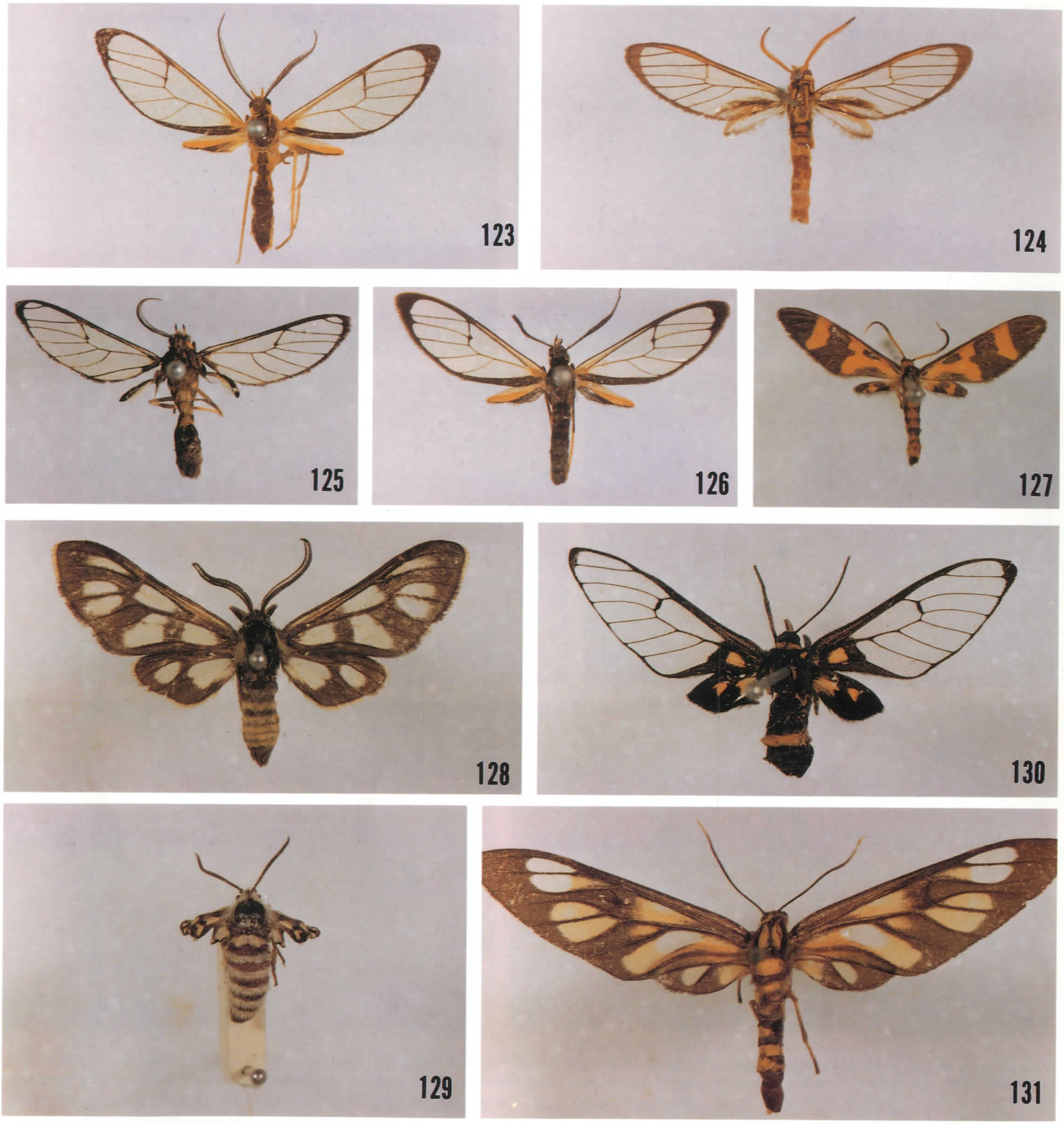


Fig. 123-131. ARCTIIDAE: 123. *Diptilon aterea* Schaus ♂ (23mm), Paraguay; 124. *Diptilon aurantipes* Rothschild ♂ (23mm), [Brazil]; 125. *Diptilon flavipalpis* Hampson ♂ (22.5mm), Argentina; 126. *Diptilon gladea* Jones ♂ (22mm), Brazil; 127. *Ceryx nacliodes* Hampson ♂ (18mm), Mozambique; 128. *Amata amazoula* (Boisduval) ♂ (26mm), South Africa; 129. same ♀ (9mm), South Africa; 130. *Amata pryeri* (Hampson) ♀ (30mm), Borneo; 131. *Amata trithyris* (Druce) ♀ (43mm), Indonesia (Sumatra) [all BMNH specimens].

Fig. 115-122. ARCTIIDAE: 115. *Gonerda breteaudeaui* Oberthür ♂ (41mm), Sikkim; 116. same ♀ (33.5mm), Sikkim; 117. *Ocnogyna corsica* Rambur ♂ (22mm), France (Corsica); 118. same ♀ (18mm), France (Corsica); 119. *Ocnogyna parasita* Hübner ♂ (28mm), [Europe]; 120. same ♀ (20mm), [Europe]; 121. *Amata rubicunda* (Mabille) ♂ (33mm), Uganda; 122. same ♀ (36mm), Cameroon [all BMNH specimens].

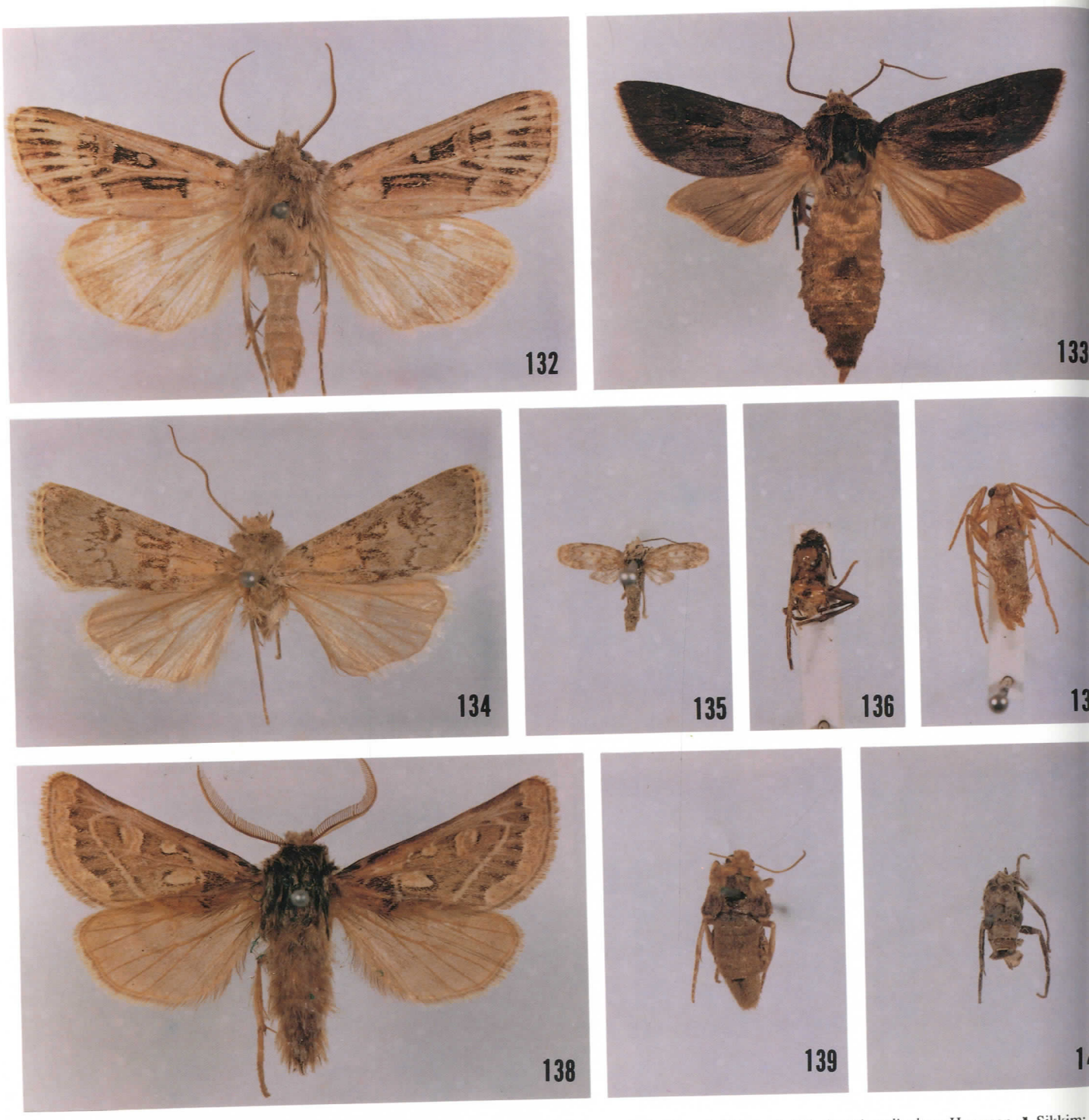
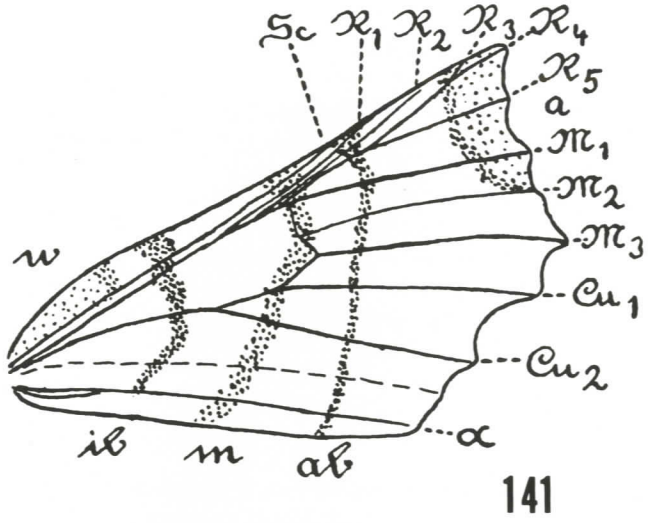


Fig. 132-140. NOCTUIDAE: 132. *Agrotis fatidica* (Hübner) ♂ (39mm), [Europe]; 133. same ♀ (31mm), [Europe]; 134. *Agrotis poliochroa* Hampson ♂, Sikkim; same ♀, Sikkim; 136. *Dimorphinoctua cunhaensis* Viette ♂ (6mm length), Tristan da Cunha; 137. *Dimorphinoctua goughensis* Fletcher ♀ (10mm length), Gough 138. *Ulochlaena hirta* (Hübner) ♂ (39mm), [Europe], 139. same ♀ (11mm length), France; 140. *Peridroma goughi* Fletcher ♂ (5mm length), Gough Id. [all BM specimens].



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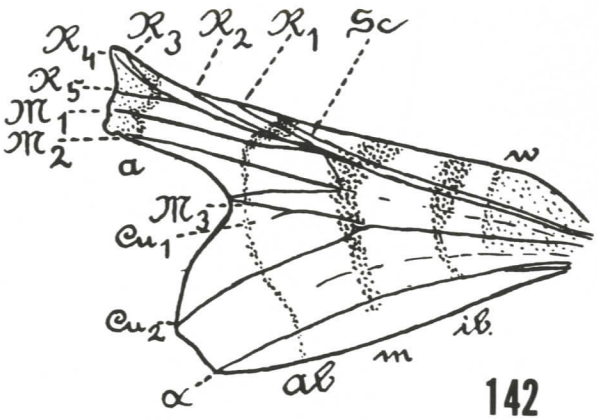

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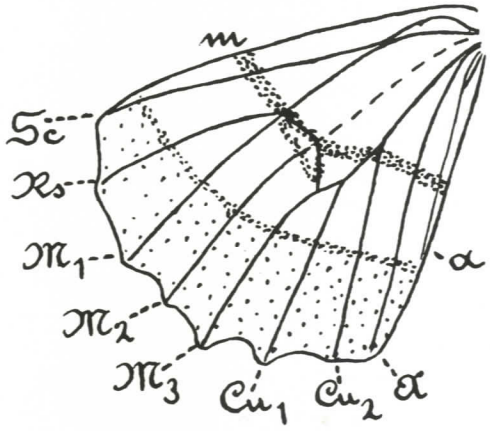

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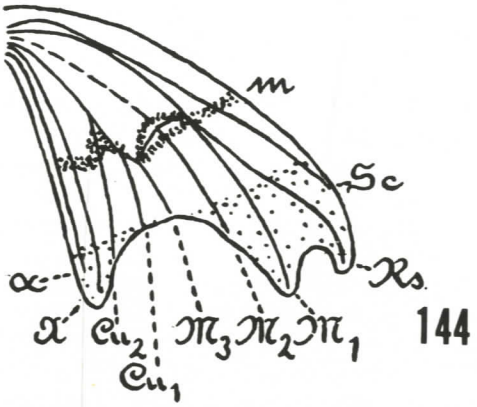

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Fig. 141-144. Wing reduction due to mutation or eclosion accidents (Geometridae: *Selenia bilunaria* Esper): 141. Forewing of normal ♂ (right dorsum); 142. Forewing of altered ♀ (left dorsum); 143. Hindwing of normal ♂ (left ventrum); 144. Hindwing of altered female (left ventrum) [after Lemche, 1933].

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