Studies on the morphology and systematics of primitive Lepidoptera (Insecta)

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Dansk resumé: Studier over primitive sommerfugles morfologi og systematik.

The monophyly and sistergroup relationship of the Lepidoptera are discussed and lepidopteran groundplan characters reviewed. Twenty-one traits are identified as probable autapomorphies of the superorder Amphiesmenoptera (i.e., they are synapomorphies of the Trichoptera and the Lepidoptera) whereas twenty-six traits are identified as probable autapomorphies of the Lepidoptera. The primary evolutionary lineages in the Lepidoptera are reviewed. Four suborders are recognized: Zeugloptera (Micropterigidae only), Aglossata (Agathiphagidae only), Heterobathmiina (Heterobathmiidae only) and Glossata. Four glossatan infraorders are recognized: Dacnonypha (Eriocraniidae + ? Lophocoronidae + ? Acanthopteroctetidae), Neopseustina (Neopseustidae only), Exoporia (Mnesarchaeoidea + Hepialoidea) and Heteroneura; the two lastmentioned constitute the monophyletic Neolepidoptera, and the Neopseustina + Neolepidoptera constitute the monophyletic Myoglossata. Arguments for and against the monophyly of the Heteroneura are presented. The phylogenetic relationships between the lepidopteran suborders are suggested to be Zeugloptera + (Aglossata + (Heterobathmiina + Glossata)), but alternative phylogenies such as Aglossata + (Zeugloptera + (Heterobathmiina + Glossata)) or Zeugloptera + ((Aglossata + Heterobathmiina) + Glossata) cannot be ruled out. Friese's (1970) "Gymnocera/Angiocera" theory of the primary lepidopteran dichotomy is examined in some detail and rejected. The genera of the non-neolepidopteran moth families are listed and representative members of these families illustrated in colour

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PREFACE

The research on which this article is based has been greatly enhanced by, indeed partly dependent on, the helpfulness of numerous colleagues, who have supplied material and information. I am particularly indebted to British Museum (Nat.Hist.) microlepidopterists Dr. G.S. Robinson, Dr. K. Sattler and Dr. P. Whalley as well as to Dr. I.F.B. Common (formerly Division of Entomology, CSIRO, Canberra), Dr. D.R. Davis (National Museum of Natural History, Washington D.C.), Mr. J.S. Dugdale (Entomology Division, DSIR, Auckland, N.Z.) and Dr. G.W. Gibbs (Victoria University, Wellington, N.Z.); my sincere thanks are also due to Dr. J.D. Bradley (Commonwealth Institute of Entomology, London), Mr. J. Heath (formerly Inst. of Terrestrial Ecology, Monks Wood, U.K.), Professor J. Powell (University of California, Berkeley), Dr. N.J. Smith (University of California, Davis), Dr. L. Vári (Transvaal Museum, Pretoria), Dr. P. Viette (Muséum national d'Histoire naturelle, Paris) and Dr. T. Yasuda (University of Osaka Prefecture, Japan). Dr. Gibbs read a draft of this article and made valuable suggestions on language and contents. Comments on the manuscript from Professor K.G. Wingstrand (University of Copenhagen), Dr. G. Mickoleit (Universität Tübingen, BRD) and the editor, Dr. H. Enghoff, are also much appreciated.

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It is probably true that to most zoologists the lowest moths are mere names in technical litterature: they are rarely conspicuous in their natural habitats even when abundant, and many taxa are represented only in a few of the most comprehensive collections. Black-and-white illustrations convey an inadequate impression of the diversity and elegance of these insects. I am greatly indebted to the Carlsberg Foundation for a grant towards the cost of the preparation of the two coloured plates accompanying this article and to the rightly renowned Microlepidoptera painter, Mr. R. Johansson (Växjö, Sweden) for his exquisite work.

In presenting this state-of-the-art review of my research on primitive Lepidoptera I wish to make a point of acknowledging my indebtedness to Dr. Anker Nielsen, emeritus reader of entomology, University of Copenhagen; his erudition and enthusiasm played a definitive role in the early shaping of my entomological interests. I similarly wish to acknowledge the impact which Professor J. Chaudonneret (Université de Dijon) and the late Professor H.E. Hinton (Bristol University) have had on my present ways of thinking about insect structure and evolution.

1. INTRODUCTION

The Lepidoptera are one of the most successful groups in the Animal Kingdom if judged by the number of extant species; the order comprises between 150.000 and 200.000 described species, and the number of undescribed ones can with certainty be stated to be very considerable. Considering the large number of species the Lepidoptera appear to be a remarkably homogeneous insect group, ecologically as well as structurally (although, of course, they exhibit abundant diversity with respect to size, shape and colour pattern in adults and immatures alike). On a geological scale the dominance of the Lepidoptera appears to be of relatively recent date. The recently described Triassic "lepidopteran" *Eocorona* Tindale, 1980 may well belong in the superorder Amphiesmenoptera (the anal veins of its fore wing exhibit the characteristic double-Y configuration) but it is devoid of obvious lepidopterous autapomorphies.

The existence of primitive Lepidoptera in the Triassic is by no means unlikely, but fossils from the lower Cretaceous remain the earliest reliable records of the order (Whalley 1978; see also the brief review by Kristensen, 1981a). In any case it appears unquestionable that by far the greatest part of the diversification of the Lepidoptera has taken place concurrently with the differentiation of angiosperm plants in the Cretaceous and later.

Modern concepts of lepidopteran phylogeny were taking shape with the writings of Hinton (1946a) and Hennig (1953). In a more general context Hennig later (1966: 227) chose to use a cladogram of the Lepidoptera (see Fig. 1) to illustrate a pattern which seems to turn up again and again during phylogenetic analyses: The "typical" derived characters of a group all occur together in one successful subordinate taxon (here the Ditrysia) and the other subordinate taxa may be arranged in a linear sequence according to the number of these "typical" characters which they have acquired; this pattern is the "additive typogenesis" of Heberer (see Hennig 1981: 24). The fact that the Lepidoptera appear to be a structurally homogeneous group is related to the numerical dominance of the
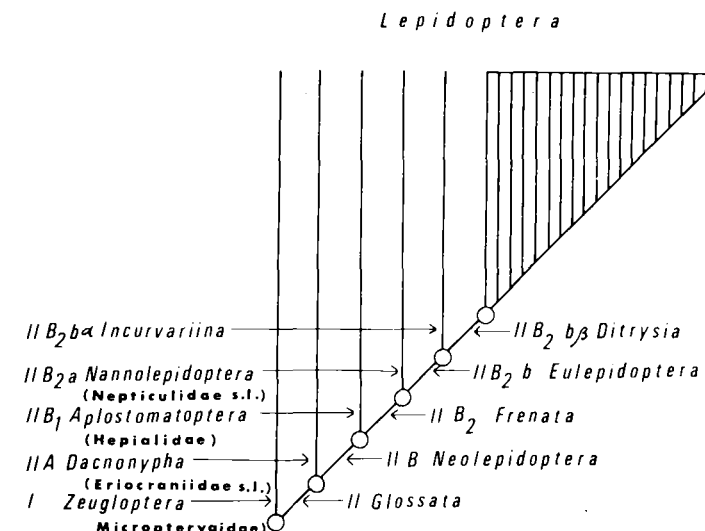

Lepidoptera

Fig. 1. Hennig's cladogram of the high-rank taxa in the Lepidoptera. (From Hennig 1966, courtesy of Illinois University Press.)

Ditrysia: The series of non-ditrysian evolutionary lineages exhibits a broad spectrum of organisational types, but all these lineages together comprise only about one per cent of the extant lepidopteran species!

Since the sixties a considerable amount of new information about the lowest Lepidoptera has become available, including descriptions of some remarkable new taxa, and certain modifications of Hennig's 1966 cladogram have been proposed. Indeed the primitive Lepidoptera do deserve particular attention, since it will be of obvious interest to elucidate details of the evolutionary pathway which has led to the emergence of one of the most successful character combinations in the Animal Kingdom. Similarly, it will be of considerable interest to clarify the details of the intrinsic evolution of each of the non-ditrysian lineages.

For a number of years the present author has been investigating selected aspects of the structure and phylogenetic systematics of the non ditrysian moths with special emphasis on the lowest homoneurous "grades"; these studies have partly been carried out in collaboration with other workers, S.J.R. Birket Smith (deceased 1983) and, particularly, E.S. Nielsen. It is the purpose of the present article to summarize the results presented in eighteen previous publications (referred to by italicized numerals and listed in the first section of the reference list) within the framework of a brief general survey of the groundplan characteristics and basic lineages of the Lepidoptera; a number of hitherto unpublished observations are also reported.

The names adopted in this survey for systematic categories above family group rank are those which appear to be in widest current use (or when this criterion is difficult to apply as in the "Heteroneura"/"Frenata(e)" case, what I consider the best descriptive name). I believe that adoption now of a strict priority criterion (as advocated by Viette 1979) would lead to unnecessary confusion in sub- and infraordinal nomenclature. The formal categorial ranks have been established according to the "phyletic sequencing" convention (see, e.g., Wiley 1981).

2. THE MONOPHYLY, SISTERGROUP RELATIONSHIP AND GROUND PLAN OF THE LEPIDOPTERA

On the basis of available knowledge the Lepidoptera must be grouped into four basic lineages, which in a formal classification may be ranked as suborders: Zeugloptera (the family Micropterigidae only), Aglossata (the family Agathiphagidae only), Heterobathmiina (the family Heterobathmiidae only) and Glossata (all other Lepidoptera) (*13*: 116); taken together the three firstmentioned suborders comprise about 0.05 per cent of the extant members of the order.

Disagreement over the monophyly of the Lepidoptera has stemmed from disagreement over the phylogenetic position of the Zeugloptera. Hinton (1946a), followed by Kiriakoff (1948) assigned the Zeugloptera the rank of a separate order[1]. Hinton claimed (1946a: 2) that the Zeugloptera are more primitive than both Lepidoptera and Trichoptera and that if they are included in the Lepidoptera the caddisflies must be included in that order as well; at a later date he even stated that the Zeugloptera are "much more closely related to the Trichoptera than to the Lepidoptera" (Hinton 1958: 203). As pointed out by Hennig (1953) and myself (Kristensen 1968, 1971, 1975, 1981a) the characters in which the Zeugloptera agree with the Trichoptera and differ from the other Lepidoptera are exclusively symplesiomorphies, and the closer "relatedness" is thus purely phenetic. Also, there are no good reasons for assuming that the caddisflies + the non-Zeuglopteran Lepidoptera should constitute a monophyletic entity. True, the two groups do share a couple of derived traits (which both can be considered regressive) viz.,

[1] Chapman had done so already by 1917, but on the basis of the erroneous belief that the non-ditrysian female genitalia of micropterigids are unique within the Lepidoptera; that this is not so had been shown already by Petersen (1900).

59.[2] *Loss of larval lacinia*, and

57. *Marked weakening of larval corporotentorium*; see Hinton (1958) and *13*. However, these traits can in no way outweigh the numerous derived traits (characters 1-26, below) now considered to be autapomorphies of the Lepidoptera inclusive of the Zeugloptera.

The two orders Trichoptera and Lepidoptera are grouped together in the superorder Amphiesmenoptera ("Trichopterida" of Boudreaux, 1979). Rohdendorf (1969) believed that the Lepidoptera phylogenetically are a subordinate group within the Trichoptera, i.e., that lepidopterous larvae are secondarily terrestrial. This assumption is totally unwarranted: The Trichoptera possess a suite of autapomorphies which clearly demonstrate their monophyly; hence, the relationship between the two orders is a genuine sistergroup relationship (Kristensen 1975, 1981a). The Amphiesmenoptera are considered to be the sistergroup of the superorder Antliophora (Mecoptera + Siphonaptera + Diptera) and the two superorders together constitute the group "Panorpida" or "Mecopteroidea" (Boudreaux 1979, 1981; Hennig 1981; Kristensen 1981b).

The following section is an enumeration of those characters in the adult and larval ground plan of the Lepidoptera which can now be considered autapomorphic of the order (Arabic numerals) or synapomorphic of the Lepidoptera and Trichoptera, i.e. autapomorphic of the Amphiesmenoptera (Roman numerals). Moreover, comments are given on a number of other groundplan traits which previously have been discussed in a phylogenetic context, or which for other reasons appear to be of particular interest.

Lepidopteran/amphiesmenopteran apomorphies in the pupal and egg stages remain to be worked out.

[2] Characters denoted by capital letters and by Roman and Arabic numerals are included in the cladogram, Fig. 13.

The term "ground plan" is here applied in its usual meaning in "Hennigian" phylogenetic systematics: The ground plan of a taxon is the hypothesized last common ancestor of the members of the taxon. The concept is equivalent to the "morphotype" as used by Nelson (1970).

The adult ground plan

A diagrammatic illustration of the hypothesized ancestral lepidopteran, wich amphiesmenopteran/lepidopteran autapomorphies indicated, is presented in Fig. 14.

Head. *Apomorphies:* Lepidopteran autapomorphies enumerated below without comments have been discussed in Kristensen (1968) and it has been checked *(19)* that the derived condition is present in the Aglossata.

1. *Median ocellus lost.*

2. *Corporotentorium with posteromedian process.* This formation, which accomodates the insertion of ventrolongitudinal neck muscles, is a characteristic lepidopteran autapomorphy. According to Boudreaux (1979) it is an amphiesmenopteran autapomorphy that the ventral neck muscles insert together on the middle of the corporotentorium; however, in the Trichoptera, which do not have the process, the muscle insertions are actually separate, paramedian *(19)*, and the muscles themselves (procoxo-tentorials, see character X) are cruciate.

3. *Presence of an intercalary sclerite laterally in the membrane between the antennal scapus and pedicellus.* A triangular or rounded intercalary sclerite is well developed in some Zeugloptera and the Aglossata *(19)* and lower Glossata (Kristensen 1968; *6*: 288); it is less distinct and probably secondarily reduced, in the Heterobathmiina (*7*: 77). A corresponding sclerite is not known to occur in the related orders and is therefore considered a lepidopteran autapomorphy.

4. *Maxillary palp with points of flexion between segments 1/2 and 3/4; segment 4 longest segment of palp; no antagonistic muscles inserting on the base of any palp segment.* It may be noted that in the Aglossata (Dumbleton 1952,

19) segment 4 is but little longer than segments 2 and 3 and all are shorter than 1. The Heterobathmiina (7: 76) have what I consider to be the groundplan proportions of the palp.

5. Presence of a slender craniostipital muscle running close to the craniocardinal muscle. Denis & Bitsch (1973) considered this muscle to be undoubtedly homologous with an "ancien cranio-stipital"; however, since the latter to my knowledge is known only from the Archaeognatha the homology seems highly questionable. I would rather consider this muscle a derivative of a tentoriostipital muscle, as suggested by Denis for a corresponding larval muscle (see *17*: 20).

6. Postlabium an arched sclerite with long piliform scales. I have previously (Kristensen 1968, 1971) referred to this trait as a "postlabial Eltringham's organ". The presence of a postlabial sclerite is in itself a plesiomorphy at the amphiesmenopteran level; a corresponding sclerite is absent in the Trichoptera (7: 118).

I. Prelabium fused with hypopharynx. It is well known that the characteristic "haustellum" of the Trichoptera is a composite formation, and the fusion is evident in primitive Lepidoptera as well. In the lowest Glossata the composite lobe is slender and resembles the mecopteran hypopharynx. Indeed the lobe has been termed the hypopharynx (Tillyard 1923, Kristensen 1968) but as pointed out by Denis & Bitsch (1973) this is wrong: the position of the salivary orifice on the anterior surface of the lobe clearly indicates the composite nature of the latter. In the non-glossatan Lepidoptera the posterior, hypopharyngeal, area of the anterior wall of the lobe is concave, forming an "infrabuccal pouch"; see below.

7. Terminal segment of labial palp with a group of chemoreceptors (or are they hygro- or thermoreceptors ?; see Chauvin & Faucheux 1981: 437) *located in a depression*; this is the socalled "vom Rath's organ".

8. Salivarium devoid of longitudinal dorsal muscle.

*9. Labral nerve and frontal ganglion connec-*tive separate just from their origin on the tritocerebrum.

10. Nervus recurrens running within cephalic aorta until reaching retrocerebral complex. This peculiar condition is mentioned from higher Lepidoptera by Bullock & Horridge (1965: 896) and from Dacnonypha-Eriocraniidae by Kristensen (1968) and its presence has now been checked *(19)* in the Aglossata (Fig. 11) and Zeugloptera (Fig. 4). In the Trichoptera the nervus recurrens has retained its primitive position below the aorta (Klemm 1966).

Notes on the ground plan of the head. Loss of the primitive tentorial adductor of the mandible has previously (Kristensen 1968) been considered a lepidopteran groundplan apomorphy, but this can no longer be upheld. The muscle, which is very small indeed, has now been identified *(19)* in the zeuglopteran genus *Micropterix* (but was not found by Hannemann 1956) as well as in the Aglossata (Fig. 8). I have previously (Kristensen 1968, 1971) suggested that the presence of lateral bundles of bristles on the labrum is another lepidopteran groundplan autapomorphy, but I now doubt that the bristles on the lateral labral corners of *Micropterix* (Hannemann 1956) can reasonably be considered direct forerunners of the characteristic "pilifer" bristles in higher Lepidoptera; lateral labral bristles are not prominent in Aglossata, Heterobathmiina, or Dacnonypha-Eriocraniidae *(19)*.

The abovementioned "infrabuccal pouch" in the hypopharynx is a remarkable point of similarity between the non-glossatan moth suborders; compare Hannemann's fig. 9 (1956) of this pouch in *Micropterix* with the illustrations presented here of the corresponding formations in Aglossata and Heterobathmiina (Figs 2-3). Since a theory of monophyly of the non-glossatan suborders would be inconsistent with the greater part of the available evidence, one has to ask whether the infrabuccal pouch is a plesiomorphy at the amphiesmenopteran or panorpid level. Within holometabolan insects a prominent infrabuccal pouch is a well known trait

in the Hymenoptera (and I still consider the Hymenoptera likely candidates of the position as the sister group of the Panorpida; I am not convinced of Boudreaux' evidence, 1979, 1981, for the monophyly of the socalled Meronida, i.e. the Panorpida + Neuropterida). It is true that an infrabuccal pouch has been said to be absent in the sawflies (Denis & Bitsch 1973) but in fact I have found a distinct infrabuccal cavity in the very primitive xyelids *(19)*. Xyelids are pollen feeders as are the Zeugloptera (and presumably the Heterobathmiina, *13*: 106) and pollen/spores might well have been a primary source of food for adult insects in a larger section of the Holometabola (see also Malyshev 1968: 11). The strongly spined pouch wall undoubtedly plays an important role for the cutting up³) of food particles through the movements of the mandibles within the preoral cavity, and the formation is unlikely to remain typically developed in groups which feed on fluid matters exclusively; this would explain its absence at least in the Trichoptera. It remains an open question whether the presence of an epipharyngeal armature (sclerites and brushes; see *7*: 78, 112) in Zeugloptera and Heterobathmiina represents a plesiomorphic condition. Again, somewhat similar formations have been found in a xyelid sawfly (*13*: 117), although in the species examined the armature is symmetrical.

Thorax. *Apomorphies.*

11. Laterocervial sclerite with "hair plate" close to the anterior apex. This trait has been mentioned as a probable lepidopteran groundplan autapomorphy since it does not appear to be known from primitive Trichoptera and Mecoptera (7: 124). It cannot be excluded, however, that it is actually a plesiomorphy which has been lost independently in the lastmentioned orders; in any case laterocervical hair plates are known to occur elsewhere among insects, e.g. in Hymenoptera.

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³) The micropterigid infrabuccal pouch has long been known as "triturating basket" in English literature.

II. *Lower posterior corner of laterocervicale produced towards the prosternum.* This trait appears to be an autapomorphy of the amphiesmenopteran ground plan (7: 119).

12. *Prothoracic endoskeleton with a prominent free arm arising from the bridge between the sternum and the lower posterior corner of the pleuron.* A lepidopteran autapomorphy (7: 119); in the lowest (i.e. non-neolepidopteran) groups the base of the arm is clearly separate from the pleuron except in cases where the arm is very broad (*5*: 14; 7: 119).

III. *Pronotum with paired setose "warts".* This Trichoptera/Lepidoptera synapomorphy was pointed out by Boudreaux (1979). The warts of the lower moths are supposedly forerunners of the stalked "patagia" in higher Lepidoptera (see 7: 130).

IV. *Pterothoracic episterna with characteristic suture pattern.* Two sutures, which have a common base, extend forwards from the pleural suture: The paraxocal suture, which runs upwards to converge or anastomose with the precoxal suture, and a short suture, which runs downwards in front of the pleurocoxal articulation (7, fig. 25). This characteristic pattern which occurs throughout the lowest lepidopteran taxa *(19)* is also found in Trichoptera (Matsuda 1970, Schmid 1970, Marshall 1979) and appears to be an amphiesmenopteran autapomorphy.

V. *Secondary furcal arms in pterothorax fused with posterior margin of corresponding epimera.* A classical amphiesmenopteran autapomorphy (Brock 1971).

13. *Mesothorax with a "tergopleural apodeme", issued from the upper part of the pleural suture and accomodating the insertion of a tergopleural muscle.* A noteworthy lepidopteran autapomorphy (Sharplin 1963, Mickoleit 1969); I have checked *(19)* the presence of this apodeme in the Aglossata.

14. *Metathorax with a "prescutal arm".* This long prescutal process, which is unknown from related orders, was identified in Zeugloptera, Glossata-Dacnonypha and Glossata-Hepialoidea

by Sharplin (1964) and I have found it *(19)* in Aglossata and Heterobathmiina also. In heteroneuran Lepidoptera this formation is secondarily modified (character 108).

VI. *Metathorax with a setose (presumably proprioceptive) sclerite in the wing base membrane below/behind the subalare.* This sclerite pertains to the groundplan of the Amphiesmenoptera and is apparently an autapomorphy of the superorder (*7*: 120). In *Micropterix (16)* and *Eriocrania (19)* the nerve supplying the setae of this sclerite curiously branches off from the dorsum I-nerve; this is in apparent conflict with current criteria for tracing segmental boundaries (*16*: 129). The innervation pattern has not yet been worked out in other Amphiesmenoptera.

15. *Fore tibia on inner surface with an "epiphysis"*; this is used for antennal grooming (see e.g. Jander 1966). The tibial wall facing the epiphysis often has a characteristic vestiture (*12*: figs 15, 34). The epiphysis is a long-established (Philpott 1924) lepidopteran peculiarity; it is known from all suborders but has been secondarily lost in some Zeugloptera (Issiki 1931) and on numerous occasions within the Glossata.

VII. *Pretarsus above the claws with a "pseudempodium", a strong seta on a socket.* A pseudempodium (*6*: 275) is found in primitive Trichoptera and Lepidoptera *(19)* and must be ascribed to the ground plan of the Amphiesmenoptera. It appears to be an autapomorphy of the superorder.

VIII. *Wings with extensive covering of setae.* There is every reason to ascribe this derived trait to the last common ancestor of Lepidoptera and Trichoptera (Boudreaux 1979, Hennig 1981), but as well known the setae have been further modified in the Lepidopteran lineage (following character).

16. *Wings with dense covering of broad scales.* The classical and still most impressive lepidopteran autapomorphy; it is true that wing scales do occur in some Trichoptera, but they do not occur in the most primitive caddisflies and there is

no basis for ascribing them to the ground plan of the order. As shown more than a decade ago *(1)* the wing-surface scales of the lowest Lepidoptera differ markedly from the previously known "normal type" of lepidopteran scales in being solid plates, i.e., their upper and lower lamellae are not separated by a lumen. In surface view these "primitive type" scales are characterized by being imperforate. The inter-ridge areas of the obverse scale surface is densely set with transverse "flutes" (nomenclature of Downey & Allyn 1975); these "flutes" were not resolved in the first SEM pictures *(1)* but have been clearly illustrated from all non-glossatan suborders as well as glossata-Dacnonypha in later works (Common 1973, Davis 1978, *7, 12*). In the three non-glossatan suborders scale types occur in which the transverse flutes are overlayered by socalled "herringbone crests" (Common 1973, Davis 1978, *7, 12*); since the non-glossatan moths are not considered to constitute a monophyletic entity, scales with "herringbone crests" are attributed to the ancestral lepidopteran.

IX. *Anal veins[4] of the fore wing apparently looping up into a double-Y configuration.* A classical amphiesmenopteran autapomorphy (Hennig 1981) which, however, is secondarily obliterated in several subordinate taxa within the Lepidoptera. The more or less oblique "distal portions of 2A and 3A" are very probably old cross veins (see *6*: 291 for discussion).

X. *One ventral (tentorial) neck muscle originating on the fore coxa.* Matsuda (1970) considered the position of this muscle (s-cx (cv) 1 in his notation) to be peculiar to the Lepidoptera, but it is known from primitive caddisflies as well (N. Klemm, personal communication, in Kristensen 1968). Bharadwaj *et al.* (1974b) note that the anterior insertion of the corresponding muscle (their lcv-cx$_1$) in some ditrysian Microlepidoptera is on the cervical sclerite, and they consider this to be the primitive con-

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[4] Following the vein nomenclature of Hamilton (1971-1972) vein 1A was termed E in 7.

dition. However, since the tentorial insertion is found in Zeugloptera (Hannemann 1956), Aglossata *(19)* and Glossata-Eriocraniidae (Kristensen 1968), the cervical insertion surely is a character reversal when present in higher moths.

XI. *Conical furcopleural muscle in the mesothorax with broad end on the pleural ridge.* A muscle between the furca and the pleural ridge is of frequent occurrence in the insect pterothorax; this muscle is often conical. Chadwick (1959) considered it a unique lepidopteran feature that the broad end of the muscle in the mesothorax is on the pleuron whereas in the metathorax it is on the furca (as usually); he claimed that this condition is not found in the Trichoptera. However, Tindall (1965) described from the caddisfly *Limnephilus* a bipartite mesothoracic furcopleural muscle, the upper bundle of which has its broad insertion on the pleural ridge. The same configuration has been found in the Aglossata *(19)* and it is presumably primitive in the Amphiesmenoptera.

17. *Metathoracic spiracle with a single, anteriorly situated, external lip.* This trait is probably a lepidopteran autapomorphy as suggested in *15*. Preliminary observations *(19)* on this spiracle in the Aglossata have now shown that it is basically similar to that of *Micropterix* described in *15*, but that it has a narrow sclerotized band in the posterior atrial wall; this band may be a vestige of the posterior lid.

Notes on the ground plan of the thorax. Ross (1967) stated that the prescutum is clearly demarcated laterally and medially in the ground plan of the Trichoptera whereas in the Lepidoptera it is not even faintly demarcated laterally. However, I consider it unlikely that the demarcation of the "wart"-bearing mesonotal area termed prescutum in Trichoptera (see also Marshall 1979) is the primitive prescutoscutal boundary. Crampton (1920) claimed that in the Lepidoptera the mesocoxal meron always extends downwards to the coxal apex whereas in the Trichoptera it does not; however, the rhyacophilid caddisfly illustrated by Schmid (1970,

fig. 3) conforms with the lepidopteran pattern (which, incidentally, would seem to be the plesiomorphic one, since it agrees with conditions in the Mecoptera; Hepburn, 1971). In the same article Crampton stated that the Lepidoptera in contrast to the Trichoptera never have a mesothoracic "basicoxite" (i.e. a basal piece of the coxa vera, delimited by a strip of membrane), but I have observed a basicoxite in zeuglopteran moths and a probably homologous formation in heterobathmiines *(19)*. A detailed comparative study of the coxal base and its associated musculature in primitive Amphiesmenoptera would surely be worthwhile. Boudreaux (1979) considered the jugo-frenate wing coupling and the forewing/metathorax locking device (see Kuyten 1974 and the earlier description of this formation in Lepidoptera by Common 1969) to be amphiesmenopteran autapomorphies; for both character complexes the trichopteran groundplan condition seems in need of further elucidation (see Riek 1967, 1970) and the possibility that a forewing/metathorax lock is plesiomorphic at the panorpid level cannot be ruled out.

The metathoracic furcal stem is simple in the Trichoptera and the Zeugloptera, but in the non-zeuglopteran primitive Lepidoptera it bears a prominent anterior process which accommodates the origin of the sternal bundle of the trochanteral depressor *(7)*. The suggestion (*7*: 138) that this process is an autapomorphy of the lepidopteran ground plan cannot be upheld in the light of the recently acquired knowledge of the Heterobathmiina *(13)*.

A skeletal bridge between the primary and the secondary metafurcal arms has been developed independently within the two amphiesmenopteran orders; the connection between the two arms is believed to have been ligamentous in the ground plan of the superorder (*16*: 26).

It was long considered an important autapomorphy of the lepidopteran ground plan that M$_4$ in both wingpairs is lacking (as a discrete vein; its base may be represented by an apparent

M-CuA crossvein). This cannot be upheld, since a distinct, complete M4 is present in the fore wing (and sometimes in the hind wing as well) of the Aglossata (Kristensen 1975, 1981a, *19*). Indeed, neither the groundplan venation of the Lepidoptera, nor that of the Trichoptera is now known to exhibit any ordinal autapomorphies; this naturally seriously impedes identification of early amphiesmenopteran fossils.

The absence of "nygmata" ("pigmented spots" or "corneous spots" of some authors) on the fore wings of Lepidoptera (Tillyard 1919) may well prove to be another autapomorphy of the order; I have checked the absence of these formations in the Aglossata and Heterobathmiina *(19)*. It should be noted that trichopteran and mecopteran nygmata (Riek 1970) are located in non-homologous wing spaces, but all may be remnants of a richer complement in ancestral Holometabola: the trichopteran nygma between the two posteriormost Rs-branches has an apparent counterpart in some primitive Neuroptera (see Riek 1970).

The tergotrochantinal muscle in the pterothoracic segments has retained its primitive (trochantinal) insertion in the Aglossata *(19)*, Zeugloptera and Glossata-Eriocraniidae (Mutuura 1956). The claim of Bharadway et *al.* (1974) that the insertion of this muscle in the Lepidoptera always is displaced into the coxa itself, is therefore incorrect.

Incidentally, Mutuura (1956: 97) considered the muscle in question to be represented by a bundle of tergosternal fibres; apparently he was not aware of the presence of a tergal coxa-promotor in any Lepidoptera.

According to Bharadwaj et *al.* (1974) the epimeral muscle to the subalare is lost in the lepidopteran metathorax; however, this trait cannot be uphold as a lepidopteran autapomorphy either, since the muscle in question has now been identified *(19)* in the Zeugloptera, Aglossata (Fig. 9) and Glossata-Eriocraniidae.

It is very surprising indeed that the "outer tergal remotor" of the mesocoxa (Figs 6-7) has now been found in the Aglossata (Kristensen 1981b); on the basis of Mickoleit's careful and extensive search (1966) for this muscle in holometabolan insects its absence has previously been considered a good autapomorphy of the entire Panorpida. If the presence of the outer tergal remotor in the Aglossata is not an autapomorphic character reversal, one has to assume that the muscle has been lost independently in the Antliophora, Trichoptera and at least once (and presumably twice, see chapter four) in the Lepidoptera.

Abdomen. *Apomorphies*:

18. *Tergum I extensively desclerotized and external layer of "short" dorsolongitudinal I/II muscles therefore lost.* This character is discussed in *16*; the muscles in question are lacking in the Aglossata also *(19)*.

19. *Tergum I with paired lateral lobes extending downwards/backwards and articulating with the anterior corners of Sternum II.* This character has been discussed in *7* (p. 121-122; see also *13*) and *16*; it is worth noting that the chordotonal organ between the secondary metafurcal arm and the upper part of the lobe is found to be well developed in the Aglossata *(19)*, although the lobe itself is indistinct in this taxon.

XII. *Presence of paired glands opening on sternum V.* This amphiesmenopteran autapomorphy is discussed in *7* and *16*; the glands have been secondarily reduced on numerous occasions within both orders.

XIII. *Male genital segment (IX) with tergum and sternum fused, forming a closed ring.* This character can only tentatively be considered an autapomorphy of the amphiesmenopteran ground plan (*7*: 125-126; *18*). If it is accepted, the separate dorsal and ventral segment IX plates in Heterobathmiina as well as the separate "tegumen" and "vinculum" in many Neolepidoptera must be considered character reversals/neoformations.

20. *Male gonopod ("valve") primarily undivided.* A possible, but by no means unproblematical autapomorphy of the lepidopteran ground plan. If it is accepted, the musculated "clasper" on the inner surface of the valve in many higher Lepidoptera must be interpreted as a character reversal or neoformation *(18)*.

21. *Protractor muscles of the male phallus originating within the gonopods.* This character is discussed in *18*.

XIV. *Anterior margin of female segments VIII and IX with long, rodlike apodemes accommodating the insertions of protractor/retractor muscles of the extensible oviscapt ("ovipositor").* This probable synapomorphy of Lepidoptera and Trichoptera was pointed out by Ross (1967), and Nielsen (1980) described further examples of long apophyses in primitive caddisflies. If the synapomorphy is accepted, the lack of one or both pairs of apophyses in several subordinate groups must be ascribed to secondary loss (*7*: 115).

22. *Cerci lacking in both sexes.* Cerci must be ascribed to the ground plan of the Trichoptera, although they are not of frequent occurrence in that order (Nielsen 1957, 1980). I am not aware that they have ever been proved present in the Lepidoptera.

Notes on the ground plan of the abdomen. Possibly it will prove to be another synapomorphy of the Trichoptera and Lepidoptera that the metapostnotal component of the definitive sclerotization on what is topographically dorsum I is quite small *(16)*. Noteworthy plesiomorphies in the lepidopteran abdominal base include the distinct sternum I and the ventral dilator muscle of spiracle I; the caddisflies are autapomorphic with respect to these traits *(16)*. It is also just possible that the paired sternal "windows" in sternum II in the lepidopteran ground plan are primitive *(16)*.

Dorsal and ventral chordotonal organs, with one and (about)four scolopidia respectively, are present in the pleural membranes of II and the following pregenital segments in *Micropterix*. The ventral organ in II is probably homologous with the sensory unit of the abdominal ears in a number of ditrysian moths *(16)*.

The ground plan of the male genitalia of the Lepidoptera is discussed in some detail in *18*.

Segment VIII was similar to the preceding segments. It is tentatively suggested that tergum and sternum IX were fused; that the gonopod was undivided and that a tubular, partly sclerotized aedeagus was present. The base of the aedeagus was probably surrounded by at least a short phallotheca. It is suggested that there was a median sclerite between the gonopod bases, but the presence of discrete, paired and muscular "valvellae" in the lepidopteran ground plan is considered doubtful. It is further suggested that dorsum X bore a pair of lobes and that there were paired sclerotizations in venter X. The X/XI boundary is very difficult to trace. Seventeen muscle sets are ascribed to the lepidopteran ground plan; it is considered an apomorphy of this ground plan that the phallic protractor originates within the gonopod. The testes presumably had large, separate follicles and there may have been two pairs of tubular accessory glands.

It is exceedingly difficult to reconstruct the groundplan configuration of the female genitalia in the Lepidoptera. If it is assumed (as above, character XIV) that an extensible oviscapt was present in the ground plan of the Amphiesmenoptera, then it might also seem reasonable to assume that a terminal cloaca was present in this ground plan. But the issue is complicated by the fact that the Heterobathmiina have the anus and gonopore separate and their abdominal apex is not extensible *(7)*; a very similar configuration is found in some caddisflies including taxa as primitive as the Rhyacophilidae-Hydrobiosinae (*7*: 126-127). I find it impossible at present to determine with certainty which of the configurations is primitive within the superorder.

Visceral anatomy. *Apomorphies.*

23. *Abdominal nerve cord with at most five ganglionic masses and with unpaired connectives.* In adult Trichoptera there may be six ganglia and the connectives are separate (Korboot 1964). Acceptance of these traits as lepidopteran autapomorphies presupposes that the six abdominal ganglionic masses known from hepialoids (see also chapter four) and the separate connectives known from neopseustoids and cer-

tain Ditrysia are interpreted as secondary modifications *(9)*.

XV. *Ventral diaphragm muscles inserting on the nerve cord.* A remarkable amphiesmenopteran autapomorphy, discussed in *8*.

24. *Mesothoracic aorta curving upwards to dorsum.* In a number of ditrysian families (Acrolophidae, Megalopygidae, Pyralidae a.o.) the mesothoracic aorta runs close to the oesophagus and does not approach the dorsum of the segment. Hessel (1969) considered this "ventral arrangement" to be primitive in the Lepidoptera, because it corresponds to the condition recorded from the Trichoptera, Mecoptera and Megaloptera; Hessel had examined ditrysian Lepidoptera exclusively. However, in Zeugloptera, Aglossata (Fig. 10) and the Glossata-Eriocraniidae the mesothoracic aorta extends upwards to the dorsum in a smooth curve *(19)*, i.e. its configuration corresponds to the "tineoid type" of Hessel. This type must consequently be assumed to represent the ancestral configuration within the order, and the abovementioned "ventral arrangement" in some higher moths must be a character reversal.

Notes on the ground plan of the viscera. The primitive configuration of the alimentary canal in the Lepidoptera remains a puzzle. It is noteworthy that the Aglossata have a very large, but delicate, stomodaeal "crop" which extends into the basal part of the abdomen (Fig. 12). A similar large crop is known from Trichoptera as well as from Neolepidoptera (Petersen 1900, Mortimer 1965), but it is not present in the Zeugloptera (Mortimer 1965) or Glossata-Dacnonypha (Kristensen 1968) where on the other hand the mesenteron is long and wide.

The identical and small number (three) of rectal papillae reported from *Micropterix* and some eriocraniids were once considered to represent the lepidopteran groundplan figure (Kristensen 1968, 1971), but this agreement proved to be spurious since some eriocraniids do have six papillae (Kristensen 1975). In the Aglossata I have found up to nine papillae *(19)*.

Cytology. *Apomorphies.*

XVI. *Female heterogamety.* A classical synapomorphy of Trichoptera and Lepidoptera.

XVII. *Apyrene sperm of usual occurrence.* This specialization has long been known from the Lepidoptera and is also present in caddisflies (Suomalainen 1966).

XVIII. *Spermatozoa with outer, accessory filaments very thick, filled with proteinaceous and glycogen-like material.* This autapomorphy of the Amphiesmenoptera is discussed by Baccetti *et al.* (1970). It may be mentioned here that it remains an open question whether the radiate "appendices laciniate", so characteristic of the testicular sperm of the ditrysian Lepidoptera examined (e.g. Phillips 1971), also occur in the most primitive members of the order and thus can be ascribed to its ground plan.

XIX. *Chromosome number specialized (high) and chromosomes probably holocentric; oogenesis achiasmatic.* For further details of caryological similarity between Lepidoptera and Trichoptera see Suomalainen (1966, 1969).

The larval ground plan

The amphiesmenopteran larval ground plan is close to that inferred for the Panorpida as a whole. Apomorphies at the superordinal and ordinal levels have so far been identified only, in a few cephalic traits.

Head. *Apomorphies.*

XX. *Each stemma with one crystalline cone cell transformed into a primary pigment cell ("Mantelzelle").* This amphiesmenopteran autapomorphy has been well discussed by Paulus & Schmidt (1978).

25. *Pleurostome elongated, craniocardinal articulation far behind mandibular base.* This feature *(17)* and the following, rather trivial, regressive trait:

26. *Maxillary palp with less than five segments (17)* are the only lepidopteran autapomorphies hitherto identified in the larva.

XXI. *Prelabium and hypopharynx fused into a lobe apically carrying the salivary (silk) gland orifice.* A classical autapomorphy of larval Amphiesmenoptera (see e.g. Hinton 1958).

Notes on the ground plan of the head. The ground plan of the lepidopteran larval head is discussed in some detail in *17*. It was supposedly prognathous, and was autapomorphic in having the craniocardinal articulation far behind the mandible; it had a complete hypostomal bridge, but neither hypostomal nor adfrontal ridges, its tentorium was probably stout and with dorsal arms. A tentative table of homologies between cranial setae in Lepidoptera and Trichoptera is presented in *17*; it differs considerably from the scheme of Williams & Wiggins (1981). The mouth parts and their musculature must have been overall very primitive for a panorpid larva, but the number of maxillary palp segments was reduced (three). The "dististipes" sensu Hinton is considered to consist of complexly fused parts of the stipes and basal palp segments. The cephalic stomodaeum must have possessed all primitive groups of extrinsic muscles. The incomplete available information on Micropterigidae impedes reconstruction of some details of the ground plan.

Boudreaux (1979) listed "muscles in larval palpi" among the plesiomorphic traits of the amphiesmenopteran ground plan, but I am not aware of reports of such muscles from either trichopteran or lepidopteran larvae (unless, of course, the stipital flexor and extensor of the dististipes are included in this category. But then these muscles are not confined to the Amphiesmenoptera within the Panorpida, see Hinton 1958).

3. THE PRIMARY EVOLUTIONARY LINEAGES IN THE LEPIDOPTERA

A synoptic list of the genera belonging to the lowest lepidopteran grades (i.e., the non-glossatan suborders and the non-neolepidopteran Glossata) is presented in the appendix, chapter 6; examples of adult moths of the families in question are illustrated in Figs 15-33. An account of the diversity within the Exoporia and lower Heteroneura is outside the scope of this survey, but reference will be made to some recent advances in the knowledge of the former taxon, which play a central role in one theory of the basal lepidopteran dichotomy (see chapter four).

Suborder Zeugloptera

Generalities and groundplan apomorphies. The single family of the suborder, the Micropterigidae, is now recorded from all zoogeographical regions. It comprises about 90 described species, and some tens of undescribed ones are recognized in collections. Micropterigids are small (wingspan reaching about 15 mm in the exceptionally large *Sabatinca delobeli* group (Fig. 16) from New Caledonia) and predominately diurnal moths with diverse metallic-coloured forewing patterns (Figs 15-22). Most adult micropterigids eat pollen, but some *Sabatinca* species are known to feed on fern spores (G.W. Gibbs, personal communication). The larvae are browsers on bryophytes (most of the known members of the *Sabatinca* group) or on the lower parts of grasses and other flowering plants as well as on decaying plant material *(Micropterix)* (Lorenz 1961, Carter & Dugdale 1982, Davis in press).

The phylogenetic key position of the Micropterigidae has long been recognized and several morphological observations on these moths have been reported. There is no recent comprehensive account of the family, but references to the principal previous works on systematics and adult skeletomuscular structure are given in *7, 12, 14* and *16*. Further morphological studies have dealt with pterothoracic structure (Mickoleit 1969, Sharplin 1963, 1964), cephalic nerve centres and eyes (Buxton 1917, Ehnbom 1948), mouthpart sensilla (Chauvin & Faucheux 1981), visceral anatomy (Mortimer 1965, Petersen 1900, Richards 1963), chorion structure (Chauvin & Chauvin 1980), embryology (Ando & Kobayashi 1978, Kobayashi & Ando 1981, 1982) and postembryonic stages (Davis in press, Hinton 1958, Lorenz 1961, Tillyard 1923, Yasuda 1962). The embryological studies in particular appear to be of considerable potential im-

portance in a phylogenetic context, but lack of comparative data on the other non-glossatan suborders so far precludes that precise inferences can be made from them.

As delimited now, after the transfer of *Heterobathmia* to a family of its own *(13)*, the family Micropterigidae is identical with the taxon denoted as subfamily Micropteriginae in *7*. The following traits can at present be considered autapomorphic of the ground plan of this taxon:

27. *Presence of antennal "ascoids"*[5] *)* (*7*: 127-128).

28. *Labrum extensively desclerotized* (*7*: 128).

29. *Mandibles asymmetrical, incisor cusps present only apically on left mandible* (*7*: 128).

30. *Pronotum with anterolateral processes and enclosing a pair of unsclerotized areas* (*7*: 128).

31. *Phallus with close-set radial folds around the gonopore* (*14*: 100).

32. *Antetior tentorial pits in larva situated close to antennal base* (Hinton 1958, see also footnote 10, p. 167).

33. *Larva with median seta on frontoclypeus* (Davis in press).

34. *Larval thoracic legs with at most four segments, the subterminal one being presumably a tibiotarsus* (*13*: 117).

35. *Larval prothorax with row of supernumary setae* (Davis in press).

36. *Larval abdomen without SD setae* (J.S. Dugdale, personal communication). Since the SD series is present in caddisfly larvae (Hasenfuss 1973) they must be attributed to the ground plan of the Amphiesmenoptera.

As far as present knowledge goes, the preceding traits are unique among the lowest Lepidoptera. However, there are several other derived features which may be considered autapomorphies of the zeuglopteran ground plan; these features are also encountered also in other primitive moths, but according to the phylo-

genetic model proposed here (chapter four) they must have been evolved independently twice (or more times).

There are at least two derived features which I believe have been evolved independently in the Zeugloptera and all other Lepidoptera except the Aglossata:

37. *Absence of a separate vein M4 in both wing pairs* (see p. 149 and *7*: 115-116).

38. *Absence of true "spurs" on fore tibia.* In the Aglossata there is an apical spur on the fore tibia; this is interpreted as a plesiomorphy (*7*: 115).

The Zeugloptera furthermore differ from the Aglossata (see later) in possessing the following four specializations which are also characteristic of the glossatan ground plan; the states of these characters in the Heterobathmiina remain unknown.

39. *"Outer tergal remotor" of mesocoxa lacking* (see p. 150 above).

40. *Follicles in testes small, closely appressed* (Petersen 1900, *18*; but see also chapter four).

41. *Male genital ducts with only one pair of accessory glands.* The interpretation of the double gland complement in the Aglossata as a primitive trait must be considered tentative; two gland pairs are recorded from some caddisflies, but whether they can reasonably be ascribed to the trichopteran and amphiesmenopteran ground plans are uncertain *(18)*.

42. *Few (five or fewer) ovarioles per ovary* (Petersen 1900; higher figures in some Heteroneura-Incurvariina are surely secondary specializations).

43. *Fewer than five abdominal ganglionic masses* (*9*; see also character 23).

The following six characters have previously (*7*: 112-115) been interpreted as synapomorphies of Micropterigidae (as here delimited) and *Heterobathmia*, but after the discovery of the immature stages of the latter this interpretation is no longer upheld. The traits in question are now *(13)* believed to be parallelisms, but it is not excluded that 44-45 could be symplesiomorphies (see also p. 146-147).

44. *Epipharynx with asymmetrical armature of sclerites and with medial bundle of bristles.*

45. *Infrabuccal pouch a "triturating basket".*

46. *Labial palps shortened.*

47. *Mesotibial spurs absent.*

48. *Male venter VIII more or less desclerotized medially.*

49. *Female segments VIII and IX without apophyses.*

The Zeuglopteran larvae known have at most six stemmata. The specialization:

50. *Larva with fewer than seven stemmata,* is believed to have evolved independently in the Zeugloptera, Aglossata and Glossata *(17)*. The same is true of another larval specialization, viz:

51. *Larval trochanter not large, bipartite and fully distinct from femur (13).*

The specialization:

52. *Malpighian tubules grouped into two bundles each discharging through a common duct* must have been evolved independently in the Zeugloptera (Petersen 1900; I have found the character also in the *Sabatinca* group, *19*) and the Neolepidoptera (or Myoglossata?) within the Glossata (Petersen 1900; I have found this character in the Exoporia-Mnesarchaeoidea also, *19*). The character state in the Heterobathmiina is not yet known.

Systematics. The problems inherent in the unravelling of the primary evolutionary lineages within the Micropterigidae (as here delimited) are discussed in *7* and *12*. There is possibly a sistergroup relationship between the predominantly West-palaearctic genus *Micropterix* (+ *Microptericina*; the latter has only very recently been separated from *Micropterix* and its distinctness awaits further evaluation) and all other micropterigid genera, the socalled *Sabatinca* group. The monobasic genera *Hypomartyria* (from Chile) and *Squamicornia* (from Ecuador), which are described in *12*, are the first genuine micropterigids to be reported from South America. There is some evidence for the assumption that the single North American genus *(Epimartyria)* together with the East Asian genera *(Paramartyria, Palaeomicroides* and *Neomicropteryx)* constitute a monophyletic entity (*16*:134, see also *14*:111) and the same may be true of *Squamicornia + Agrionympha* (S.Africa) + *Sabatinca* (Australian region) (*12*:

515, *16*: 36). *Hypomartyria* is phenetically overall close to the ground plan of the *Sabatinca* group, but the cladistic affinities of this genus remain uncertain. All suggestions concerning the systematics of the *Sabatinca* group must be considered tentative until more information of its constituent genera becomes available; particularly the very fragmentarily known Australian fauna of *Sabatinca* s.lat. appears to include taxa of considerable phylogenetic significance (see chapter 6 and also *12*: Addendum).

Morphological contributions. The head. The epipharyngeal armatures (see character 44) described from *Sabatinca* (Tillyard 1923) and *Micropterix* (Hannemann 1956) are very elaborate and probably close to the groundplan condition in the family; it is shown in *7* (pp. 112, 123) that the armature is much less elaborate in some northern hemisphere taxa of the *Sabatinca* group. A sclerotized rod on the right side of the epipharynx is shown (*7*: 112) to be located on the inner side of the procuticle. A distinct intercalary sclerite between scapus and pedicellus (character 3) is found in *Micropteryx* as well as some members of the *Sabatinca* group *(19)*. A costa on the basal piece of the maxilla is shown not to be transcardinal as hitherto believed; it separates the cardo from the basistipes (*7*: 117). The tentorial mandible adductor does occur in *Micropterix* (*19*, see p. 146). On the other hand I have been unable to confirm the presence of the muscle described by Hannemann (1956) as m.mentosalivarialis; this muscle cannot be of general occurrence in *M.calthella*. The recurrent nerve runs inside the cephalic aorta (Fig. 4, see character 10).

The thorax. The pattern of the mesopleural sutures is discussed in *7* (p. 120). The Zeugloptera are the only primitive Lepidoptera with a simple metafurcal stem (*7*:131; see p. 149). The setose sclerite below the metasubalare (character V) is fused with the epimeron in some *Sabatinca*-group taxa (*7*: 120). A hindwing/body lock is described from *Micropterix calthella* (*16*: 117). The primary and secondary metafurcal arms are united by ligaments (*16*: 118, 130; p. 149 above). The metepimeral muscle to the subalare is retained (*19*; see p. 150 above). The scales on the wing surface *(1, 12)* are of the "primitive type" and often have "herringbone crests"; the latter are usually lacking from the forewing scales of *Hypomartyria* (*12*: 517).

Visceral anatomy. There are four abdominal ganglionic masses in *Micropterix*, but only two in *Paramartyria (9)*. The perineural sheath around the abdominal connectives in *Micropterix* may consist of large cells, but its development is very variable (*8*: 127, 139). The muscle fibres in the ventral diaphragm do insert on the nerve cord (character XIV) contrary to the statements by Richards (1963). The mesothoracic

aorta is of the "tineoid type" *sensu* Hessel (1969) (*19*; see character 24).

Male genital segments. The skeleton of the male genital segments of *Paramartyria immaculatella* Issiki, 1931 is redescribed in *3*. Issiki's report of a "transtilla" is due to a misinterpretation of the gonopod base (which ventromedially carries a strong, posteriorly directed process) and the median plate. What Issiki described as a "thick membranous portion" near the middle of the phallus is actually the double-walled phallobase. The socalled "gnathos" probably belongs to venter X (further substantiation in *14*:109), its processes are not articulated.

The skeleton and musculature of the genital segments of *Epimartyria pardella* (Walsingham, 1880) are described in some detail in *14*. The anteroventrally produced segment IX ring and the bilobed tergum X are considered ground plan traits in the *Sabatinca* group. The gonopod base carries a strong dorsomedian process. The posterolateral sclerotizations of the anal cone are unusually strong and well demarcated, the venter X plates are simple and weakly sclerotized. The phallus consists of a double-walled phallobase and an aedeagus which is divided into a dorsal and a ventral branch; the gonopore is located distally on the latter. A section of the ejaculatory duct is anchored to the inner wall of the phallobase. Fibres from a VIII/IX dorsolongitudinal muscle occasionally insert in the gonopod. There are no muscles from the segment IX ring to the gonopod; such muscles are lacking also in *Paramartyria*, but they do pertain to the ground plan of the *Sabatinca* group. Gonopod adduction is apparently performed through contraction of a median muscle which inserts on the median plate between the gonopod bases. A comparison is made in *14* between the genital musculature in *Epimartyria, Micropterix* and *Eriocrania*.

The pregenital abdomen. Article *16* is devoted to a treatment of the skeletomuscular system and chordotonal organs in the pregenital abdomen of *Micropterix calthella*; the diversity in the skeletal structure of this body region in the *Sabatinca* group is briefly outlined, and an account is given of the sternum V gland which in the Zeugloptera is confined to the *Sabatinca* group. The morphological thoracoabdominal boundary is discussed; see the notes on character V above. Specializations in the structure of dorsum I have been mentioned previously (characters 18 and 19); a large chordotonal organ between the secondary arm of the metafurca and the lateral lobe of tergum I is believed to register movements of II + following segments. *Micropterix* males have a pair of very powerful, oblique muscles in dorsum I; these muscles, which probably perform a twisting of the abdomen during copulation, have not been found in members of the *Sabatinca* group. The

presence of a distinct sternum I is undoubtedly plesiomorphic (p. 151), but no muscles originate on this sclerite; the "windows" in the anterior part of sternum II may be plesiomorphic too. The body-wall musculature of the pregenital abdomen exhibits considerable intraspecific variability. Sometimes the adult moth possesses supernumerary muscles interpreted as persisting pupal muscles; the socalled "tuberculate plates" (see also *6*: 277-278) are insertion areas of such muscles. All spiracles have intrinsic occlusor muscles. Spiracle I has an extrinsic (ventral) dilator muscle, which arises on the secondary arm of the metafurca; the following spiracles are devoid of dilator muscles or ligaments. The pleural chordotonal organs in II and following segments have been mentioned above (p. 151). The sternum V gland cells (character XI) are situated on the saccular reservoir; this is interpreted as a plesiomorphy. In some genera *(Sabatinca* and, presumably, *Agrionympha* and *Squamicornia)* the sternal protuberance bearing the gland orifice is set with long piliform scales; this arrangement is suggestive of a pheromone "sender". In the Nearctic/East Asian genera the orifice is located on a non-elevated sternal area devoid of specialized vestiture. Both conditions are interpreted as deviations from the ground plan and hence as evidence for the monophyly of the two genus groups.

The respiratory system. The respiratory system of *Micropterix calthella* is described in *15*. The atrium of the first thoracic spiracle is T-shaped in cross section and can be occluded by contraction of muscle fibres which extend between the dorsal and ventral wall on both the anterior and posterior side. The second thoracic spiracle is of the specialized structure mentioned above, character 17. The functional spiracles on abdominal segments I-VII all have a "closing bow" and a "closing lever". A dorsal and ventral tracheal trunk extend into the head from the first spiracle. The mouthparts and antennae are supplied from the ventral trunk; there is no connection between the branches of the two trunks. A single series of connectives unites the spiracles of each side. A ventral commissural trachea is present in both segments of the pterothorax but is lacking in the prothorax. In each pterothoracic segment an anterior and a posterior tracheal "arch" give off branches to the wings, and the arch trunks anastomose with each other on their downwards course into the leg. The wing tracheation is much reduced. The anterior and posterior tracheal stem of each wing are independent of each other. In the abdomen a dorsal commissure is present in segment VIII; ventral abdominal commissures are lacking in *Micropterix* but they do occur in other micropterigids. The tracheal supply of the genital segments partly originates in segment VII. Air sacs have been found only in the tibiae. Some phylogenetic aspects of the tracheal con-

figuration in holometabolan insects are discussed in *15*.

Larval thoracic legs. Hinton's (1958) interpretation of the thoracic legs in micropterigids is briefly discussed in *13* (p. 117-118); it is suggested that the four segments, which sometimes can be recognized, are the coxa, trochanter + femur, tibia + tarsus and pretarsus, respectively.

Suborder Aglossata

Generalities and groundplan apomorphies. The single family of the suborder, the Agathiphagidae ("kauri moths"), contains only the genus *Agathiphaga* with two, structurally very similar species described from the Southwest Pacific some thirty years ago. The adult moths (Fig. 23) are nocturnal, small to mediumsized and superficially very similar to "typical" caddisflies. Only very few adult specimens have been found in nature. Examination of such individuals have not so far yielded any evidence as to whether the moths feed at all; it should be noted, however, that although the mandibles are rather large and have a distinct basal articulation (and a very powerful musculature) they are devoid of genuine incisivus cusps and are probably incapable of biting *(19)*; they are used, of course, for moving the huge pupal mandibles (see *13*: fig. 35) during the pharate phase. The apodous larvae are miners in seeds of kauri pines, *Agathis* (Araucariaceae). The very limited previous knowledge of the bionomics, structure and taxonomy of *Agathiphaga* largely came from Dumbleton's pioneer study of the genus (1952), as well as from observations by Common (1970, 1973) and Robinson & Tuck (1976).

Autapomorphies in the aglossatan ground plan include, e.g., the lack of ocelli, the structure of the sternum V gland in the male (*16*: 134) and the lack of this gland in the female, the presence of apophyses on tergum *and* sternum VIII in the female, some details in the male genital apparatus *(18)* and a number of regressive traits in the endophagous larva *(17)*. If the elaborate epipharyngeal armature and the strong, regularly arranged spines in the infrabuccal pouch in

the Zeugloptera and Heterobathmiina are indeed symplesiomorphies (see. p. 146-147 and characters 44-45 above), then the absence of these traits in the Aglossata *(19)* is most likely autopomorphic too (and paralleled in the Glossata).

The Aglossata share with the Heterobathmiina and primitive Glossata a suite of characters, which with variable degree of certainty are interpreted as apomorphies (discussion/references in *13*):

53. Paraglossae lost.

54. Stem of metafurca with anterior process.

55. Ductus spermathecae with thinwalled and thickwalled compartments.

56. Pupal mandible hypertrophied, angularly bent.

57. Larval corporotentorium slender.

58. Medial labral retractors in larva lost.

59. Larva with only one maxillary endite lobe (probably the galea).

60. Larva with metathoracic spiracle nonfunctional.

61. Cranial flexor of dististipes in larva lost.

62. Larva with dorsoventral cranial muscle laterally spanning the foramen magnum. The absence of this noteworthy specialization in the Zeugloptera has only very recently been confirmed *(17)*.

Another suite of more or less evident apomorphies are also shared with the Heterobathmiina, but do not pertain to the glossatan ground plan (discussion/references in *13*):

63. Anterior tentorial arms fused into a Y-shaped formation.

64. Postlabium posteriorly widened.

65. Metepisternal pre- and paracoxal sutures anastomosing below anapleural cleft.

66. Lateral process from tergum I indistinct.

67. Male with phallotheca strongly developed, entirely enclosing aedeagus.

68. Pupal mandible with strong subapical tooth on lower surface.

69. Labral compressors in larva lost.

70. Intrinsic maxillary muscles in larva lost.

71. Dorsal postcerebral dilators of pharynx in larva lost.

Morphological contributions. Successful rearing of *Agathiphaga vitiensis* in the British Museum (Natural History) (Robinson & Tuck 1976) led to the procurement of Bouin-fixed adult moths, suitable for study of the internal structure; a few of the field-collected moth specimens have been fixed also. Detailed studies of the larval anatomy have been made possible by the finding, in 1979, of non-diapausing, non-histolyzed mature larvae *(17)*. Investigations on the male genitalia *(18)* and the larval head *(17)* are now completed, and preliminary observations have been made on several other aspects of the internal structure of these insects.

The head exhibits characters I, 1-10, 53 and 63-65. The epipharynx is simple and the infrabuccal pouch (Fig. 3) is not armed as a "triturating basket". The antennae are devoid of sensilla auricillica *(13:* 119). As in the Zeugloptera the basal maxillary piece consists of a cardo and a basistipes separated by a costa (7: 117-118). The distal lobe of the galea is somewhat larger than in the Zeugloptera, but this is perhaps a plesiomorphic trait; in any case the aglossatan galea lobe (Fig. 5) is strikingly similar to the maxillary endite lobe in the primitive caddisfly genus *Rhyacophila*; according to Klemm (1966) the caddisfly lobe is the lacinia, but this interpretation is questionable (see also Denis & Bitsch 1973). The musculature of the mouth parts *(19)* is almost as primitive as that of the Zeugloptera (described by Hannemann, 1956). It includes a slender tentorial adductor of the mandible (Fig. 8, see also p. 146 above), cranial muscles of the prelabium as well as the homologue of the prelabial flexor glossae (but not of the flexor paraglossae). The tritocerebral commissure runs above the ventral dilator of the cibarium (Fig. 11).

The thorax exhibits characters II-X, 11-16, 54 and 65. The primary and secondary metafurcal arms are united by ligaments *(16:* 26), the pterothoracic tergo-trochantinal muscles have retained the primitive ventral insertion, the metepimeral muscle to the subalare (Fig. 9) is retained and so is the "outer tergal remotor" of the mesocoxa (Figs 6-7) (see p. 150 above).

The abdomen exhibits characters XI-XII, 18, 20-22. The lateral lobe of tergum I (character 19) is indistinct, but probably secondarily so; it may be noted that the cuticle of Agathiphaga on the whole is rather weakly melanized. In the sternum V gland (present in males only) the secretory section is a long, twined tube *(16:* 134); this condition is unique in primitive Amphiesmenoptera, as far as known. The highly complex male genitalia are described in some detail in *18*. Sternum VIII is anteriorly produced into blunt paired apophyses and posteriorly into a tongueshaped median lobe. Segment IX is a complete ring, very short in the dorsal and ventral midlines; its anterolateral lobes are largely apodemal. The long and curved gonopod con-

sists of a single piece. There is no median sclerite between the gonopod bases, but an open, softwalled "subgenital crypt" below the entrance of the phallocrypt may be homologous with the "median plate" in other primitive homoneurous moths. Tergum X bears a pair of broad "superior lobes" and the postgenital complex terminates in a medially indented, partly sclerotized "terminal lobe" above the eversible perianal area. The roof of the posterior part of the genital chamber bears a median aggregation of cuticular spines (the "spiny plate") and a pair of smooth lateral sclerotizations ("presocii") tentatively attributed to venter X; a pair of setose sclerites ("socii") are tentatively attributed to the paraprocts. The area bearing the spiny plate and presocii may in repose be folded down behind the phallus, thereby closing the phallocrypt. The phallus comprises a tubular phallotheca and an eversible aedeagus; the thick basal margin of the phallotheca is posteriorly expanded and forms the floor of the greater part of the phallocrypt; there is no ventral aedeagal branch. The musculature comprises two IX/X muscles, a segment IX muscle inserting on the subgenital crypt, phallic pro- and retractors (the former originating in the gonopod), intrinsic phallic muscles, a single segment IX muscle (adductor) of the gonopod and five intrinsic muscles of the postgenital complex. Each testis comprises four large, separate follicles. The spermatozoa do not remain grouped in discrete bundles in the vas deferens. Seminal vesicles are located on the vasa deferentia close to the testes and are doubtfully homologous with the vesicles in other Lepidoptera. The unpaired ejaculatory duct is very short. There are two pairs of tubular accessory glands.

The visceral anatomy exhibits characters XIV and 23-24. Five ganglionic masses are present in the abdominal nerve cord *(9)* and the connective sheath may have conspicuous dorsal thickenings which appear to be largely cellular (*8:* 127, 139). The stomodaeal crop (Fig. 12) is large (see p.152) whereas the mesenteron is short; the six malpighian tubules discharge separately into the gut. The ovariole number in female *Agathiphaga* is far greater than in any other examined Lepidoptera; a count from serial sections of a single ovary yielded 45 ovarioles *(19)*.

The larval head is described in some detail in *17*. The head capsule has a complete hypostomal bridge, but no hypostomal ridges. Adfrontal ridges and distinct ecdysial lines are absent. There are two vestigial stemmata (without lenses) on each side. The antenna is one-segmented. All "typical lepidopteran" head setae have been identified. The corporotentorium is very slender, dorsal tentorial arms are present. Intrinsic labral muscles are lacking. The mandible has retained a tentorial muscle. The maxilla is without a discrete cardo and has but a single endite lobe; intrinsic maxillary

muscles and the "cranial flexor of the dististipes" are lacking. The postlabium is undivided and without setae, the labial palp is one-segmented and the lateral prelabio-hypopharyngeal sclerotization is continued into an oral arm. Some of the ventral pharyngeal dilators arise on the tentorium; mouth-angle retractors and dorsal postcerebral pharynx dilator are absent. The two brain lobes have almost parallel long axes and are united by a narrow (almost pure neuropile) bridge. The corpora cardiaca and c. allata are contiguous. In front of the retrocerebral complex the aorta is an open gutter.

Suborder Heterobathmiina

The single family of the suborder, the Heterobathmiidae, contains only the recently discovered genus *Heterobathmia*, which occurs in temperate South America. Less than ten *Heterobathmia* species are known and only two species are at present named. Heterobathmiids are small, diurnal moths, some of the species being superficially strikingly similar to certain Glossata-Eriocraniidae; examples are illustrated in *7* and in Fig. 24. They may be found on flowering *Nothofagus* where they presumably eat pollen. The larvae are leaf miners in deciduous *Nothofagus*. *Heterobathmia* was described *(7)* in the Zeugloptera-Micropterigidae (as a separate subfamily), but after the subsequent discovery of the immature stages it was realized that this systematic placing cannot reasonably be upheld; a separate suborder has consequently been erected for these moths *(13)*. An account of the skeletal structure of adult heterobathmiids is given in *7*, and the larval and pupal structure is outlined in *13*, in which also the available knowledge on the bionomics of the family is presented.

Presumed autapomorphies of adult heterobathmiids comprise *(7)* the absence of a costa between the cardo and the basistipes, the shape of the proximal prelabial sclerite as well as of the laterocervicale, the pro-katepisternum and the profurcal arm, the fusion of the metepimeron and the setose sclerite behind the subalare, the unforked veins Sc and R in the forewing, the proximally forked vein CuP ("E"), the structure of the obverse surface of the forewing scales, and details in the genital structure of

both sexes. Characters 44-49 have presumably been evolved independently in the Zeugloptera and the Heterobathmiina (if 44-45 are not symplesiomorphies). As mentioned in the Aglossata section above, characters 53-62 are shared by the Aglossata, Heterobathmiina and Glossata, whereas characters 63-71 are shared by the two firstmentioned suborders only. However, the Heterobathmiina also possess a series of presumedly derived traits which are absent from Zeugloptera and Aglossata, but which do occur in the ground plan of the Glossata (discussion/references in *13*):

72. Antennae with sensilla auricillica.

73. Crossvein Sc-R lost.

74. Pupal mandibles with coarse apical teeth.

75. Larval head with adfrontal ridges.

76. Larval hypostoma unsclerotized in middle.

77. Larval head with hypostomal ridges.

The abovementioned features have been found particularly important for the assessment of heterobathmiine affinities. The following traits are also of particular interest for one reason or another: The antennal intercalary sclerite is indistinct, presumably secondarily reduced (see character 3); the male genital segment has a separate dorsal and ventral sclerotization (see character XIII); the male postgenital complex bears "spine plates" reminiscent of the "spiny plate" in the Aglossata *(18)*; the female postabdomen does not form an eversible oviscapt and the anus is separate from the gonopore (see p. 151); the larva is more primitive than any other known caterpillar in having seven stemmata and a large, bipartite trochanter (see characters 50-51). As in the preceding suborders the imaginal mandible has a distinct articulation with the head capsule, the maxilla has an unspecialized galea and a sclerotized lacinia lobe, the tritocerebral commissure is "free" (*13:* 120), the pupal anteclypeus is setose and well demarcated, and the larva has no "spinneret".

As mentioned in *13* an extensive and well preserved material of *Heterobathmia* was procured by O. Karsholt and E.S. Nielsen in 1981-

82. Detailed studies of the internal structure of these insects and descriptions of the new taxa will be made by E.S. Nielsen and the present author in the foreseeable future.

Suborder Glossata

Generalities and groundplan apomorphies. The suborder Glossata, then, comprises all the remaining Lepidoptera. According to present knowledge the glossatans can be grouped into four higher taxa which in a formal classification may be ranked as infraorders: Dacnonypha, Neopseustina, Exoporia, and Heteroneura (= Frenatae). The following traits are considered to be autapomorphic of the ground plan of the Glossata:

78. *Mandible non-functional after pupal/ adult ecdysis, without genuine articulation basally (and often strongly reduced).* See, e.g., Kristensen (1968).

79. *Maxilla devoid of sclerotized lacinia.* I have previously (Kristensen 1968) interpreted a membranous fold on the inner side of the maxillary base in the Dacnonypha-Eriocraniidae as a lacinia vestige; the cranial lacinia flexor muscle is also retained in these moths. However, a sclerotized distal lobe of the lacinia is absent in the Glossata whereas it has been retained in the other suborders (see also chapter four).

80. *Maxillary galeae forming a proboscis, spirally coiled in repose.* The classical and very convincing autapomorphy of the Glossata. The proboscis has been secondarily reduced on numerous occasions within the Exoporia and Heteroneura (see also chapter four).

81. *Prelabio-hypopharyngeal lobe narrow, hypopharyngeal base without infrabuccal pouch.* The lobe is actually distinct only in the lowest infraorders, i.e., Dacnonypha and Neopseustina (Kristensen 1968, Davis 1975, 1978).

82. *Tritocerebral commissure incorporated into suboesophageal ganglionic mass.* This derived trait has been found in the Dacnonypha-Eriocraniidae (Kristensen 1968) as well as Exoporia and Heteroneura (Ehnbom 1948) and can

surely be attributed to the ground plan of the Glossata.

83. *Pupal antecypeus non-setose and not distinctly demarcated.* This condition has been recorded from the lowest Glossatan grades i.e. the taxa with decticous pupae (Eriocraniidae, Acanthopteroctetidae; Davis 1978 and in press) and it is tentatively attributed to the glossatan ground plan; see *13.*

84. *Larva with articulated "spinneret" on the apex of the prelabio-hypopharyngeal lobe.* See, e.g., Hinton (1958).

As mentioned in the preceding sections the ground plan of the Glossata exhibits several relatively derived traits which also occur, as parallelisms or synapomorphies (see chapter four) in one or more of the non-glossatan (or "preglossatan") suborders, viz., the characters 37-43, 50-51, 53-62, 72-77. Particular reservations must be made concerning the larval leg character (no. 51), since the Dacnonypha-Eriocraniidae have apodous larvae, the larval legs of Dacnonypha-Acanthopteroctetidae have not been analyzed in details yet, and the larvae of Dacnonypha-Lophocoronidae as well as of the Neopseustina are unknown altogether.

The development of the coilable proboscis (an unusual piece of animal mechanics, see Bänziger 1971 and Hepburn 1971) was undoubtedly an important event in the evolution of the Lepidoptera *(10).* It is well known that the food channel is usually the space enclosed between the concave medial walls of the two galeae; however, an early "evolutionary experiment" in which a separate suction tube is formed in each galea has now been reported from the Neopseustina *(11).*

As is well known, nectar-feeding is very widespread among higher Lepidoptera and the co-evolution of long moth proboscises and deep flower corollas is a classical textbook story. However, the evolutionary origin of the lepidopteran proboscis is not necessarily related to the origin of floral nectaries, indeed it may well have predated the latter. The lowest glossatan moths whose adult habits have been observed

are not nectar feeders, and even in members of the higher grades the proboscis is used for the uptake of a variety of fluid nutrients and, of course, water.

Glossatan infraorders and their interrelationships

Infraorder Dacnonypha

The taxon Dacnonypha was erected (as a suborder) by Hinton (1946a) to accommodate the families Eriocraniidae and (tentatively) the Mnesarchaeidae; the latter has subsequently been transferred to the Exoporia. At present two other families besides the Eriocraniidae are included in the Dacnonypha, viz., the Acanthopteroctetidae and the Lophocoronidae. It must be stressed, however, that no synapomorphies of these three taxa have yet been established, and the arrangement is therefore only tentative.

Family Eriocraniidae. This is a long-established, exclusively Holarctic family comprising some twenty described species. Eriocraniids are small, predominantly diurnal moths with iridescent forewing patterns; some characteristic species are shown in Figs 25-28. They do not frequent flowers but they do use the proboscis for drinking water and I have also observed them to suck up sap exuding from injured leaf buds *(19).* The larvae are apodous leafminers, almost exclusively associated with trees of the order Fagales. An excellent account of the family, including a revision of the Nearctic taxa, has recently been given by Davis (1978).

Morhphological contributions. The first ultrastructural observations on eriocraniid wing scales are presented in *1.* The wing-surface scales were found to be of the "primitive type", whereas "normal type" scales were identified along the wing margins (see also notes pertaining to character 16).

The skeleto-muscular anatomy of the male genitalia in some Palaearctic eriocraniids is described in *2* and considered in comparative contexts in *14* and *18.* Segment IX is largely exposed behind the pregenital segments; paired apophyses on its anterior margin accommodate the origins of the phallic retractors. The gonopods are believed to be fragmented into a proximal sclerotization (bp in *2*) which is synscleritous with

the segment IX ring and the distal gonopod proper ("valve"); the latter is very short and only in *Dyseriocrania* [6]) are muscles inserted on it. A sclerotized median plate (Davis' "juxta") supporting the intromittent organ is considered, on the base of its musculature, to contain elements homologous with (at least part of) the "median plate" in Zeugloptera ("Zwischenstück" of Hannemann, 1957) and Heterobathmiina; it may also contain elements homologous with the phallotheca in Aglossata and Heterobathmiina *(18).* The intromittent organ has a dorsal and a ventral branch apparently comparable with the dorsal and ventral aedeagal branches of the Zeuglopteran *Epimartyria (14).* The phallic protractor originates caudally on segment IX, in *Dyseriocrania* partly inside the "valve". Tergum X is bilobed. There are postgenital muscles interpreted as X dorsoventrals and X/XI ventrolongitudinals respectively, and there are segmental sets of dorsal diaphragm fibres in IX and X.

In all female eriocraniids examined there are only three ganglionic masses in the abdomen, whereas in most eriocraniid males there are four (the "typical" lepidopterous number). However, male *Eriocrania haworthi* Bradley, 1966 have three masses, and this pattern has also been observed (as an individual abnormality) in a male *Dyseriocrania subpurpurella* (Haworth, 1828) *(9).* The ventral diaphragm is strongly reduced; it consists of a series of segmental pairs of slender muscle fibres. The abdominal nerve cord sheath is tenuous *(8).*

Family Lophocoronidae. This family comprises only the small Australian genus *Lophocorona.* Lophocoronids are small, predominately nocturnal moths; the most frequently collected species is illustrated in Fig. 29. The substantial original account by Common (1973, summarized 1974) presents all yet available knowledge of lophocoronid moths. Female specimens and the immature stages still await discovery and nothing is known of the internal anatomy of the male moths. The assignment of the Lophocoronidae to the Dacnonypha is based on symplesiomorphies exclusively.

Family Acanthopteroctetidae. Another very small family. The West-Nearctic genus *Acanthopteroctetes* was described in "Micropterygidae-Eriocraninae" but appropriately transferred to a family of its own by Davis (1978) who pre-

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[6]) In *2 Dyseriocrania* is treated as a subgenus of *Eriocrania.*

sented a detailed morphological/taxonomic treatment of the few specimens known by that year. Acanthopteroctetids are small, probably predominately diurnal moths, and the few species exhibit a remarkable diversity in forewing pattern; the largest described species is illustrated in Fig. 30. Nothing is known about the internal anatomy of these moths. Davis listed a suite of presumed synapomorphies of Eriocraniidae and Acanthopteroctetidae, but these must be weighted against the evidence from the presence in the latter family of "normal type" (i.e. hollow) wing-surface scales; this is suggestive of a closer phylogenetic relationship to the Myoglossata (see below). On the other hand speculations (Davis 1978: 32; *10*: 301) that the acanthopteroctetid pupae would be adecticous have been proven wrong: The life history of one of the *Acanthopteroctetes* species (*A.unifascia* Davis, 1978) has very recently been elucidated by D. Frack, and descriptions of the pupae and larvae (leafminers on Rhamnaceae: *Ceanothus*) are forthcoming (Davis in press).

Infraorders Neopseustina + Exoporia + Heteroneura: The Myoglossata

The proboscis of Dacnonypha-Eriocraniidae is devoid of an intrinsic musculature; nothing is known about the internal proboscis structure in the two other families currently assigned to the Dacnonypha. The other glossatan infraorders share the synapomorphy of having:

85. *Proboscis with an intrinsic musculature.* The simple arrangement of this musculature in the non-ditrysian taxa is described in *10*. The name Myoglossata has been introduced *(10)* for the entity characterized by apomorphy 85. The Myoglossata possess another apomorphy, viz.,

86. *Presence of "normal type" wing-surface scales.* In some families in the Exoporia "primitive type" scales occur together with "normal type" scales on the wing surface; this condition is also of frequent occurrence in primitive Heteroneura (E.S. Nielsen, pers. communication) and probably primitive in the Myoglossata (see also 6: 288).

As mentioned above the Acanthopteroctetidae also have "normal type" wing-surface scales. It remains an open question whether this family actually belongs in the Myoglossata (in which case the alleged eriocraniid/acanthopteroctetid synapomorphies must be parallelisms or even symplesiomorphies) or whether the "normal type" of wing-surface scales have twice evolved independently.

It is tempting to speculate that the heat insulating effects of the hollow "normal type" wing scales has been an important factor for the success of the higher Lepidoptera as strong fliers even at low temperatures (nocturnal activity!) and with wing surface/body volume proportions which are unusually high for pterygote insects.

Within the Myoglossata there is apparently a sistergroup relationship between the Neopseustina and the Exoporia + Heteroneura.

Infraorder Neopseustina

The Neopseustina (Davis & Nielsen, 1980) comprise the single family Neopseustidae with less than a dozen described species from southern Asia and southern South America. Neopseustids are mediumsized moths; they are predominately nocturnal, but diurnal swarming has been recorded from *Synempora*. In *Archepiolus* and *Synempora* (Fig. 31) the wings have rather commonplace proportions and are densely scaled; on the other hand the members of *Neopseustis* (Fig. 33) and *Apoplania* (Fig. 32) are probably the most odd-looking homoneurous moths with their broad and semitransparent (the scales are narrow and widely spaced) wings. Neopseustid morphology, taxonomy and behaviour has been fully reviewed by Davis (1975) and Davis & Nielsen (1980 and in press). Most neopseustid species are known from very few specimens and material suited for anatomical study has only very recently become available *(11)*. The immature stages remain inknown.

Morphological contributions. The neopseustid moth examined in *10 (Synempora)* has well developed mandibular muscles and it is therefore likely that the pupa is decticous. The abovmentioned curious double-tube proboscis is described in *11*. There are four abdominal

ganglionic masses, the interganglionic connectives are partly separate (interpreted as an autapomorphic character reversal) and have a tenuous sheath; there is no trace of a ventral diaphragm *(8,9)*.

Infraorders Exoporia + Heteroneura: The Neolepidoptera

There is good evidence that the Exoporia and the Heteroneura constitute together a monophyletic entity; the name Neolepidoptera is available for this taxon. Character 52 (see the Zeugloptera section above) and the following ten characters are possible synapomorphies of the two infraorders; it must be noted, however, that for characters 52, 87, 91, 94-96 the states in Neopseustina are unknown; some of these characters may eventually prove to be myoglossatan autapomorphies.

87. *Brain and suboesophageal ganglion broadly united to form a compact mass with a very narrow aperture for the stomodaeum and aorta.* This similarity between Hepialidae (Exoporia) and primitive Heteroneura was pointed out by Ehnbom (1948).

88. *Anterior notal wing process and first axillary of fore wing at least 1/50 of wing length.* A specialization noted in Hepialoidea (Exoporia) and primitive Heteroneura by Sharplin (1963, 1964).

89. *Hind wing median plates replaced by "cubital plates".* Another specialization noted in Hepialoidea and Heteroneura by Sharplin (1963, 1964).

90. *Free profurcal arm displaced laterally* (*5*: 14, but note also *7*: 119).

91. *Thoraco-abdominal boundary region specialized, with enlarged meta-laterophragmata and strong development of acrotergite I.* Brock (1971) has pointed to these similarities in the modifications of the "thoraco-abdominal articulation" in Hepialidae (Exoporia) and primitive Heteroneura, but his account is very summary and partly difficult to understand. A more extensive study of this body region in primitive Myoglossata is much needed.

92. *Muscle fibres of ventral diaphragm in abdominal segment II arising in regular succession*

over a considerable portion of the segment. This condition has been found in Hepialidae (Exoporia) and primitive Heteroneura *(8)*.

93. *Dorsal enlargement of sheath on abdominal interganglionic connectives, when present, largely a true connective tissue formation with copious extracellular material.* This character is discussed in *8*; further study of the sheath swelling in Aglossata is needed to establish whether this formation is in fact mainly cellular.

94. *Pupa adecticous* (Hinton 1946 a, b).

95. *Pupa obtect, with rows of spines on several abdominal segments* (Hinton 1946b). The spines on the pupal cuticle play an important role for the movement of the pharate adult insect out of the pupal shelter just prior to the final ecdysis.

96. *Larva with musculated, crochet-bearing prolegs on abdominal segments III-VI and X.* It is a subject of long-standing debate whether abdominal prolegs in larvae of holometabolan insects are derivatives of the primitive segmental limbs or purely secondary formations (see e.g. Hinton 1955, Matsuda 1976, Bitsch 1979). Among larvae of non-myoglossatan Lepidoptera only some Zeugloptera have abdominal prolegs; these are non-musculated, devoid of crochets and occur on segments I-VIII (Hinton 1955). There is no evidence that a complement of prolegs with the abovementioned distribution and structural characteristics was ever present outside the Neolepidoptera, and I consequently consider it an autapomorphy of this taxon. Note that this does not preclude the possibility that proleg development in Neolepidoptera is partly controlled by ancient "limb genes"; in any case they are borne on areas which would seem to comprise the limb base territories.

Infraorder Exoporia

The Exoporia comprise the superfamilies Mnesarchaeoidea and Hepialoidea, which share the following apomorphies (discussion/references in *6*).

97. *Female genitalia exoporian, without colleterial glands.*

98. *Dicondylous articulation of antennal base.*

99. *Scales on more or less extensive wing areas with secondary ridges* (see also *4*).

100. *Male genitalia without sclerotized tubular intromittent organ.*

(An alleged mnesarchaeoid/hepialoid synapomorphy in proboscis surface structure was later proved wrong; see Kristensen, 1979).

Superfamily Mnesarchaeoidea. Only the family Mnesarchaeidae with the single genus *Mnesarchaea* Meyrick, 1886 is included here[7]). *Mnesarchaea* contains less than ten species and is confined to New Zealand[8]). Mnesarchaeid moths are small and diurnal, they have a well developed proboscis and are known to drink water, but have not been observed in flowers (Gibbs, personal communication). The immature stages have been discovered only very recently (Gibbs 1979); the ground dwelling larvae are reminescent of minute hepialid caterpillars. The family was long associated taxonomically with the eriocranioid assemblage; its close relationships with the hepialoids only become clear through reassessments of the female genital configuration by Mutuura (1972) and, particularly, Dugdale (1974).

Superfamily Hepialoidea. Five families are at present recognized in the Hepialoidea, viz., Palaeosetidae (Australian/Oriental), Neotheoridae (S.American), Anomosetidae (Australian), Prototheoridae (S.African) and Hepialidae (cosmopolitan). Possible synapomorphies of these families are:

101. *Backwards displacement of posterior fork of radial sector, Rs3[9]) reaching termen, not costa* (6: 284).

102. *Reduction of maxillary appendages* (6: 285).

It is possible that the presence of a pair of

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[7]) *Nematocentropus*, originally described in the Mnesarchaeidae (see *6*: 282) is now known to be a neopseustid (see Davis & Nielsen 1980).

[8]) A mnesarchaeid-like moth from Siberian Cretaceous amber (Skalski 1979) awaits closer scrutiny.

[9]) Termed S3 in *6*, cp. footnote four.

small lateral processes on the pronotum can be ascribed to the hepialoid ground plan as a further apomorphy, but if so, the processes must have been lost independently on several occasions (*5*: 14). Whether a specialized sperm transport tract is generally present between the copulatory orifice and the ovipore awaits confirmation (6: 285).

The status and interrelationships of the hepialoid families are reviewed in *6* (p. 286-288). It is tentatively suggested that there is a sistergroup relationship between the Palaeosetidae and the remaining families, but it must be stressed that the family Palaeosetidae is itself of doubtful monophyly. Possible synapomorphies of the non-palaeosetid hepialoids are the presence of an inter-M crossvein (a character reversal) and a marked elongation of the intercalary plate between scapus and pedicellus. A key to the hepialoid families is presented in *5*.

Systematic and morphological contributions. The family Neotheoridae was described in *6* on the basis of *Neotheora chiloides* Kristensen, 1978, known from a single female specimen from Brazil (Matto Grosso). *N. chiloides* is a mediumsized moth with numerous autapomorphies (6: 292). Its proboscis is less reduced than that of other hepialoids, like anomosetids it has retained a layer of "primitive type" wing scales and like both anomosetids and prototheorids it has retained two pairs of metatibial spurs. The question of the sister group of Neotheoridae must remain open, since the distribution patterns of relevant derived characters suggest a variety of possible phylogenies in the Neotheoridae + Anomosetidae + Prototheoridae + Hepialidae group (6: 288-292); it is considered most likely, however, that the sistergroup of the new family is either the family Anomosetidae or the family Prototheoridae.

The family Anomosetidae was removed from synonymy with Prototheoridae in *6* (p. 287). Its single constituent species *Anomoses hylecoetes* Turner, 1916, is reviewed in *5* and new information on its integumental structure is presented. *Anomoses* is an overall primitive hepialoid taxon (*5*: 14-15); the large and distinctly separate tergal sclerotizations of IX and X in the male and the presence of a papilla spermathecae in the female are particularly noteworthy plesiomorphies.

A remarkable wing-scale specialization, the "second order ridge", which involves a longitudinal folding of the entire upper scale lamella (or both upper and lower lamellae), is described from hepialid moths in *4*.

Infraorder Heteroneura

The Heteroneura comprise the Incurvariina + Nepticulina + Tischeriina + Ditrysia (Nielsen, in press, provides an updated discussion of basic heteroneuran interrelationships). Several derived traits have been claimed to be characteristic of the ground plan of this entity (see Common 1975):

103. *Venation heteroneurous due to simplification of the hindwing Rs.* The classical diagnostic trait.

104. *Wingcoupling retinaculo-frenate and jugum reduced in males.* In the vast majority of the Heteroneura the female also has a specialized, reticulo-frenate type of wing coupling; see Braun 1919, 1924. Although not prominent the jugum remains distinctly discernible throughout the lower heteroneuran grades (Sharplin 1963, 1964).

105. *Fusion of anterolateral corners of prosternum with pleuron* (Brock 1971).

106. *Connection of second basalare to episternum loosened in both wingbearing segments* (Sharplin 1963, 1964).

107. *Forewing articulation specialized: Joint present at radius/medial plate junction and bending cuticle between second axillary sclerite and first median plate strongly reduced* (Sharplin 1963, 1964).

108. *Metaprescutal arm not discrete, probably fused with second basalare; insertion of metathoracic "third tergopleural muscle" (sensu Sharplin; it is the "Pleuralleiste-Subtegulamuskel" of Mickoleit, 1969) displaced to metaprescutum itself, intersegmental region, or mesolaterophragma* (Sharplin 1963, 1964).

109. *Sternum I sclerotization obliterated* (8: 144).

According to Brock (1971) further autapomorphies of the Heteroneura are the specialized "dorsal plates", patagia and parapatagia on the prothoracic dorsum. However, this character complex certainly needs reinvestigation throughout the lower Lepidoptera. According to the early survey by Schultz (1914) the patagia in some of the lower Ditrysia are elongate and have

a broad base; they thus would seem to be basically similar to the pronotal "warts" in homoneurous moths.

However, the monophyly of the Heteroneura is not entirely unproblematical: It can be argued that the separate copulatory and ovipository openings as well as the dorsal position of the oviduct (relative to the bursa copulatrix) in the Exoporia indicate that this taxon rather than one of the monotrysian heteroneuran groups is the sister group of the Ditrysia; this is the view of Dugdale (1974). Like Common (1975), I am inclined to favour the hypothesis of a monophyletic taxon Heteroneura as evidenced by the suite of characters just enumerated and hence to believe that the similarities in female genital structure in Exoporia and Ditrysia are parallelisms, but further inquiry into this problem is greatly needed (including i.a., a study of the morphogenesis of the female genitalia in monotrysian and exoporian moths). In any case, however, the monophyly of the taxa Neolepidoptera/Myoglossata appears to be well supported (characters 52, 85-96). Mutuura (1972) suggested that the somewhat similar piercing ovipositors in Eriocraniidae and Incurvariina indicate that the latter have been derived from an eriocranoid ancestor independently of other Neolepidoptera/Myoglossata, but this view has not gained acceptance (Common 1975, Davis 1978, *10*: 301). Indeed one might rather ask whether the piercing ovipositor was a groundplan trait of the Glossata; this would provide a simple explanation for the presence of this ovipositor type the Acanthopteroctetidae even if the latter prove not to be cladistically closely related to the Eriocraniidae.

Morphological contributions. The intrinsic proboscis musculature of Incurvariina and Nepticulina is shown in *10* to be as simple as that of the homoneurous Myoglossata. The absence of a discrete sternum I in the non-ditrysian Heteroneura is discussed in *8* (p. 144). Observations on the ventral diaphragm and abdominal nerve cord configuration of Incurvariina and Nepticulina are reported in *8* and *9*; some specializations present in Opostegidae (two ganglionic masses and a long, stout stem of the terminal nerves; close-set diaphragm

muscles which mostly extend across the nerve cord) are particularly noteworthy. The diaphragm pattern with several alae per segment, considered typical of Lepidoptera by Richards (1963) cannot even be ascribed to the ground plan of the Ditrysia.

4. THE QUESTION OF THE BASIC DICHOTOMIES IN LEPIDOPTERAN PHYLOGENY

Tentative phylogeny of Lepidopteran high-rank taxa

A tentative phylogenetic arrangement of the lepidopteran suborders and infraorders is shown in Fig. 13.

I have stated earlier that "there must have been a substantial amount of parallel evolution during the differentiation of the earliest lineages" (Kristensen 1981a: 414), and as noted in *13* this statement has since been confirmed to an unimagined degree by the discovery of the *Heterobathmia* immatures. The neat picture drawn by Hennig (1953, 1966) of "additive typogenesis" in early lepidopteran evolution is now severely blurred by numerous parallelisms/character reversals. No phylogeny of the order can be proposed which will obviate this problem.

The phylogenetic model proposed here is "conservative" in that it places the Zeugloptera as the sister group of all other Lepidoptera which are held together by the derived traits 53-62. Obviously, however, the alternative possibility that the basic dichotomy lies between the Aglossata and all other Lepidoptera also deserves serious attention. Surely the larger of the two *Agathiphaga* moths (*A.vitiensis,* see Fig. 22) is in general appearance more similar to a typical primitive caddisfly – and hence presumably to the last common ancestor of the two amphiesmenopteran orders – than any other extant moth; also the loss of the discrete vein M4 in the non-aglossatans is a kind of character to which at least many insect palaeontologists (which often have to base systematic decisions

exclusively on venational characters) would attribute considerable significance! Nevertheless, I am inclined to assume that the suite of derived characters (nos. 37-38 and perhaps nos. 39-43 also) at present known to be common to Zeugloptera and other non-aglossatans have been evolved independently twice, rather than to make this assumption for the abovementioned apomorphies shared by the non-zeuglopterans. Evidence from further character complexes is much needed.

The primary dichotomy within the non-zeuglopteran assemblage also remains most problematical. Are the Heterobathmiina the sister group of the Glossata (characters 37-38, 72-77 and perhaps 39-43) or the Aglossata (characters 63-71)? As expounded elsewhere (*13*: 15-16) the firstmentioned hypothesis is preferred at the moment, but again further inquiry into this matter is surely needed. Note, however, that acceptance of the second hypothesis would require additional parallelisms in characters 37-38 (and perhaps 39-43).

The "Gymnocera/Angiocera theory" of the primary dichotomy in the Lepidoptera

Friese in 1965 (published 1970) proposed a theory on early lepidopteran phylogeny which radically deviates from those discussed in the preceding section. According to this theory,the Hepialoidea are the sistergroup of all other Lepidoptera, and in the belief that one of the uniquely primitive features of the hepialoid moths is the absence of scales on the antennae Friese named the two entities suborder Gymnocera and suborder Angiocera respectively. Friese's theory has not gained acceptance (see Common 1975, Davis 1978, *6*: 282) but since it was developed with apparently sound application of the principles of phylogenetic systematics it does deserve some further comments (see Kristensen 1981a).

Initially it may be noted that Friese makes no mention at all of *Agathiphaga*; by 1965 this genus was still formally placed in the Micropterigidae although Hinton 1958 had stated that it

"belongs to the Eriocraniidae or a closely related family".

Obviously, Friese's theory requires on one hand discarding of the presumed synapomorphies of Hepialoids and other Neolepidoptera as well as of the autapomorphies of the successively higher taxa of non-zeuglopteran Lepidoptera, (i.e. of the characters 37-43, 50-62, 72-100) and on the other hand recognition of synapomorphies of all non-hepialoid Lepidoptera; indeed, Friese attempted to fulfill both requirements. However, among the characters of the first category Friese discussed only nos. 78-80, 59, 75 and 96, i.e., those considered by Hennig in 1953 to be synapomorphies of non-zeugloptera[10]), and his rejection of the significance of these characters appears entirely unconvincing to me. With respect to the imaginal mandible Friese's statement that "auch bei den Hepialiden und Eriocraniiden die Mandibeln ziemlich gut ausgebildet sind" conveys no appropriate description of the profound differences between the functional significance of the mandibles of the two groups, of which the former has adecticous and the latter decticous pupae (character 94). Friese's statement that the mouthparts of hepialids are of "laciniaten Typ" is without any foundation, and the statement that the hepialid galea is "noch in einer ursprünglichen Form erhalten" is similarly misleading: Whereas it it true that most hepialids have very small galea vestiges which *could* be interpreted as unmodified galeae, the members of the long-established small hepialoid families Anomosetidae and Prototheoridae (but also some members of the hepialid genus *Fraus* Walker, 1856 (syn. *Hectomanes* Meyrick, 1890) have rather long maxillary

lobes which surely have been evolved from a genuine proboscis through regression; in the recently described hepialoid family Neotheoridae the maxillary lobe is particularly long and its derivation from a functional proboscis appears very evident *(6).* Moreover, of course, the evidence of a sistergroup relationship between mnesarchaeoids and hepialoids is indirect evidence that the small size of the galeae in the latter is secondary. Friese's critique of the proleg character does not apply to a formulation as given above (no. 96) and his general remark on the low value of characters of immature stages because "bisher erst sehr wenige Larven von den ursprünglichen Lepidopteren-Familien bekannt und näher untersucht sind" was not even justified by 1965. Altogether I do consider that the characters 37-43, 50-62 and 72-100 provide strong evidence for a relatively subordinate position of the hepialoids in lepidopteran phylogeny.

What, then, of the series of characters Friese considered to be synapomorphies of non-hepialoid Lepidoptera? It included the following: (a) thoracic segments firmly united (against "separate" in hepialoids); (b) pronotum smaller relative to mesonotum, in dorsal view hidden by head capsule; (c) mesonotum with incomplete, weakly indicated mediolongitudinal suture; (d) wing coupling device with a frenulum; (e) non-exoporian female genitalia; (f) presence of female accessory (colleterial) glands; (g) presence of telescope-like "ovipositor"; (h) follicles of each testis appressed, enclosed in peritoneal capsule; (i) antennae scaled; and (j) less than five abdominal ganglia in adult. However, I find myself in disagreement with Friese concerning either facts or interpretations pertaining to these points: (a) I am not aware of any evidence which can support the claim that the thoracic segments in hepialoids are less firmly united than in other primitive Lepidoptera. (b) The pronotum in Aglossata and Heterobathmiina is distinctly larger relative to the mesonotum than is the *Micropterix* pronotum depicted by Friese; conditions in the two firstmentioned taxa are rather

[10]) Hennig (and hence Friese) mentioned one further, larval, character in this category, viz., the position of the anterior tentorial pit, which was said to be "nahe d. Clypeus" in Zeugloptera and "fern v. Clypeus" in non-zeuglopterans. However, the pit probably remains situated at what is morphologically the clypeal boundary, even if the postclypeus itself may not be distinctly delimited; this is the condition found in the Aglossata *(17).*

similar to those of a rhyacophiline caddisfly (see Schmid 1970) and therefore probably close to those of the ancestral amphiesmenopteran. Further investigations on thoracic proportions in the Zeugloptera are needed to establish whether pronotal reduction is another groundplan autapomorphy of this suborder. (c) Whether a complete longitudinal mesoscutal suture is primitive in the Lepidoptera remains an open question; the suture is complete in some *(19)* but not in all (Schmid 1970) rhyacophiline caddisflies. The suture is variably developed in primitive Lepidoptera, but its anterior portion is generally strong, and besides in hepialids I have found it fully developed also in heterobathmiids and mnesarchaeids, it is also complete in some Ditrysia (Weber 1924). (d) Frenulum bristles actually do occur in primitive hepialoids (6: 277, 287) but they are not distinctly differentiated from the costal hairs (*sensu* Braun 1919, 1924); there is every reason to believe that conditions in hepialoids are secondarily modified. The homology of the somewhat aberrant "frenulum" in mnesarchaeoids (Philpott 1922) needs reinvestigation. (e) The "outgroup criterion" conclusively shows that the monotrysian and not the exoporian female genital configuration is primitive in the Lepidoptera. Friese himself actually considered it most likely that the exoporian pattern was derived from a monotrysian one, so it is not at all clear in which way the character of the female genital opening should support his theory. (f) The presence of colleterial female glands is a plesiomorphic insect trait; the absence of these glands can straightforwardly be considered an autapomorphy of the Exoporia (character 97). (g) As discussed in chapter 2 the presence of a telescope-like "ovipositor" may be a plesiomorphy at the Lepidopteran level. Moreover, in the recently described hepialoid family Neotheoridae rather typical "anal papillae" (albeit without apophyses) are retained. (h) The free testes follicles certainly appear to represent a plesiomorphic condition, but in the light of the evidence on hepialoid relationships provided by other characters I would rather interpret them as a case of autapomorphic character reversal; in any case they are not unique among primitive Lepidoptera, since the Aglossata are now known to have very prominent, free follicles *(18)*. (i) Where unscaled antennae occur in hepialoids they are autapomorphic of smaller taxonomic groups; several hepialoids do have the antennae extensively scaled (6: 290) and this condition can certainly be ascribed to the ground plan of the superfamily. (j) As with character (h) this certainly appears to represent a plesiomorphic condition, but again I suppose that it is a case of character reversal. As suggested in 9 the high number of abdominal ganglia in adult hepialids (actually some hepialoids have as many as six masses) could be explained in terms of neoteny, i.e. as an autapomorphic arrest of the ganglionic concentration which usually takes place during metamorphosis.

5. CONCLUDING REMARKS

As outlined in the preceding chapter the distributional pattern of derived characters in the earliest differentiated lepidopteran lineages is not by far as "neat" as was believed a couple of decades ago. But certainly the pattern known today, with its intricate network of parallelisms/character reversals is no less interesting.

It is noteworthy how many of the most important discoveries of homoneurous moths have been reported since the middle of this century; Agathiphagidae in 1952, the primitive neopseustid *Nematocentropus* in 1965, the Lophocoronidae in 1973, S. American neopseustids in 1975 and 1980, the Neotheoridae in 1978, the Heterobathmiidae and mnesarchaeid immatures in 1979, S.American micropterigids in 1982, heterobathmiid immatures in 1983, and reports on acanthopteroctetid immatures are forthcoming. It can safely be assumed that further discoveries will fill some of the structural gaps between the presently known taxa — and, to be sure, con-

front us with unwieldy new character combinations! With respect to detailed comparative study on the internal structure of the lowest moths we are really still in an initial phase. However, adequately preserved material of representatives of important higher taxa has been rapidly accumulating within the last few years, and major advances in this field are to be expected within the next decade.

Considering the number of recent discoveries of new high-rank taxa within the lowest moth grades it appears not altogether unlikely that future search could disclose new extant taxa even at the ordinal level: A sister group of the hitherto known Lepidoptera, a sister group of the hitherto known Trichoptera, a sister group of the hitherto known Amphiesmenoptera. Attention should be drawn to the fact that such insects, as far as the adult stage is concerned, might be superficially exceedingly similar to primitive caddisflies: The few presently known imaginal autapomorphies of the order Trichoptera are notoriously inconspicuous. The suites of lepidopteran and amphiesmenopteran autapomorphies drawn up in chapter 2 will help assessing the affinities of new high-rank taxa in this section of the panorpid complex, and a detailed inquiry into the trichopteran ground plan is now very desirable.

6. APPENDIX: A SYNOPSIS OF THE FAMILIES AND GENERA OF NON-NEOLEPIDOPTERAN MOTHS

Nomenclature details, numbers of currently recognized species and distribution of the genera in the non-neolepidopteran moth families are presented; an asterisk denotes that I am aware of the existence of further, undescribed, species. The coloured illustrations, Figs 15-32, convey some impression of the diversity exhibited by the adult moths of this grade.

Zeugloptera: Micropterigidae Herrich-Schaeffer, 1855 (as *Micropterygina*) (= Eriocephalidae Chapman, 1894).

Micropterix Hübner, [1825]. Type-species *Tinea podevinella* Hübner, [1813] (= *Micropterix aruncella* (Scopoli, 1763)). Synonyms: *Micropteryx* Zeller, 1839 (unjustified emendation); *Eriocephala* Curtis, 1839.
51 species*. Temperate/subtropical Eurasia and North Africa.

Microptericina Zagulajev, 1983. Type-species *Micropteryx amasiella* Staudinger, 1880.
3 species. Caucasia, Asia Minor.

Sabatinca Walker, 1863. Type-species *S.incongruella* Walker, 1863 (= *S.eodora* Meyrick, 1918). Synonyms/subgenera: *Palaeomicra* Meyrick, 1886; *Micropardalis* Meyrick, 1912.
24 species*. New Zealand, New Caledonia, (Eastern Australia).
Note: *Sabatinca* is a very heterogeneous assemblage, but the New Zealand taxa *Palaeomicra* (Type-species *P.chrysargyra* Meyrick, 1886) and *Micropardalis* (type-species *Palaeomicra doroxena* Meyrick, 1888) seem to be at most subgenerically distinct from the similarly New Zealand *S.incongruella* group. On the other hand the Australian species groups as well as a few undescribed New Caledonian species and the New Zealand *S.zonodoxa* Meyrick, 1888 exhibit no particular resemblance to (let alone synapomorphies with) true *Sabatinca* and appear to have their closest relatives elsewhere in the family. The majority of the numerous undescribed micropterigids now known from New Caledonia are true *Sabatinca*. A revision of *Sabatinca* s.lat. is now being undertaken by J.S. Dugdale, G.W. Gibbs and the present author.

Agrionympha Meyrick, 1921. Type-species *A.pseliacma* Meyrick, 1921.
3 species. South Africa.

Hypomartyria Kristensen & Nielsen, 1982. Type-species *H.micropteroides* Kristensen & Nielsen, 1982.
1 species. Temperate Chile.

Squamicornia Kristensen & Nielsen, 1982. Type-species *S.equatoriella* Kristensen & Nielsen, 1982.
1 species. Ecuador.

Epimartyria Walsingham, 1898. Type-species *Micropteryx pardella* Walsingham, 1880.
2 species*. North America.

Paramartyria Issiki, 1931. Type-species *P. immaculatella* Issiki, 1931.
9 species*. Japan, Taiwan, China.

Palaeomicroides Issiki, 1931. Type-species *P.discopurpurella* Issiki, 1931.
7 species*. Taiwan.

Neomicropteryx Issiki, 1931. Type-species *N.nipponensis* Issiki, 1931.
6 species*. Japan.

† *Parasabatinca* Whalley, 1978. Type-species *P. aftimacra* Whalley, 1978.
1 species. Lower Cretaceous of Lebanon.

Aglossata: Agathiphagidae Kristensen, 1967.
Agathiphaga Dumbleton, 1952. Type-species *A.vitiensis* Dumbleton, 1952.
2 species. Queensland, Fiji, New Hebrides, Solomon Isles, New Caledonia.

Heterobathmiina: Heterobathmiidae Kristensen & Nielsen, 1979 (as Micropterigidae-Heterobathmiinae).
Heterobathmia Kristensen & Nielsen 1979. Type-species *H.pseuderiocrania* Kristensen & Nielsen, 1979.
2 species*. Temperate Argentina and Chile.

Glossata-Dacnonypha: Eriocraniidae Tutt, 1899 (as Eriocraniides) (= Micropterygidae Chapman, 1894)
Dyseriocrania Spuler, 1910. Type-speceis *Tinea subpurpurella* Haworth, 1829. Synonym: *Mnemonica* Meyrick, 1912.
3 species*. Temperate/subtropical North America and Eurasia.

Eriocraniella Viette, 1949. Type-species *Micropteryx aurosparsella* Walsingham, 1880.
7 species. North America.

Neocrania Davis, 1978. Type-species *N.bifasciata* Davis, 1978.
1 species. California.

Heringocrania Kuznetzov, 1941. Type-species *Adela unimaculella* Zetterstedt, 1839.
2 species. Europe.

Eriocrania Zeller, 1850. Type-species *Lampronia semipurpurella* Stephens, 1834.

Synonyms: *Chapmania* Spuler, 1910 preoccupied; *Allochapmania* Strand, 1917.
8 species. Temperate Eurasia and North America.

Issikiocrania Moriuti, 1982. Type-species *I.japoniella* Moriuti, 1982.
1 species. Japan.

Lophocoronidae Common, 1973.
Lophocorona Common, 1973. Type-species *L.pediasia* Common, 1973.
3 species*. Southern Australia.

Acanthopteroctetidae Davis, 1978.
Acanthopteroctetes Braun, 1921. Type-species *A.tripunctata* Braun, 1921.
3 species*. Western U.S.A.

Glossata-Neopseustina: Neopseustidae Hering, 1925.
Nematocentropus Hwang, 1965. Type-species *N.omeiensis* Hwang, 1965. Synonym: *Archepiolus* Mutuura, 1972.
1 (2 ?) species. Himalayas.

Neopseustis Meyrick, 1909. Type-species *N.calliglauca* Meyrick, 1909. Synonym: *Formopseustis* Matsumura, 1931.
5 species. Himalayas, Taiwan.

Synempora Davis & Nielsen, 1980. Type-species *S. andesae* Davis & Nielsen, 1980.
1 species. Temperate Argentina and Chile.

Apoplania Davis, 1975. Type-species *A.chilensis* Davis, 1975.
2 species*. Temperate Argentina and Chile.

Presumed non-neolepidopteran moth genera, *incertae sedis*
† *Electrocrania* Kuznetzov, 1941. Type-species *E. immensipalpia* Kuznetzov, 1941.
1 species. Eocene Baltic amber.

† *Undopterix* Skalski, 1979. Type-species *U. sukatshevae* Skalski, 1979.
1 species. Lower Cretaceous of Siberia.

Dansk resumé: Studier over primitive sommerfugles morfologi og systematik.

1. Indledning
Sommerfuglene, ordenen Lepidoptera, er med 150-200.000 beskrevne arter en af dyrerigets artsrigeste grupper. De ældste sikre sommerfuglefossiler er fra nedre kridt, og størsteparten af ordenens uddifferentiering er utvivlsomt foregået samtidig med de dækfrøede blomsterplanters uddifferentiering igennem kridt- og tertiærtiden. Det er sandsynligt, at primitive sommerfugle har eksisteret i hvert fald i trias, men ingen af de hidtil beskrevne triassiske "sommerfugle" (heller ikke den i 1980 beskrevne *Eocorona*) udviser karakterer, som tillader en sikker bestemmelse til orden.

Sommerfuglenes basale uddifferentiering er blevet anvendt som illustration af et udviklingsmønster, som synes at genfindes i mange dyregrupper (Hennig 1966, se Fig. 1): gruppens "typiske" afledte karakterer findes samlet i én, meget artsrig underordnet delgruppe (her Ditrysia), og de andre underordnede delgrupper kan arrangeres i en lineær sekvens, efter hvor mange af disse "typiske" karakterer, de har erhvervet. Når sommerfuglene forekommer at være en strukturelt homogen gruppe, skyldes det Ditrysia's talmæssige dominans: De "primitive", ikke-ditryse udviklingslinier udviser faktisk et bredt spektrum af organisationstyper, men de udgør tilsammen kun omkring én procent af de nulevende sommerfuglearter.

Siden 1960'erne er der indvundet en del ny viden om de primitiveste sommerfugles morfologi og systematik, og det ovennævnte udviklingsskema har måttet modificeres. Nærværende arbejde sammenfatter resultater fremlagt i en række tidligere publikationer (referenceliste 1, referencer i tekst ved kursiverede tal), samt nogle hidtil upublicerede observationer, indenfor rammen af en kortfattet generel oversigt over sommerfuglenes grundplanskarakterer; desuden diskuteres de primære udviklingsliniers karakteristika og fylogenetiske systematik.

2. Sommerfuglenes monofyli, søstergruppeforhold og grundplan
De kendte sommerfugle grupperes i fire basale udviklingslinier (underordner): Zeugloptera, Aglossata, Heterobathmiina og Glossata; de tre førstnævnte er meget artsfattige (tilsammen ca. en halv promille af ordenen). Det har været omdiskuteret, hvorvidt sommerfuglene som her afgrænset er monofyletisk, idet zeugloptererne har været betegnes som "mere primitive end både Lepidoptera og Trichoptera" (Hinton 1946a) eller endog som "meget nærmere beslægtet med Trichoptera" (Hinton 1958). Imidlertid er der aldrig påvist mulige synapomorfier for zeuglopterer og trichopterer,

og kun et par afledte træk (regressive karakterer i larvehovedet, karaktererne 57 og 59) er fælles for trichopterer og ikke-zeugloptere sommerfugle; disse træk tydes her som parallellismer. Der kan nemlig påpeges talrige sandsynlige synapomorfier for Zeugloptera og de andre sommerfuglegrupper; disse karakterer er altså autapomorfier for ordenen Lepidoptera som her afgrænset og er overbevisende evidens for gruppens monofyli. Det er almindelig anerkendt, at Trichoptera (vårfluerne) er sommerfuglenes nærmeste slægtninge. Relationen mellem de to ordner er et ægte søstergruppeforhold: Rohdendorfs teori (1969), om at Trichoptera er parafyletisk m.h.t. Lepidoptera, afvises; tilsammen udgør sommerfuglene + vårfluerne overorden Amphiesmenoptera.

Der gives en oversigt, baseret på andres og egne undersøgelser, over de nu kendte, mulige autapomorfier i grundplanerne af såvel overordenen Amphiesmenoptera som ordenen Lepidoptera. De klassiske amphiesmenopter-autapomorfier er "dobbelt-Y" konfigurationen af forvingens analribber, larvens sammensatte (prelabio-hypopharyngeale) silkekirtel-lobe, og den hunlige heterogameti, men der kendes nu ialt godt en snes karakterer (I-XXI) i denne kategori: Sammenvoksning af hypopharynx og labium også hos imago, adskillige detaljer i den imaginale thorakalmorfologi, parrede (defensive/feromon-) kirtler med udmunding på sternum V, muligvis fusion af tergum og sternum IX hos hannen og tilstedeværelse af stavformede apofyser på VIII og IX hos hunnen, strukturen af den ventrale diaphragma, flere cytologiske detaljer samt larveøjnenes finstruktur.

Den mest påfaldende sommerfugle-autapomorfi er naturligvis vingeskællene, men det er påvist *(1)*, at vingefladens skæl hos de primitiveste sommerfugle afviger påfaldende fra de "typiske" sommerfugleskæl ved ikke at være hule og ved at have uperforeret oversidelamel. Ialt kendes nu over en snes sommerfugle-autapomorfier i den imaginale anatomi (karaktererne 1-24), mens der for larvestadiets vedkommende kun kan peges på det forlængede pleurostom, samt en så triviel karakter som reduktionen i antallet af maxillarpalpeled (kar. 25-26).

Foruden karaktererne i de to autapomorfi-sæt diskuteres i kapitel 2 en lang række andre træk i sommerfuglenes/amphiesmenopterernes grundplan, og for såvel det hanlige genitalapparats som for larvehovedets vedkommende forsøges en sammenfattende rekonstruktion af sommerfugle-grundplanen (udførlige fremstillinger i hhv. *18* og *17*).

3. De primære udviklingslinier inden for sommerfuglene
I dette kapitel gives en oversigt over de fire underordners grundplansapomorfier og systematik.

Underordenen Zeugloptera rummer en enkelt familie, Micropterigidae, med ca. 90 beskrevne arter; den er nu kendt fra alle zoogeografiske regioner. Voksne micropterigider er primært pollenædere. Larverne er "jordbundsdyr", som lever i og af mosser, jordnære plantedele og henfaldende planterester. Der opregnes 26 karakterer, i hvilke zeuglopterernes grundplan afviger fra sommerfuglegrundplanen. Ti af disse (kar. 27-36) synes at være enestående for underordenen, mens de øvrige 16 forekommer i andre sommerfuglegrupper også; efter den i kap. 4 foreslåede fylogenetiske model er der imidlertid tale om paralellisme (eller evt. fejltolkede symplesiomorfier). Mindst to af disse træk (bortfald af separat ribbe M$_4$ i forvingen og bortfald af tibialsporer på forbenet, kar. 37-38) genfindes hos alle andre sommerfugle undtagen Aglossata. Yderligere fem karakterer (bortfald af mesocoxas ydre tergalremotor, hannens kønsveje med kun et par accessoriske kirtler, testesfollikler små og sammenpressede, ovarioletal reduceret og bagkroppens gangliekæde stærkt koncentreret, med færre end fem ganglier; kar. 39-43) genfindes i samme udformning i glossaternes grundplan (for forbehold m.h.t. testesstruktur og gangliekæde se dog kap. 4), men for disse kendes tilstanden ikke hos Heterobathmiina. Seks specialiseringer (kar. 44-49) er fælles for Zeugloptera og Heterobathmiina. Disse overensstemmelser var forklaringen på, at *Heterobathmia* blev beskrevet i Zeugloptera *(7)*, en placering som måtte forlades efter opdagelsen af *Heterobathmias* ungdomsstadier *(13)*. Nogle af overensstemmelserne er nu fremdeles meget bemærkelsesværdige, specielt børste/skleritbevæbningen på epipharynx og den som "rivejern" udformede "infrabuccallomme" i hypopharynx; for disse træks vedkommende kan det dog ikke afvises, at der er tale om symplesiomorfi. Zeuglopterlarver har højst seks larveøjne og deres thorakallemmers trochanter er ikke bevaret i den primitive tilstand (frit og tvedelt; kar. 50-51); syv larveøjne (det oprindelige amphiesmenopter-tal) og en primitiv larvetrochanter er bevaret hos Heterobathmiina, og reduktionen af øjetal samt modifikation af larvebenet må være foregået uafhængigt hos Zeugloptera, Aglossata og Glossata. Endelig er zeuglopterernes specialiserede ved, at imagos seks malpighiske rør er arrangeret i to grupper, hver med en fælles udførselsgang; en tilsvarende specialisering er fundet hos Neolepidoptera (kar. 52).

Der gives en oversigt over originale bidrag til zeuglopterernes systematik og morfologi. Slægterne *Hypomartyria* og *Squamicornia* (beskrevet i *12*) er de første ægte micropterigider, der er fundet i Sydamerika. Der består muligvis et søstergruppeforhold mellem *Micropterix* (og den herfra nylig udskifte slægt *Microptericina*) og alle andre micropterigideslægter, den s.k. *Sabatinca*-gruppe. Indenfor sidstnævnte er der måske et sø-

stergruppeforhold mellem den nordamerikanske + de østasiatiske taxa på den ene side og de sydamerikanske + afrikanske + australske/pacifiske taxa på den anden; dette må dog anses for ganske foreløbige arbejdshypoteser. Tidligere beskrivelser af hovedet, thoracalskelettet og den viscerale anatomi hos zeuglopterer suppleres m.h.t. en række detaljer; bl.a. findes *(8)*, at det ventrale diaphragma ikke er principielt forskelligt fra de øvrige sommerfugles (*contra* Richards 1963). De hanlige genitalsegmenter af *Paramartyria immaculatella* vises at være af mere ordinær *Sabatinca*-gruppe type, end originalbeskrivelsen lader formode *(3)*. Skelet/muskelanatomien af det hanlige genitalapparat hos den nordamerikanske *Epimartyria* beskrives *(14)*; forhold af særlig interesse er den reducerede gonopodmuskulatur samt strukturen af phallus og "analkeglens" sklerotisering. Den pregenitale bagkrop beskrives, særlig på grundlag af *Micropterix (16)*; forhold af særlig interesse er bl.a. formen af tergum I-sklerotiseringen, bevarelsen af et tydeligt sternum I, udformningen af det proprioceptive apparat (et pleurall chordotonalorgan med fire sensoriske enheder er muligvis forløber for de preabdominale tympanalorganer hos flere dityse familiegrupper), variabiliteten i kropsvæggens muskulatur samt spirakelstrukturen. Specialiseringen af åbningsfeltet for sternum-V kirtlen tillægges systematisk værdi på slægtsgruppeniveau. I *15* beskrives for første gang respirationssystemet hos en primitiv sommerfugl *(Micropterix calthella)*; af særlig interesse er bl.a. strukturen af thorakalspiraklerne, manglen på forbindelse mellem hovedets dorsale og ventrale trachéstammer, manglen på forbindelse mellem den forreste og bageste trachéstamme til hver vinge, manglen af ventrale abdominale kommissurer (sådanne findes dog inden for *Sabatinca*-gruppen) samt den delvise forsyning af genitalsegmenterne fra trachéer, som udspringer i segment VII. Larvebenets struktur diskuteres *(13)*; det næstyderste led foreslås at være tibiotarsus.

Underordenen Aglossata rummer en enkelt familie, Agathiphagidae, hvis eneste slægt *(Agathiphaga)*, kun omfatter to arter; *Agathiphaga* findes i Australien og på nogle SV-pacifiske øer. Larverne minerer i frøene af kaurifyr (*Agathis*, Araucariaceae); imagines (som i live ligner vårfluer til forveksling!) er nataktive, og det vides ikke, om de optager næring. *Agathiphaga* er først beskrevet i 1952 og endnu er kun ganske få imagines fundet i naturen.

Der opregnes en række autapomorfier for *Agathiphaga*. Af særlig interesse er imidlertid en række specialiseringer (kar. 54-62), som denne slægt har fælles med Heterobathmiina og Glossata; hertil hører bl.a. en påfaldende modifikation af metafurca, en specialisering af spermathek-kanalens struktur og flere detaljer i larvehovedet. Et andet sæt specialiseringer (kar. 63-

71) hos *Agathiphaga* genfindes hos Heterobathmiina alene. Hertil hører bl.a. imagos Y-formede tentorium, hannens veludviklede phallotheca og nogle regressive træk i larvehovedets muskulatur.

De første observationer over *Agathiphagas* muskel- og visceralanatomi samt en række nye observationer over dyrenes skeletstruktur er fremlagt i *7-9, 17, 18* og nærværende arbejde; de er baseret på materiale modtaget fra British Museum (Nat.Hist.). Blandt de interessanteste træk kan foruden de netop nævnte anføres bevarelsen af mesocoxas "ydre tergalremotor" (enestående blandt panorpide insekter!), den relativt ukoncentrerede gangliekæde, hvis skede kan udvise dorsale (tilsyneladende overvejende cellulære) fortykkelser, den store stomodaeale kro og de meget talrige ovariolefollikler. Det hanlige genitalapparat behandles i nogen udførlighed *(18)*: Dets skeletale struktur er meget kompleks (delvis stærkt autapomorf) og i de indre organer er forekomsten af 2x4 store og frie testesfollikler utvivlsomt, forekomsten af to par accessoriske kirtler muligvis, primitive træk. Larvehovedets anatomi behandles i *17*. Hintons påstand (1958) om, at *Agathiphaga*-larven er "en typisk sommerfuglelarve", vises at være helt ukorrekt; bl.a. har den komplet hypostomalbro og mangler adfrontal- og hypostomalsuturer samt tilleddet "spindetap".

Underordenen Heterobathmiina rummer en enkelt familie, Heterobathmiidae, hvis eneste slægt *(Heterobathmia)* først er beskrevet så sent som i 1979 (i *7*); den forekommer i det tempererede Sydamerika. Både larverne og de voksne sommerfugle er knyttet til "sydbøge", *Nothofagus*; larven er bladminerer, og imago fourager (formentlig på pollen) i træernes blomster.

Som før nævnt blev *Heterobathmia* først beskrevet i Zeugloptera-Micropterigidae (som selvstændig underfamilie), men efter den helt nylige opdagelse af ungdomsstadierne kan denne placering ikke opretholdes, og dyrene er derfor placeret i egen familie og underorden *(13)*. Al eksisterende viden om gruppen er fremlagt i afhandlingerne *7* (imagos skeletstruktur, sammenligning med andre primitive sommerfugle, taxonomisk beskrivelse af de to hidtil navngivne arter) og *13* (bionomi, præliminær beskrivelse af ungdomsstadiernes morfologi).

Heterobathmias autapomorfier opregnes; opmærksomheden henledes yderligere på tre sæt specialiseringer hos disse dyr, nemlig dels de tidligere nævnte, som er fælles med henholdsvis Aglossata + Glossata (kar. 53-62) og Aglossata alene (kar. 63-71), dels et sæt, som er fælles med Glossata alene (kar. 72-77); særlig bemærkelsesværdige karakterer i sidstnævnte kategori er nogle detaljer i larvens hovedkapsel (tilstedeværelse af adfrontale og hypostomale suturer og det mediant usklerotiserede hypostom). Endelig nævnes en række

andre strukturelle ejendommeligheder hos *Heterobathmia*; af særlig gådefulde træk skal fremhæves de adskilte dorsale og ventrale skleritplader på genitalsegmentet hos hannen samt den ikke-retraktile bagkropsspids og de adskilte køns- og analåbninger hos hunnen. Plesiomorfier eller autapomorfe karakter-"reverseringer"?

Underordenen Glossata omfatter alle de resterende sommerfugle, som i øjeblikket grupperes i fire infraordner: Dacnonypha, Neopseustina, Exoporia og Heteroneura. Glossaternes monofyli begrundes overbevisende ved en række autapomorfier (kar. 78-84), hvoraf den mest bemærkelsesværdige naturligvis er spiralsugesnablen, dannet af maxillernes galeae.

Infraordenen Dacnonypha omfatter i gængs systematik familierne Eriocraniidae, Lophocoronidae og Acanthopteroctetidae. Der kendes dog ingen sikre synapomorfier for de tre familier.

Familien Eriocraniidae er holarktisk; den omfatter godt en snes beskrevne arter, hvis larver er bladminerende, praktisk talt altid på træer tilhørende bøgeordenen (Fagales). Skelet/muskelanatomien af eriocraniidernes ejendommelige hanlige genitalia omtales (beskrivelse i *2*, yderligere diskussion i *14* og *18*). Det bemærkes endvidere, at der hos flere eriocraniider er fundet kønsdimorfi m.h.t. gangliekoncentrationen i bagkroppen *(9)* samt at det ventrale diaphragma er stærkt reduceret i denne familie.

Familierne Lophocoronidae (australsk, 3 arter) og Acanthopteroctetidae (nearktisk, 3 arter) er endnu meget dårligt kendt. Sidstnævnte har hule, d.v.s. "normaltype"-skæl på vingefladen, hvilket taler for en placering i Myoglossata (jfr. nedenfor), men på den anden side har Davis (1978) ment at kunne påpege synapomorfier med Eriocraniidae; spørgsmålet om familiens placering må anses for helt åbent.

Infraordnerne Neopseustina + Exoporia + Heteroneura: Myoglossata. Tilstedeværelsen af en indre snabelmuskulatur (kar. 85) er en interessant synapomorfi for de ikke-dacnonyphe glossater (NB, den indre snabelstruktur hos Lophocoronidae og Acanthopteroctetidae kendes ikke) *(10)*. En anden tilsyneladende synapomorfi for myoglossaterne er tilstedeværelsen af "normaltype" skæl på vingefladen, evt. sammen med "primitiv-type" skæl (kar. 86); se noten vedr. Acanthopteroctetidae ovenfor.

Infraordenen Neopseustina omfatter en enkelt familie, Neopseustidae, som med en halv snes arter forekommer disjunkt i SØ-Asien og det sydlige Sydamerika. Ungdomsstadierne er ukendt, og materiale til studier over sommerfuglenes indre anatomi er først helt nyligt blevet tilveiebragt. Det er påvist, at der i denne fa-

milie forekommer en (såvidt vides) enestående "dobbelt-rør" snabeltype *(11)* samt endvidere, at bagkroppens gangliekæde har parrede kommissurer (autapomorf karakter-"reversering"?), og at det ventrale diaphragma er helt bortfaldet *(8, 9)*.

Infraordnerne Exoporia + Heteroneura: Neolepidoptera. Der kendes adskillige afledte karakterer, som er fælles for underordnerne Exoporia og Heteroneura (kar. 52, 87-96), men for en del af disse karakterers vedkommende (kar. 52, 87, 91, 94-96) kendes tilstanden ikke hos Neopseustina, og de kan derfor muligvis vise sig at være synapomorfier for hele gruppen Myoglossata. Specielt bemærkelsesværdige specialiseringer i grundplanen hos begge neolepidoptergrupper er at finde hos ungdomsstadierne (kar. 94-96); det drejer sig om velkendte forhold som de "adecticous" mumiepupper med abdominale tornrækker og larvernes udstyr af gangvorter (med sklerotiserede kroge og extrinsikke muskler) på segment III-VI og X.

Infraordenen Exoporia omfatter overfamilierne Mnesarchaeoidea og Hepialoidea, som synes at kunne holdes sammen *(6)* af fire synapomorfier (kar. 97-100); en af disse, de "sekundære køle" på vingeskællene (kar. 99) omtales nærmere i *4* (ligesom en beslægtet skælmorfologisk ejendommelighed, "andenordens køle", som kendes fra nogle hepialider).

Overfamilien Mnesarchaeoidea omfatter kun den lille familie Mnesarchaeidae, som er endemisk på New Zealand.

Overfamilien Hepialoidea omfatter fem familier: Palaeosetidae (orientalsk/australsk), Neotheoridae (sydamerikansk), Anomosetidae (australsk), Prototheoridae (sydafrikansk) og den artsrige Hepialidae (kosmopolitisk). Hepialoideas monofyli er begrundet *(6)* ved en ribbekarakter og ved reduktionen af maxillens vedhæng (kar. 101-102). De enkelte familiers status indenfor overfamiliens fylogeni er diskuteret i *6*, og en familienøgle gives i *5*. Den monobasiske familie Neotheoridae omtales; den er beskrevet i *6*. Det er en i adskillige henseender autapomorf sommerfugl, men dens snabel er mindre reduceret end hos nogen anden hepialoid. Den ligeledes monobasiske familie Anomosetidae er i *6* flyttet bort fra synonymi med Prototheoridae, og dens skeletstruktur omtales (genbeskrivelse og diskussion i *5*).

Infraordenen Heteroneura omfatter i gængs systematik grupperne Incurvariina + Nepticulina + Ditrysia. En behandling af de heteroneure sommerfugles fylogeni falder uden for nærværende arbejdes rammer. Det bemærkes dog, at mens Heteroneuras monofyli understøttes af en række specialiseringer (kar. 103-109) i vinge- og thorakalstruktur samt bortfaldet af sternum

l-sklerotiseringen *(8)*, så *kunne* på den anden side nogle ligheder i det hunlige kønsapparat (adskilt æglægnings- og parringsåbning, bursas ventrale position i forhold til oviducten) hos Exoporia og Ditrysia tolkes som evidens for, at disse grupper er hinandens nærmeste slægtninge (Dugdale 1974); Commons (1975) støtte til det gængse system følges her, men yderligere belysning af problemet er ønskelig. Under alle omstændigheder forekommer imidlertid monofylien af de højere taxa Neolepidoptera/Myoglossata så velfunderet, at Mutuuras (1972) afledning af Incurvariina fra en eriocraniide-lignende form uafhængigt af andre neolepidopterer/myoglossater må afvises.

4. Spørgsmålet om de basale dichotomier i sommerfuglenes fylogeni
I cladogrammet, Fig. 13, illustreres den her foretrukne arbejdshypotese om slægtskabsforholdene mellem sommerfuglenes hovedudviklingslinier. M.h.t. den basale dichotomi er diagrammet "konservativt" ved at foreslå zeugloptererne som søstergruppe til alle andre sommerfugle (sammenholdt af de afledte træk A-B og 53-62). Men det er klart, at en alternativ model med Aglossata som søstergruppe til de øvrige sommerfugle (sammenholdt af kar. 37-38 og måske 39-43) stadig fortjener opmærksomhed.

Også den primære dichotomi indenfor de ikke-zeugloptere sommerfugle er problematisk, men teorien om et søstergruppe-forhold mellem Aglossata og Heterobathmiina + Glossata (sidstnævnte sammenholdes af kar. 37-38, 72-77 og måske 39-43) foretrækkes frem for en alternativ model med et søstergruppe-forhold mellem Glossata og Aglossata + Heterobathmiina (sidstnævnte sammenholdt af kar. 63-71).

Endelig diskuteres Frieses 1970-teori om, at den primære dichotomi i sommerfuglenes fylogeni ligger mellem Hepialoiderne ("Gymnocera") og alle andre sommerfugle ("Angiocera"). Frieses argumenter mod den her angivne (og i de senere årtier gængse) relativt underordnede placering af hepialoiderne afvises, og hans formodede synapomorfier for ikke-hepialoide sommerfugle tydes på anden måde.

5. Afsluttende bemærkninger
Her bemærkes, at sommerfuglenes tidligste evolution er langt mere kompleks, end man troede for et par årtier siden. Men det nu kendte evolutionsmønster med de mange paralellismer (og/eller karakter "reverseringer") er ikke mindre interessant end den tidligere foreslåede simple model.

Det fremhæves med udgangspunkt i de senerste årtiers mange opsigtsvækkende fund af primitive sommerfugle, at fremtidige fund utvivlsomt vil udfylde nogle strukturelle diskontinuiteter mellem de nu kendte former − samt med sikkerhed også vil konfrontere

os med uventede karakterkombinationer! Det detaljerede sammenlignende studium over de primitive sommerfugles indre bygning befinder sig endnu i en begynderfase, men store fremskridt kan ventes i det kommende årti.

Endelig omtales muligheden af fund af nye recente taxa på ordens-niveau (d.v.s. søstergrupper til de kendte sommerfugle, vårfluer eller amphiesmenopterer) og det påpeges, at for imagostadiets vedkommende kan

sådanne taxa forventes at have en overordentlig stor ydre lighed med primitive vårfluer. I denne sammenhæng fremhæves behovet for en detaljeret rekonstruktion af vårfluernes grundplan.

6. Appendix
Her gives en fortegnelse over slægterne af de ikke-neolepidoptere sommerfuglefamilier. For hver slægt anføres typeart, artstal og udbredelse i store træk.

REFERENCES (1)

1. Kristensen, N.P., 1971: Morphological observations on the wing scales in some primitive Lepidoptera. J.Ultrastruct.Res. *30*: 402-410.

2. Birket-Smith, S.J.R. & Kristensen, N.P., 1974. The skeleto-muscular anatomy of the genital segments of male *Eriocrania* (Insecta, Lepidoptera). Z.Morph.Tiere 77: 157-174.

3. Kristensen, N.P., 1976. A redescription of the male genital morphology of *Paramartyria immaculatella* (Insecta, Lepidoptera, Micropterigidae). Steenstrupia *4*: 27-32.

4. – 1978. Ridge dimorphism and second-order ridges on wing scales in Lepidoptera: Exoporia. Int.J.Insect Morph. Embryol., 7: 297-299.

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

6. – 1978. A new familia of Hepialoidea from South America, with remarks on the phylogeny of the subordo Exoporia (Lepidoptera). Ent. Germ., *4*: 272-294.

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

8. – 1980. The ventral diaphragm of primitive (non-ditrysian) Lepidoptera. A morphological and phylogenetic study. Z.zool.Syst.Evol.Forsch., *18*: 123-146.

9. – 1981. Abdominal nerve cord configuration in adult non-ditrysian Lepidoptera. Int.J.Insect. Morph.Embryol.,*10*: 89-91.

10. – 1981. Intrinsic proboscis musculature in non-ditrysian Lepidoptera-Glossata: Structure and phylogenetic significance. *In* Cederholm, L. (ed.): Advances in insect systematics and phylogeny. Ent.scand.Suppl. *15*: 299-304.

11. – 1981. Double-tube proboscis configuration in neopseustid moths (Lepidoptera: Neopseustidae). Int.J.Insect Morph.Embryol. *10*: 483-486.

12. – 1982. South American micropterigid moths: two new genera of the *Sabatinca* group. Ent. scand., *13*: 513-529.

13. – 1983. The *Heterobathmia* life history elucidated: Immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). Z. zool.Syst.EvolForsch. *21*: 101-124.

14. Kristensen, N.P., 1984. Skeletomuscular anatomy of the male genitalia of *Epimartyria* (Lepidoptera: Micropterigidae. Ent.scand. *15*: 97-112.

15. Kristensen, N.P., 1984. Respiratory system of the primitive moth *Micropterix calthella* (Linnaeus) (Lepidoptera: Micropterigidae). Int.J. Insect Morph. & Embryol. *13*: 137-156.

16. – 1984. The pregenital abdomen of the Zeugloptera (Lepidoptera). Steenstrupia *10*: 113-136.

17. – 1984. The larval head of *Agathiphaga* (Lepidoptera Agathiphagidae) and the lepidopteran ground plan. Syst.ent. *9*: 63-81.

18. – 1984. The male genitalia of *Agathiphaga* (Lepidoptera, Agathiphagidae) and the lepidopteran ground plan. Ent.scand. *15*.

19. – Unpublished observations.

REFERENCES (2)

Ando, H. & Kobayashi, Y., 1978: The formation of germ rudiment in the primitive moth, *Neomicropteryx nipponensis* Issiki (Micropterygidae, Zeugloptera, Lepidoptera) and its phylogenetic significance. – Proc. Jap. Soc. syst. Zool. 15: 46-50.

Baccetti, B., Dallai, R. & Rosati, T., 1970: The spermatozoon of Arthropoda 7. Plecoptera and Trichoptera. – J.Ultrastruct.Res. 31: 212-228.

Bänziger, H., 1971: Extension and coiling of the lepidopterous proboscis – a new interpretation of the blood-pressure theory. – Mitt.schweiz.ent.Ges. 43: 225-239.

Bharadway, R.K., Chandran, R.S. & Chadwick, L.E., 1974: The cervical and thoracic musculature of lepidoptera. Part II. Comparison of published reports. – J.nat.Hist. 8: 311-331.

Bitsch, J., 1979: Morphologie abdominale des insectes. Pp. 291-600. In Grassé, P.P. (ed.). – Traité de Zoologie VIII (2), Masson et Cie, Paris.

Boudreaux, H.B., 1979: Arthropod phylogeny with special reference to insects. – J. Wiley & Sons, New York, Chichester, Brisbane & Toronto.

– 1981: About the panorpoid complex. – Ann.ent. Soc.Am. 74: 155-157.

Braun, A.F., 1919: Wing structure of Lepidoptera and the phylogenetic and taxonomic value of certain persistent Trichopterous characters. – Ann.ent. Soc.Am. 12: 349-366.

– 1924: The frenulum and its retinaculum in the Lepidoptera. – Ann.ent.Soc.Am. 17: 234-256.

Brock, J.P., 1971: A contribution towards an understanding of the morphology and phylogeny of the Ditrysian Lepidoptera. – J.nat.Hist. 5: 29-102.

Bullock, J.H. & Horridge, G.A., 1965: Structure and function in the nervous systems of invertebrates. W.H. Freeman, San Francisco & London.

Buxton, P.A., 1917: On the protocerebrum of *Micropteryx*. – Trans.ent.Soc.Lond. 1917: 112-153.

Carter, D.J. & Dugdale, J.S., 1982: Notes on collecting and rearing *Micropterix* (Lepidoptera: Micropterigidae) larvae in England. – Ent.Gaz. 33: 43-47.

Chadwick, L.E., 1959: The furcopleural muscles of Lepidoptera. – Ann.ent.Soc.Am. 52: 665-668.

Chapman, T.A., 1917: *Micropteryx* entitled to ordinal rank; order Zeugloptera. – Trans.ent.Soc.Lond.: 310-314.

Chauvin, G. & Faucheux, M., 1981: Les pièces buccales et leurs recepteurs sensoriels chez l'imago de *Micropterix calthella* L. (Lepidoptera: Micropterigidae). – Int.J.Insect Morph.Embryol. 10: 425-439.

Chauvin, J.T. & Chauvin, G., 1980: Formation des reliefs externes de l'oeuf de *Micropteryx calthella* L. (Lepidoptera: Micropterigidae). –Can.J.Zool. 58: 761-766.

Common, I.F.B., 1969: A wing-locking or stridulatory device in Lepidoptera. – J.Aust.ent.Soc. 8: 121-125.

– 1970: Lepidoptera. Pp. 765-866 *in* CSIRO (sponsor), The Insects of Australia, Melbourne University Press, Carlton.

– 1973: A new family of Dacnonypha (Lepidoptera) based on three new species from Southern Australia, with notes on the Agathiphagidae. – J.Aust.ent. Soc. 12: 11-23.

– 1974: Lepidoptera. Pp. 98-107 *in* CSIRO (sponsor) The Insects of Australia, Supplement 1974, Melbourne University Press, Carlton.

– 1975: Evolution and classification of the Lepidoptera. – A.Rev.Ent. 20: 193-203.

Crampton, G.C., 1920: A comparison of the external anatomy of lower Lepidoptera and Trichoptera from the standpoint of phylogeny. – Psyche, Camb. 27: 23-34.

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

– 1978: A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family Acanthopteroctetidae (Lepidoptera). – Smithson.Contr.Zool. 251: i-iii, 1-131.

– (in press): Micropterigidae, Eriocraniidae, Acanthopteroctetidae. *In* Stehr, F. (ed.) An introduction to the immature insects of North America.

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

– in press: The South American neopseustid genus *Apoplania* Davis: a new species, distribution records and notes on adult behaviour (Lepidoptera: Neopseustina). – Ent.scand. 15.

Denis, J.R. & Bitsch, J., 1973: Morphologie de la tête des insectes. Pp- 1-593 *in* Grassé, P.P. (ed.) Traité de Zoologie VIII (1), Masson et Cie, Paris.

Downey, J.C. & Allyn, A.C., 1975: Wing-scale morphology and nomenclature. – Bull.Allyn Mus. 31: 1-32.

Dugdale, J.S., 1974: Female genital configuration in the classification of Lepidoptera. – N.Z.J. Zool. 1: 127-146.

Dumbleton, L.F., 1952: A New Genus of seed-infesting Micropterygid Moths. – Pacif.Sci. 6: 17-29.

Ehnbom, K., 1948: Studies on the central and sympathetic nervous system and some sense organs in the head of neuropteroid insects. – Opusc.ent.Suppl. 8: 1-162.

Friese, G., 1970: Zur Phylogenie der älteren Teilgruppen der Lepidopteren. – Ber. 10 Wanderversamml. dt.Ent.: 203-222.

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

Hamilton, K.G.A., 1971-72: The insect wing. I-IV. – J.Kans.ent.Soc. 44: 421-433; 45: 54-58, 145-162, 295-308.

Hannemann, H.J., 1956: Die Kopfmuskulatur von *Micropteryx calthella* (L.) (Lep.). Morphologie und Funktion. – Zool.Jb. (Anat.) 75: 177-206.

– 1957: Die männlichen Terminalia von *Micropteryx calthella* L. (Lep. Micropterygidae). – Dt.ent.Z. (N.F.) 4: 209-222.

Hasenfuss, I., 1973: Vergleichend-morphologische Untersuchung der sensorischen Innervierung der Rumpfwand der Larven von *Rhyacophila nubila* Zett. (Trichoptera) und *Galleria mellonella* L. (Lepidoptera). Ein Beitrag zum Problem der Homologie und Homonomie ihrer larvalen Sensillenmuster. – Zool.Jb. (Anat.) 90: 1-54, 175-253.

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

– 1966: Phylogenetic systematics. – Illinois University Press, Urbana.

– 1981: Insect Phylogeny. (Pont, A.C. & Schlee, D., eds.). Joyn Wiley & Sons, Chichester, New York, Brisbane, Toronto.

Hepburn, H.R., 1971: Proboscis extension and recoil in Lepidoptera. – J.Insect Physiol. 17: 637-656.

Hessel, J.H., 1969: The comparative morphology of the dorsal vessel and accessory structures of the Lepidoptera and its phylogenetic implications. – Ann. ent.Soc.Am. 62: 355-370.

Hinton, H.E., 1946a: On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. – Trans. R.Ent.Soc.Lond. 97: 1-37.

Hinton, H.E., 1946b: A new classification of insect pupae. – Proc.zool.Soc.Lond. 116: 282-328.

– 1955: On the structure, function and distribution of the prolegs of Panorpoidea, with a criticism of the Berlese-Imms theory. – Trans.R.Ent.Soc.Lond. 106: 455-545.

– 1958: The phylogeny of the panorpoid orders. – A.Rev.Ent. 3: 181-206.

Issiki, S.T., 1931: On the morphology and systematics of Micropterygidae (Lepidoptera: Homoneura) of Japan and Formosa, with some considerations on the Australian, European, and North American Forms. – Proc.zool.Soc.Lond. 1931: 999-1039.

Jander, U., 1966: Untersuchungen zur Stammesgeschichte von Putzbewegungen von Tracheaten. – Z.Tierpsychol. 23: 799-844.

Kiriakoff, S.G., 1948: A classification of the Lepidoptera and related groups, with some remarks on taxonomy. – Biol.Jaarb. 15: 118-143.

Klemm, N., 1966: Die Morphologie des Kopfes von Rhyacophila Pict. (Trichoptera). – Zool.Jb.Anat. 83: 1-51.

Kobayashi, Y. & Ando, H. 1981: The embryonic dedelopment of the primitive moth, Neomicropteryx nipponensis Issiki (Lepidoptera, Micropterygidae): Morphogenesis of the embryo by external observation. – J. Morph. 169: 49-59.

– 1982: The early embryonic development of the primitive moth, Neomicropteryx nipponensis Issiki (Lepidoptera, Micropterygidae). – J.Morph. 172: 259-269.

Korboot, K., 1964: Comparative studies of the external and internal anatomy of three species of caddis flies (Trichoptera). – Pap.Dept.Ent.Univ.Qd 2 (1): 1-44.

Kristensen, N.P., 1968: The anatomy of the head and the alimentary canal of adult Eriocraniidae. – Ent. Meddr. 36: 239-315.

– 1971: The systematic position of the Zeugloptera in the light of recent anatomical investigations. – Proc.13th Congr.Ent.Moscow 1968, 1: 261.

– 1975: The phylogeny of hexapod "orders". A critical review of recent accounts. – Z.zool.Syst.Evol Forsch. 13: 1-44.

– 1979: The Mnesarchaea proboscis, a correction. (Lepidoptera: Exoporia: Mnesarchaeidae). – Ent. Gen. 5: 267-268.

– 1981a: Amphiesmenoptera. Trichoptera, Lepidoptera (Revisionary notes). Pp. 325-330, 412-415 in Hennig, W., Insect Phylogeny, Pont, A.C. & Schlee, D. (eds.), John Wiley & Sons, Chichester, New York, Brisbane, Toronto.

– 1981b: Phylogeny of insect orders. – A.Rev.Ent. 26: 135-157.

Lorenz, R.E., 1961: Biologie und Morphologie von Micropterix calthella (L.). – Dt.ent.Z. (N.F.) 8: 1-23.

Malyshev, S.J., 1968: Genesis of the Hymenoptera and the phases of their evolution. Methuen, London, 319 pp.

Marshall, J.E., 1979: A review of the genera of the Hydroptilidae (Trichoptera). – Bull.Br.Mus.nat.Hist. (Ent.) 39: 135-239.

Matsuda, R. 1970: Morphology and evolution of the insect thorax. – Mem.Can.ent.Soc. 76: 1-431.

– 1976: Morphology and Evolution of the Insect Abdomen. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris & Frankfurt, 534 pp.

Mickoleit, G., 1966: Zur Kenntnit einer neuen Spezialhomologie (Synapomorphie) der Panorpoidea. – Zool.Jb. (Anat.) 83: 483-496.

– 1969: Vergleichend-anatomische Untersuchungen an der pterothoracalen Pleurotergalmuskulatur der Neuropteria und Mecopteria (Insecta, Holometabola). – Z.Morph.Tiere 64: 151-178.

Mortimer, J.F., 1965: The alimentary canals of some adult Lepidoptera and Trichoptera. – Trans.R.ent. Soc.Lond. 117: 67-94.

Mutuura, A., 1956: On the homology of the body areas in the thorax and abdomen and new system of the setae on the lepidopterous larvae. – Bull.Univ. Osaka Prefect. (B) 6: 93-122.

– 1972: Morphology of the female terminalia in Lepidoptera and its taxonomic significance. – Can. Ent.104: 1055-1070.

Nelson, G.J., 1970: Outline of a theory of comparative biology. – Syst.Zool.19: 373-384.

Nielsen, A., 1957: A comparative study of the genital segments and their appendages in male Trichoptera. – Biol.Skr.8 (5): 1-159.

– 1980: A comparative study of the genital segments and the genital chamber in female Trichoptera. – Biol.Skr. 23 (1): 1-200.

Nielsen, E.S., in press: The monotrysian heteroneuran phylogeny puzzle: a possible solution (Lepidoptera). – Nota Lepidopterologica.

Paulus, H.F. & Schmidt, M., 1978: Evolutionswege zum Larvalauge der Insecten: Die Stemmata der Trichoptera und Lepidoptera. – Z.zool.Syst.Evol-Forsch. 16: 188-216.

Petersen, W., 1900: Beiträge zur Morphologie der Lepidopteren. – Mém.Acad.Sci.St.Petersb. 8 (9) 6: 1-144.

Philips, D.M., 1971: Morphogenesis of the lacinate appendages of Lepidoptera spermatozoa. – J.Ultrastruct.Res. 34: 567-585.

Philpott, A., 1922: The wing coupling apparatus in the Mnesarchaeidae. – N.Z.J.Sci.Tech. 5: 275-276.

– 1924: The tibial strigil of the Lepidoptera. – Trans. Proc.N.Z.Inst. 55: 215-224.

Richards, A.G., 1963: The ventral diaphragm of insects. – J.Morphol. 113: 17-48.

Riek E.F., 1967: Structures of unknown, possibly stridulatory, function on the wings and body of Neuroptera; with an appendix on other endopterygote orders. – Austr.J.Zool. 15: 337-348.

– 1970: Neuroptera (Lacewings), Mecoptera (Scorpion-flies), Trichoptera (caddis-flies, caddises). Pp. 472-494, 636-646, 741-764 in CSIRO (sponsor) The insects of Australia, Melbourne University Press, Carlton.

Robinson, G.S. & Tuck, K.R., 1976: The kauri moth Agathiphaga. A preliminary report, 8 pp. British Museum (Natural History), London.

Rohdendorf, B.B., 1969: Phylogenie. – Handb.Zool. 4 (2): 1/4: 1-28.

Ross, H.H., 1967: The evolution and past dispersal of Trichoptera. A.Rev.Ent. 12: 169-206.

Schmid, F., 1970: Le genre Rhyacophila et la famille des Rhyacophilidae (Trichoptera). – Mém.Soc.ent. Canada 66: 1-230, 52 pl.

Schultz, H. 1914: Das Pronotum und die Patagia der Lepidopteren. – Dt.ent.Z. 1914: 17-42.

Sharplin, J. 1963: Wing base structure in Lepidoptera. I. Fore wing base. II. Hind wing base. – Can.ent. 95: 1024-1050, 1121-1145.

-- 1964: Wing base structure in Lepidoptera. III. Taxonomic characters. – Can.Ent. 96: 943-949.

Skalski, A.W., 1979: Records of oldest Lepidoptera. – Nota Lepidopterologica 2: 61-66.

Suomalainen, E., 1966: Achiasmatische Oogenese bei Trichoptera. – Chromosoma Berl. 18: 201-207.

– 1969: Chromosome evolution in the Lepidoptera.

Pp. 132-138 in Darlington, C.D. & Lewis, K.R. (eds.), Chromosomes today, 2. Oliver & Boyd, Edinburg.

Tillyard, R.J., 1923: On the larva and pupa of the genus Sabatinca (Order Lepidoptera, family Micropterygidae). – Trans.R.ent.Soc.Lond. 1923: 437-453.

Tindale, N., 1980: Origin of the Lepidoptera, with description of a new Mid-Triassic species and notes on the origin of the butterfly stem. – J.Lepid.Soc. 34: 263-285.

Tindall, A., 1965: The functional morphology of the thorax of Limnophilus marmoratus Curtis (Trichoptera: Limnophilidae). – Trans.R.ent.Soc.Lond. 117: 127-166.

Viette, P., 1979: Réflexions sur les classifications en sous-ordres de l'Ordre des Lepidoptera. – Bull.ent. Soc.Fr. 84: 68-78.

Weber, H., 1924: Das Thorakal-Skelett der Lepidopteren. – Ein Beitrag zur vergleichenden Morphologie des Insekten-thorax. – Z.Anat.EntwGesch. 73: 277-331.

Wiley, E.O., 1981: Phylogenetics. The theory and practice of phylogenetic systematics. – J.Wiley & Sons, New York, Chichester, Brisbane & Toronto.

Whalley, P. 1978: New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of the Lepidoptera (Insecta). – Ann.Transv.Mus. 31: 72-86.

Yasuda, T., 1962: On the larva and pupa of Neomicropteryx nipponensis Issiki, with its biological notes (Lepidoptera, Micropterygidae). – Kontyu 30: 130-136.

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ADDENDA

After this article went to press, some interesting new contributions to the understanding of the earliest evolution of the Lepidoptera have come to my notice.

1) Two small, scaly-winged insect fossils which in all probability are genuine Lepidoptera have now been identified in pre-Cretaceous deposits (see chapter one). The younger fossil, *Eolepidopterix jurassica* Rasnitsyn, 1983, comes from the Soviet Upper Jurassic and is by its author assigned to a new family, Eolepidopterigidae, and suborder, Eolepidopterigina (Rasnitsyn 1983, Doklady Akademii Nauk SSSR, 269: 467-471). Parts of the legs of *Eolepidopterix* are visible, including the fore tibia, but an epiphysis has not been identified; it must be remembered, however, that the epiphysis in extant Lepidoptera is often largely concealed by the tibial vestiture. I therefore consider it an open question whether the epiphysis of *Eolepidopterix* was actually absent, and hence whether the fossil should be assigned to the "stem-group" (*sensu* Hennig, see, e.g., Hennig 1981: 30) of the Lepidoptera. The wing scales of *Eolepidopterix* have not been studied in detail, and the venation is largely obscured.

The older fossil is from the Lower Jurassic (Lias) of Dorset, UK, and is likewise being assigned to a new family of its own (Whalley in press, Bull. Br. Mus. nat. Hist. (Geol.)). This insect is known only from a single wing (apparently a hindwing), but some of the scales are sufficiently well preserved to permit SEM examination. The phylogenetic position of this fossil within the Lepidoptera remains uncertain.

2) The alleged occurrence of apyrene sperm in the Trichoptera (see chapter two, character XVII) has been reexamined by Friedländer (1983, J. Ultrastruct. Res. 83: 141-147). None of the several caddisfly taxa examined by Friedländer have apyrene sperm, and he concludes that previous reports of apyrene sperm in the Trichoptera have stemmed from the occasional occurrence of degeneration of nucleate sperma-

tozoa in members of this order. The presence of apyrene sperm in the Zeugloptera and Glossata-Hepialidae was confirmed by TEM observation, and it is concluded that apyrene sperm are "an evolutionary novelty of the Lepidoptera", i.e., they are another autapomorphy of that order. Friedländer also considered the question of the occurrence of "appendices laciniatae" in lepidopteran sperm (see character XVIII); these formations were not found on the testicular sperm of the homoneurous moths examined, and hence they cannot be considered a lepidopteran ground-plan autapomorphy.

3) The monophyly of the Heteroneura is now being questioned by Minet (in press, Nouvelle Rev. Ent. (n.s.)) but not on the same grounds as by Dugdale (see chapter three). Minet suggests that there is a sistergroup relationship between the Nepticulina and the remaining Neolepidoptera (i.e., the Exoporia + Incurvariina + Tischeriina + Ditrysia). As possible autapomorphies of the last-mentioned entity Minet envisages the crochet-bearing prolegs (character 96) and the connective-tissue pads on the ventral nerve cord (character 93). In including the proleg complement among the probable neolepidopteran autapomorphies I have, of course, assumed (as have previous authors) that the absence of these formations in the leaf- and stem-mining larvae of the Nepticulina is due to secondary reduction, as it certainly is in a number of apodous larvae of similarly endophagous Ditrysia (see, e.g., Hinton 1955). It is true that there is no certain proof that this is indeed correct, but the assumption remains a reasonable one. With respect to the absence of connective-tissue pads on the nepticulinan nerve cord I believe there can be little doubt that this is a case of secondary reduction: The hitherto examined members of the Nepticulina do not even have a dorsal enlargement of the cellular nerve-cord sheath, although such enlargements have been found in members of the non-glossatan grade (8). It should be noted that there is considerable variation in the development of the sheath

in some primitive moths, and it would come as no great surprise if future investigations of further representatives of the Nepticulina should indeed disclose the presence of connective-tissue pads.

Minet reports the important finding that the fusion of the anterior prosternal corners with the propleuron cannot, as claimed by Brock (1971), be upheld as an autapomorphy of the Heteroneura (character 105): The fusion is present in the Incurvariina, Tischeriina and Ditrysia, but is actually not (or only weakly, a parallelism?) developed in the Nepticulina. This naturally weakens the case for the monophyly

of the Heteroneura. With respect to character 104 Minet correctly notes that the subcostal male retinacula in primitive Heteroneura are not structurally uniform; it remains possible, however, that they pertain to a single transformation series. Altogether, in the light of the evidence from characters 103, 104, 106-109, and in the absence of stronger evidence for alternative phylogenies, I still consider the monophyly of the Heteroneura to be a justified and useful working hypothesis.

Corrections to previous articles
Among those misprints and errors in the previous articles which have come to my notice, a few are likely to cause confusion to the reader:

Article *14*, fig. 12. The posterior termination of the upper fibres of muscle 11 should have been shown as in fig. 11.

Article *16*, p. 124 (right), line 3 up. For "M4" read "M7".

Article *17*, p. 79 (right), l. 19-20 up. For "ground-plan apomorphies" read "groundplan traits".
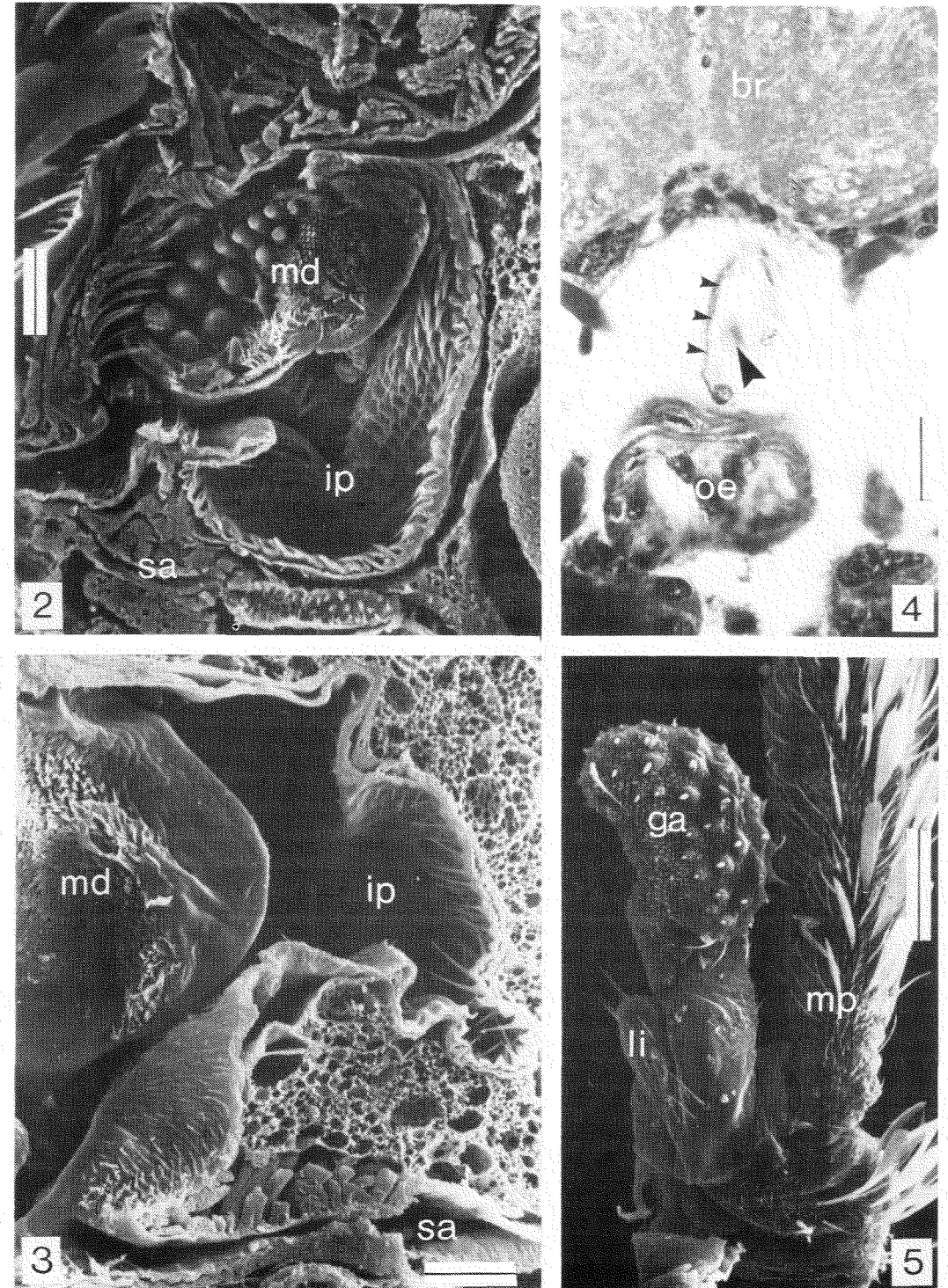
Figs 2-3. Preoral cavities in adult non-glossatan moths; sagittal sections in medial views, SEM. 2. *Heterobathmia pseuderiocrania*. 3. *Agathiphaga vitiensis*. Fig. 4. *Micropterix calthella*, horisontal section of head showing recurrent nerve (large arrow) running inside aorta (small arrows). Fig. 5. *Agathiphaga vitiensis*, base of left maxilla, ventral view, SEM. br: brain; ga: galea; ip: infrabuccal pouch; li: lacinia; md: inner surface of mandible; mp: maxillary palp; oe: oesophagus; sa: salivarium. Scales: 2-3, 40 μm; 4, 20 μm; 5, 100 μm.
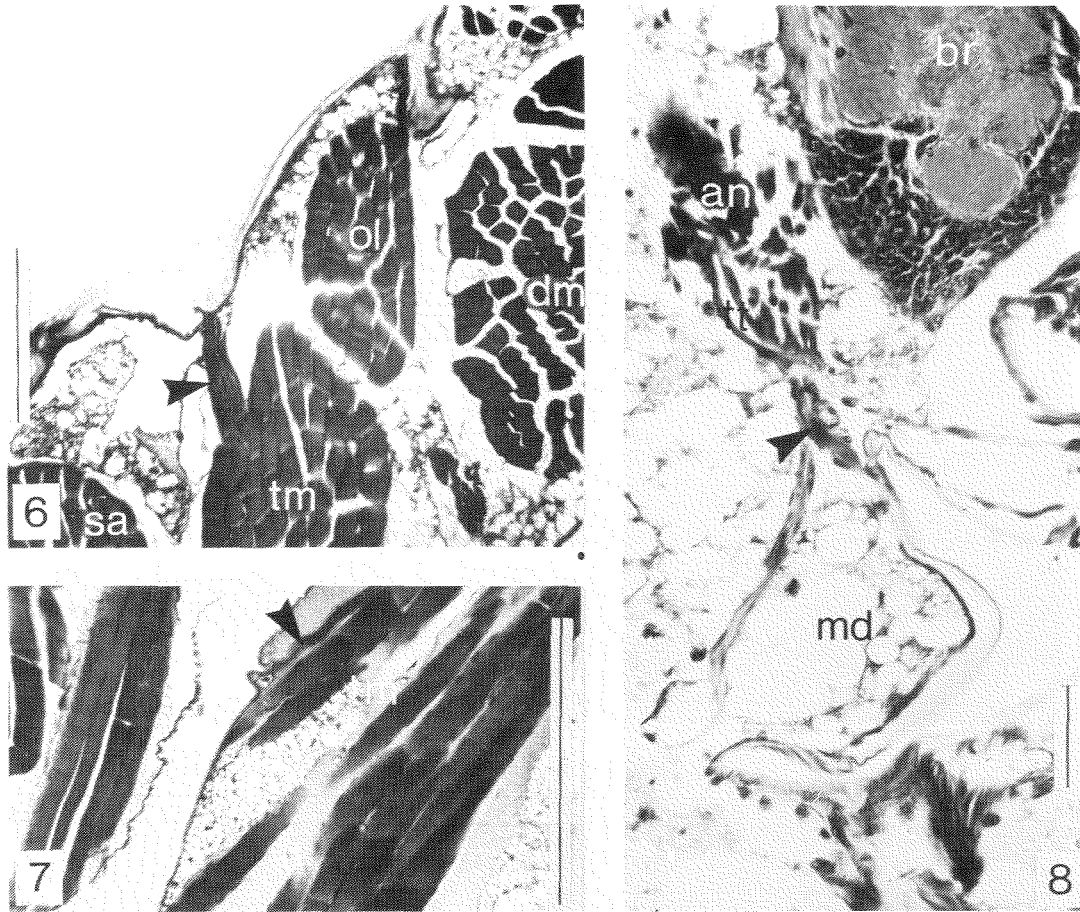
Figs 6-12. *Agathiphaga vitiensis*. 6-7. The "outer tergal remotor" (arrows) of the mesocoxa. 6. Origin of the muscle on lateral margin of scutum, transverse section. 7. Insertion of the muscle on slender tendon just above insertion of "inner tergal remotor", sagittal section. 8. Horisontal section of head, showing small tentorial adductor of mandible (arrow). 9. Lateral sagittal section of metathorax showing epimero-subalar muscle (arrow). 10. Medial sagittal section of mesothorax showing mesothoracic aorta (large arrows) curving upwards and running adjacent to the scutellar wall behind the scutoscutellar suture (small arrow). 11. Horisontal section of head showing free tritocerebral commissure (large arrows); also note recurrent nerve (small arrow) inside aorta. 12. Paramedial sagittal section of abdominal base, showing large, thinwalled stomodaeal crop and location of stomodaeum/mesenteron transition; the arrow at lower left points to the anterior rim of sternum II. an: tentorial antennal muscles; ao: (cephalic) aorta; br: brain; cr: stomodaeal crop; dm: median dorsolongitudinal muscle; md: mandible; me: mesenteron; ol: oblique/lateral dorsolongitudinal muscle; sa: coxosubalar muscle; sg: suboesophageal ganglion; st: stomodaeum; tm: (inner) tergomeral muscle; tt: tentorium; vc: ventral cibarial dilator. Scales 6, 7, 9, 10, 12, 200 μm; 8, 11, 50 μm.
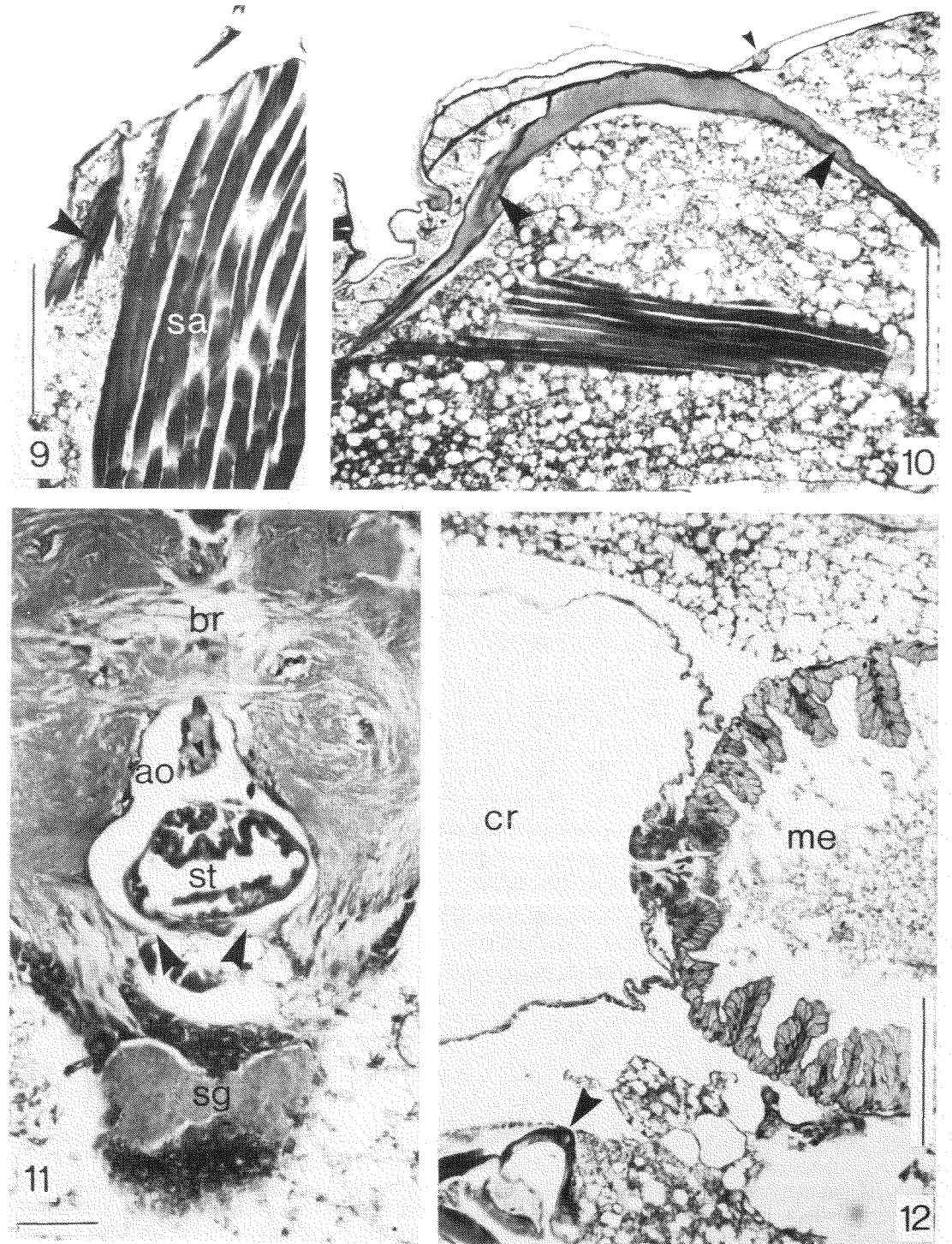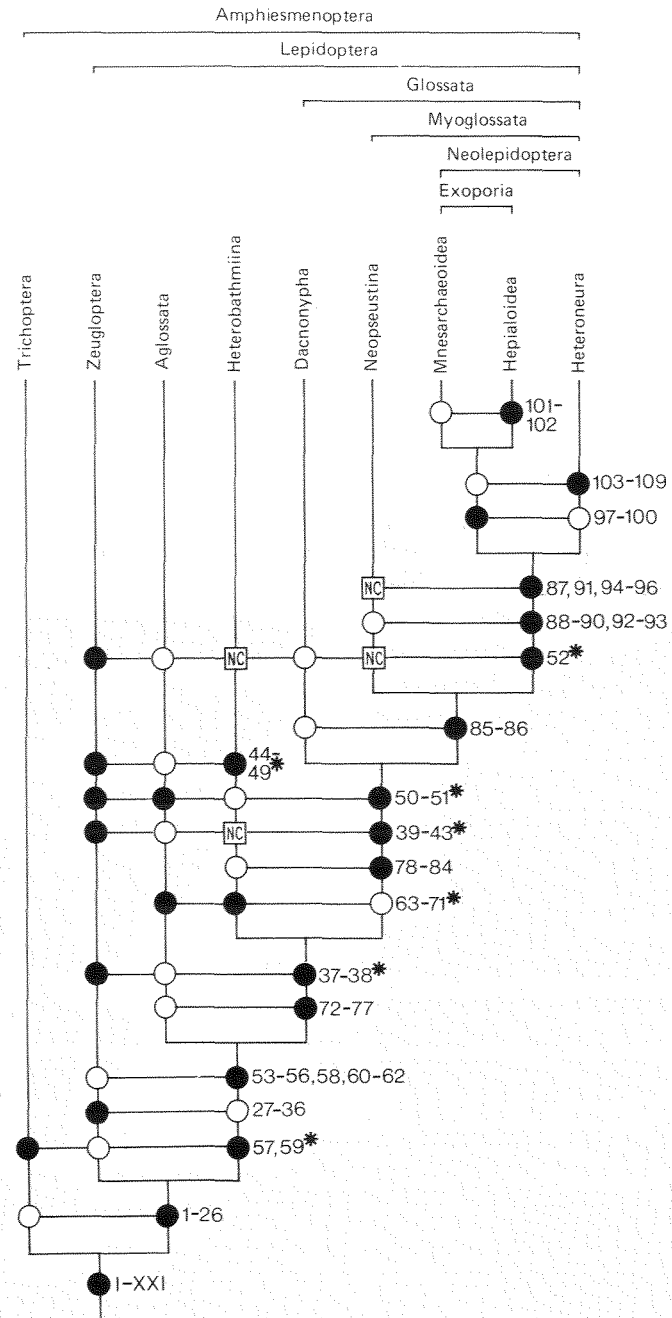
Fig. 13. Cladogram of the basic lineages of the Amphiesmenoptera and Lepidoptera. Roman and Arabic numerals refer to character enumeration in text. Filled circles are apomorphic character states, open circles plesiomorphic states. NC denotes "no comparison". Asterisks indicate supposed evolution of derived character states on more than one occasion. Unparalleled autapomorphies of the Trichoptera, Aglossata, Heterobathmiina, Neopseustina and Mnesarchaeoidea are not included. No autapomorphies of the Dacnonypha (as currently delimited, i.e., Erio-craniidae + Acanthopteroctetidae + Lophocoronidae) are known.
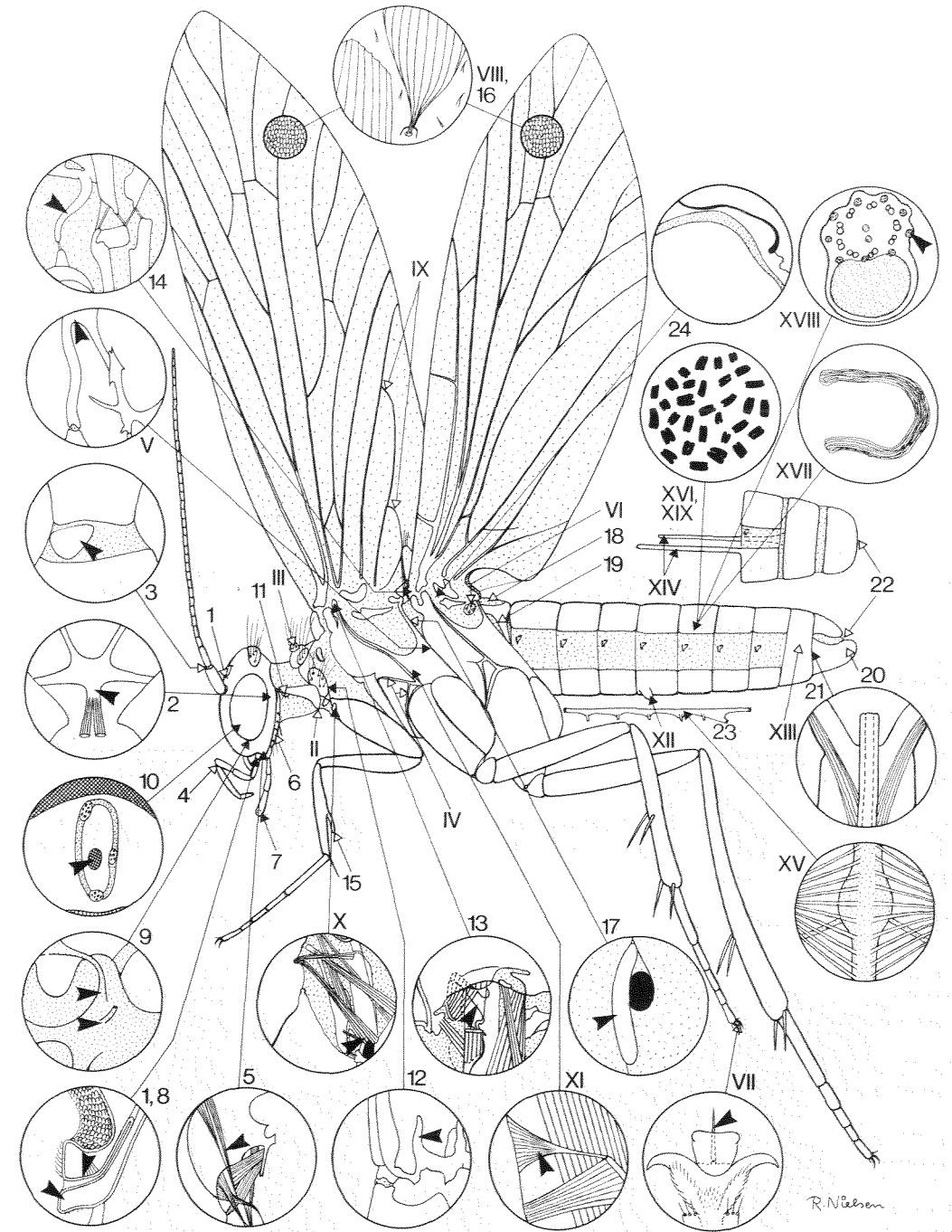

Fig. 14. Diagram of hypothetical ancestral moth. Roman and Arabic numerals refer, respectively, to the amphies-menopteran and lepidopteran ground-plan autapomorphies enumerated in chapter two. Drawings of details partly original, partly based on figures from Baccetti et al. (1970), Common (1970), Hannemann (1956), Matsuda (1970), Mickoleit (1969), Sharplin (1963), Suomalainen (1969) and Tindall (1965).

Habitus figures: Zeugloptera and Aglossata

Fig. 15. *Micropterix calthella* (Linnaeus, 1761). This species is locally very abundant in the Western Palaearctic and it is the most thoroughly studied non-neolepidopteran moth. Very many *Micropterix* species have a more elaborate forewing pattern with bright transverse bands.

Fig. 16. *Sabatinca* sp. near *delobeli* Viette, 1978. The *S. delobeli* species group contains the largest and most magnificent members (and so far the only named one) of the recently discovered "swarm" of micropterigid moths from New Caledonia. Although the majority of the New Caledonian micropterigids may be closely interrelated, they exhibit remarkable diversity in size and wing patterns.

Fig. 17. *Sabatinca (Micropardalis) doroxena* (Meyrick, 1888). One of the most widespread New Zealand *Sabatinca* species. It is interesting that the characteristic forewing pattern of *S. doroxena* is rather closely paralleled in *S. (Sabatinca) calliarcha* Meyrick, 1912, although on structural grounds these species clearly belong in different sections within the genus. Wing patterns in New Zealand *Sabatinca* are otherwise quite diverse.

Fig. 18. *Agrionympha vari* Whalley, 1978. The few *Agrionympha* species all have dark forewings with prominent transverse bands.

Fig. 19. *Paramartyria semifasciella* Issiki, 1931. One of the most frequently collected *Paramartyria* species. Some other members of the genus have an additional costal spot, while *P. immaculatella* Issiki, 1931 is devoid of forewing pattern.

Fig. 20. *Palaeomicroides obscurella* Issiki, 1931. A typical member of this overall uniform genus.

Fig. 21. *Neomicropterix nipponensis* Issiki, 1931. A frequently collected species which has been studied in considerable detail; it is, e.g., the only non-neolepidopteran moth for which information on the embryonic development is available. The *Neomicropteryx* species are superficially very uniform.

Fig. 22. *Epimartyria pardella* (Walsingham, 1880). The strikingly patterned western *Epimartyria*. The eastern *Epimartyria auricrinella* Walsingham, 1898 has unicolorous forewings.

Fig. 23. *Agathiphaga vitiensis* Dumbleton, 1952. The larger of the two *Agathiphaga* species. The caddisfly-like appearance of this moth is more striking in its natural resting posture where the antennae are directed forwards.

Paintings by R. Johansson from specimens/photographs of specimens in the collections of the British Museum (Natural History) (Figs 16, 17, 23), National Museum of Natural History, Washington D.C. (Figs 19-22), Transvaal Museum, Pretoria (Fig. 18) and Zoological Museum, University of Copenhagen (Fig. 15).

The figures are about 4.5 times natural size.
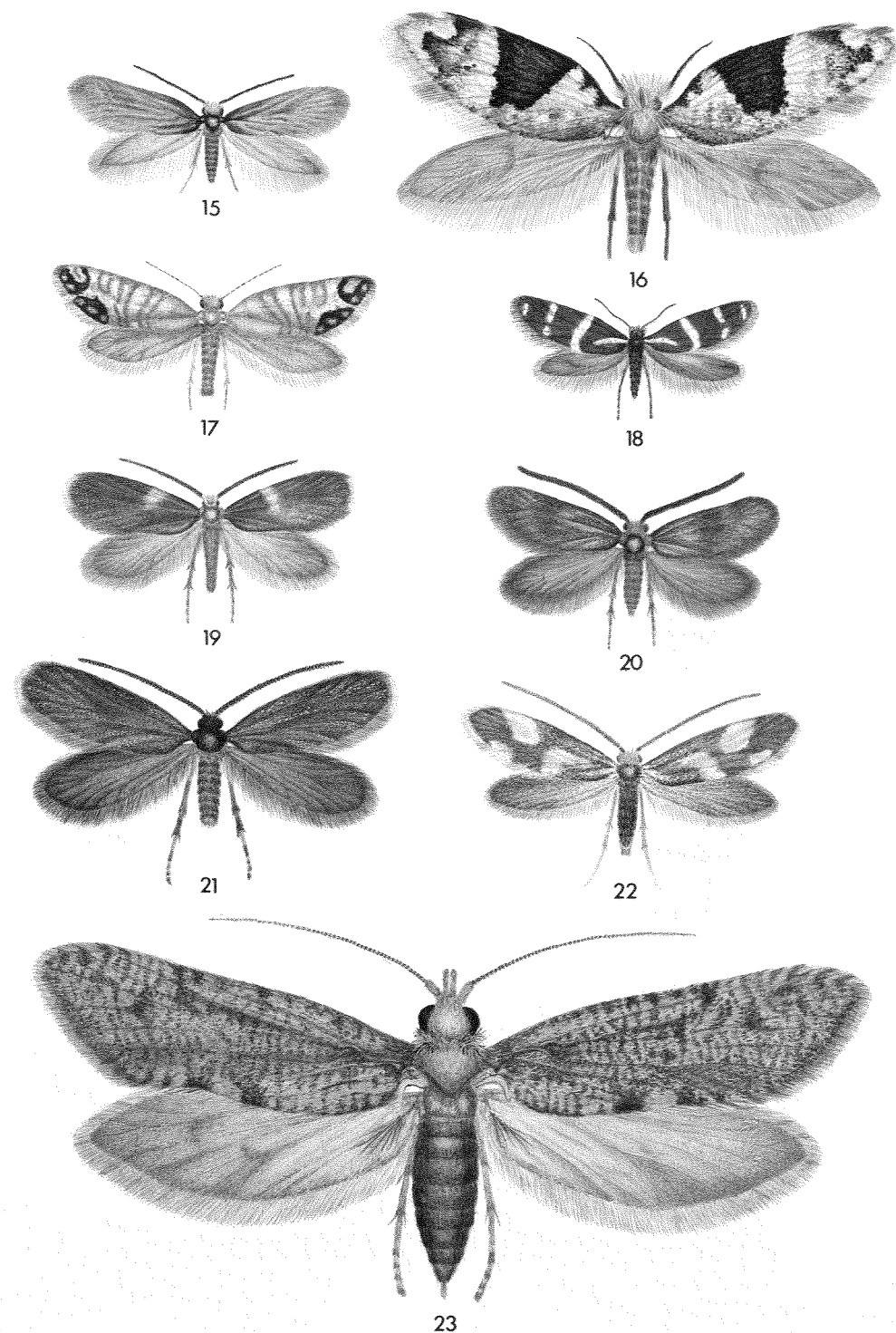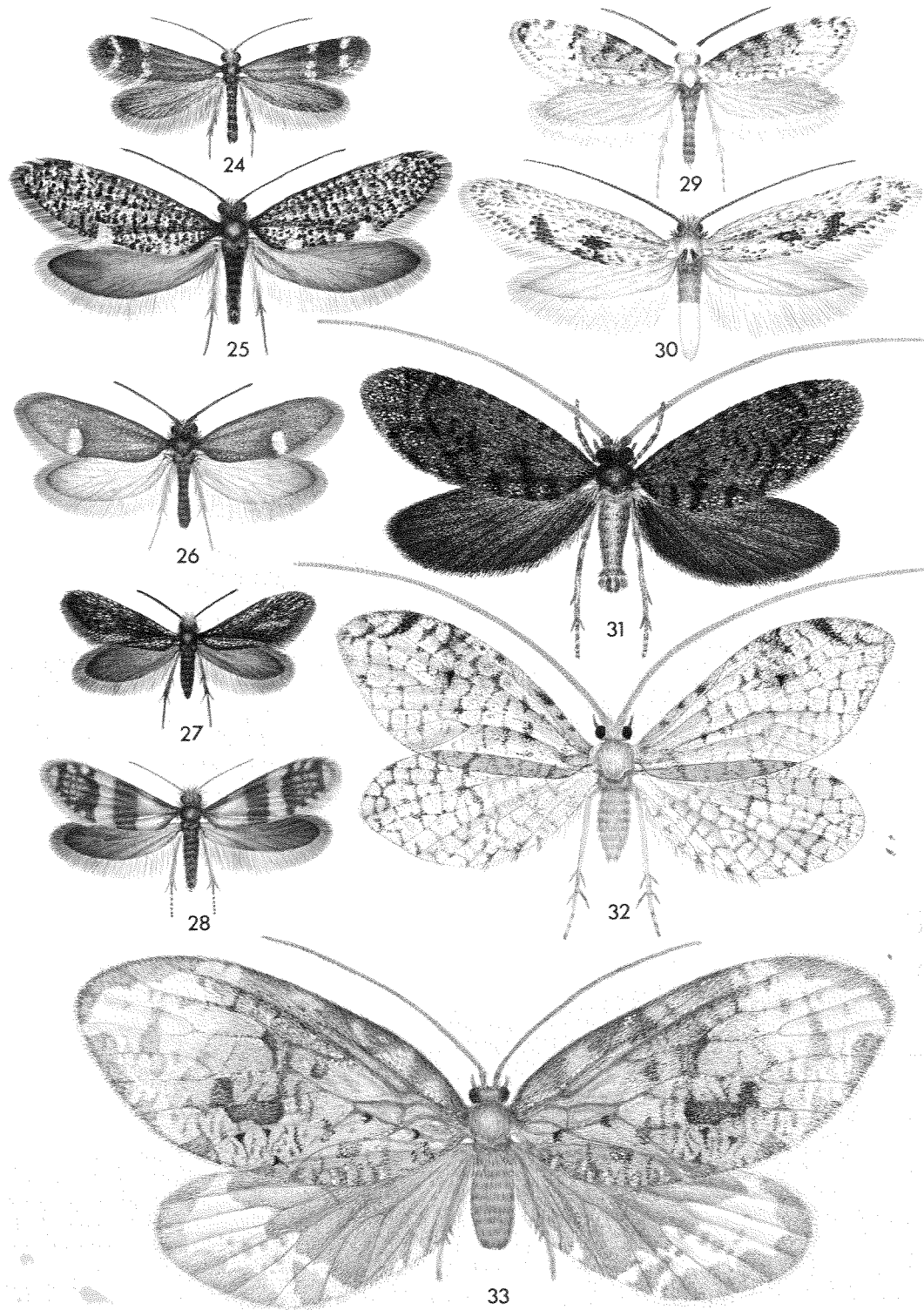
Habitus figures: Heterobathmiina, Glossata-Dacnonypha and Glossata-Neopseustina

Fig. 24. *Heterobathmia* "species A". The two named *Heterobathmia* species are illustrated in colour in 7. *H.* "species A" is perhaps the most strikingly patterned among the subsequently discovered, yet unnamed species.

Fig. 25. *Dyseriocrania subpurpurella* (Haworth, 1829). A common West-palaearctic species. It is characteristic of the members of this genus that golden rather than purple scales are predominant on the forewing.

Fig. 26. *Heringocrania unimaculella* (Zetterstedt, 1839). A common West-palaearctic species. Most members of the genus *Eriocrania* are very similar.

Fig. 27. *Eriocraniella xanthocara* Davis, 1978. A Californian species characteristic by the yellow cephalic vestiture and greenish forewing iridescence. Most members of the genus have similarly patternless forewings.

Fig. 28. *Neocrania bifasciata* Davis, 1978. A most unusual eriocraniid by virtue of the elaborate forewing pattern; the genital segments of both sexes are also strikingly aberrant.

Fig. 29. *Lophocorona pediasia* Common, 1973. This is the so far most frequently collected *Lophocorona* species. The bicoloured, dark-and-light forewings surely make the moth simulate a bird-dropping when at rest; similar wing patterns turn up again and again in higher Microlepidoptera also. Other lophocoronids have very different, prominently banded, forewings.

Fig. 30. *Acanthopteroctetes bimaculata* Davis, 1969. This is the largest *Acanthopteroctetes* species. The other named members of the genus have quite different forewing patterns (fuscous with light bands and spots).

Fig. 31. *Synempora andesae* Davis & Nielsen, 1980 (male). A neopseustid moth with densely scaled wings. The female is slightly larger and somewhat lighter, particularly on the apical half of the forewing (approaching a "bird-dropping pattern").

Fig. 32. *Apoplania penai* Davis & Nielsen, 1980. The thinly scaled *Apoplania* species are superficially uniform.

Fig. 33. *Neopseustis archiphenax* Meyrick, 1928. The largest, and hence most striking, neopseustid; the members of the genus are overall uniform.

Paintings by R. Johansson from specimens/photographs of specimens in the collections of the British Museum (Natural History) (Fig. 33), National Museum of Natural History, Washington D.C. (Fig. 30), University of California, Berkeley (Figs 27, 28) and Zoological Museum, University of Copenhagen (Figs 24–26, 29, 31, 32).

The figures are about 4.5 times natural size.