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Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity

NIELS P.KRISTENSEN[1], MALCOLM J. SCOBLE[2] & OLE KARSHOLT[1]

[1] *Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen Ø, Denmark; npkristensen@snm.ku.dk; okarsholt@snm.ku.dk*
[2] *Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK; M.Scoble@nhm.ac.uk*

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Abstract

The currently recognized robust support for the monophyly of the Lepidoptera (and the superorder Amphiesmenoptera comprising Lepidoptera + Trichoptera) is outlined, and the phylogeny of the principal lineages within the order is reviewed succinctly. The state of the taxonomic inventory of Lepidoptera is discussed separately for ‘micro-moths’, ‘macro-moths’ and butterflies, three assemblages on which work has followed historically somewhat different paths. While currently there are about 160,000 described species of Lepidoptera, the total number of extant species is estimated to be around half a million. On average, just over one thousand new species of Lepidoptera have been described annually in recent years. Allowing for the new synonyms simultaneously established, the net increase in species numbers still

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exceeds 800/year. Most of the additions are foreseeable in the micro-moth grade, but even for butterflies ca 100 species are added annually. Examples of particularly interesting new high-rank taxa that have been described (or whose significance has become realized) since the middle of the 20th century include the non-glossatan lineages represented by *Agathiphaga* and *Heterobathmia* and the heteroneuran families Andesianidae, Palaephatidae, Hedylidae and Micronoctuidae. Some thoughts on how present and future systematic lepidopterology might be prioritised are presented.

Key words: Lepidoptera, phylogeny, taxonomy, species numbers

Introduction

A combination of features has conspired to render the Lepidoptera one of the most studied groups of organisms. The order is species-rich and occurs in nearly all regions and a wide variety of habitats. The dense covering of scales on the wings not only gives the order its scientific name, but also forms the basis for the attractive colour patterns present in many species. The resultant conspicuousness of a variety of Lepidoptera explains much of the attention these insects have received. That attention, as we note below, has resulted in taxonomic work that while extensive exhibits much variation in quality. The state of Lepidoptera taxonomy, therefore, is partly a function of the visibility of these insects.

According to some newer estimates (Hammond 1992, T. Pape pers. comm. on Diptera , L. Vilhelmsen pers.comm. on Hymenoptera) the number of described extant species of Lepidoptera may be exceeded only by beetles and flowering plants. In the best known of all biota, those of NW Europe, Lepidoptera species numbers are also surpassed markedly by fungi, hymenopterans and flies, and the same observation will almost certainly prove to apply (at least in the case of the said insect taxa, likely also mites and nematodes?) on a global scale. Despite the unquestionable species richness of the Lepidoptera, they are far more homogeneous, structurally and ecologically, than the other larger insect groups: The point has been made repeatedly, that the most structurally diverse lineages, composed of the lower (non-ditrysian) grade in the order, account for only about 1-2 per cent of its total species number. The combination of a large number of species and little structural diversity can impede progress in the overall taxonomic treatment of an animal group.

The conspicuousness and attractiveness of such lepidopterans as butterflies, hawk moths and emperor moths, have made these insects popular 'beginners items' with amateur entomologists. And when advanced amateur lepidopterists seek challenges in groups other than those most easily accessible, they often proceed to less conspicuous lepidopterans rather than to other orders of insects. Paradoxically, the popular appeal of Lepidoptera may have adversely affected professional research on the order. A student of systematic entomology will often enter the field through working on the local fauna, and in some countries may then find it easier to make 'immediate new discoveries' by studying insects other than Lepidoptera. Also, the study of aesthetically pleasing insects sometimes elicits the charge of being *ipso facto* intellectually second-rate! Negative attitudes held towards allegedly 'philatelistic' butterfly workers (Paul R. Ehrlich (1960) mentioned the sometime influential insect morphologist/taxonomist G. F. Ferris as an instructive example) may well reflect adversely on lepidopterology as a whole. Faced with such an attitude from their superiors, it is hardly surprising that some potential lepidopterists have chosen to turn for their graduate studies to insect taxa that are judged to be more academically respectable.

The colourful vestiture of scales and hairs on the wings, body and appendages of Lepidoptera certainly often offers excellent diagnostic features at the lower taxonomic levels, but at the same time this vestiture conceals most of those exoskeletal traits found to be so useful in supraspecific classification, and which are more easily and routinely studied in insect taxa where the exoskeleton is exposed. Vestiture, thus, has invited literal superficiality in Lepidoptera taxonomy. Not only has this impeded taxonomic progress, but it may well have contributed to the aforementioned disdain for Lepidoptera studies within parts of the ‘establishment’ of systematic entomology, hence creating a vicious circle. Yet Lepidoptera have been used often as model organisms in a wide range of investigations in related disciplines. Furthermore, given that these insects lend themselves to colour- and pattern-based identification, they have attracted the attention of a variety of non-professional lepidopterists (e.g., ornithologists) where identification is primarily visual. Given such interest in Lepidoptera, professionals would do well to encourage this broader engagement, and help the group to become the flagship taxon of the invertebrates for inventorying biodiversity.

This article combines a succinct outline of Lepidoptera phylogeny (essentially a condensed and updated version of the corresponding sections in Kristensen & Skalski 1998) with information and discussion on the state of the inventory and classification of this major insect order.

Lepidoptera monophyly and affinities

The monophyly of the 'order' Lepidoptera is firmly established by an impressive suite of synapomorphies of its constituent basal lineages. The position of the group within the insect hierarchy is similarly well established: It has a strongly supported sistergroup relationship to the Trichoptera (caddisflies), constituting with the latter the high-rank taxon Amphiesmenoptera. The Amphiesmenoptera, in turn, together with the (similarly monophyletic?) Antliophora (Mecoptera *s.lat.* [including the Nannomecoptera, Neomecoptera and Siphonaptera] + Diptera), constitute the Mecopterida or 'panorpoid' clade within the Endopterygota; for supra-ordinal relationships see, e.g., Kristensen (1999), Beutel & Pohl (2006).

A detailed reconstruction of the lepidopteran ground plan was presented by Kristensen (1984) and updated in Kristensen & Skalski 1998). Several apomorphies arguably unique to the Lepidoptera were identified, and another set of groundplan traits was identified as probable synapomorphies with the Trichoptera, i.e., autapomorphies of the Amphiesmenoptera. The great majority of the characters in question occurs in the adult insect. Subsequent work has suggested little in the way of change.

The following morphological character states are currently considered likely lepidopteran groundplan autapomorphies: ***Adult*** (numbers in brackets refer to figured details in Fig.1): Median ocellus lost (1). Corporotentorium with posteromedian process, accommodating insertions of ventral neck muscles (2). Intercalary sclerite present laterally in membrane between antennal scapus and pedicellus (3). Maxillary palp with points of flexion between segments 1/2 and 3/4; segment 4 longest; intrinsic palp musculature not comprising antagonistic pairs (4). Craniostipital muscle present, slender and running close to craniocardinal muscle (5). Postlabium an arched sclerite with long piliform scales (6). Terminal segment of labial palp with group of sensilla in depression ('vom Rath's organ') (7). Labral nerve and frontal ganglion connective separating immediately at their origin on the tritocerebrum (9). Nervus recurrens running inside aorta until reaching retrocerebral complex (10). Laterocervical sclerite with proprioceptive 'hair plate' close to anterior apex (11). Prothoracic endoskeleton with prominent free arm arising from bridge between sternum and lower posterior corner of pleuron (12). Mesothorax with 'tergopleural apodeme' issued from upper part of pleural suture and accommodating insertion of a tergopleural muscle (13). Metathorax with 'prescutal arm' (14). Fore tibia with movable 'epiphysis' on inner surface, and with at most a single spur (15). Wings with dense covering of broad scales (16). Metathoracic spiracle with single, anteriorly situated, external lip (17). Tergum I extensively desclerotized, with concomitant loss of external layer of 'short' dorsolongitudinal I/II muscles (18). Tergum I with lateral lobes extending posteroventral to articulate with anterior corners of sternum II (19). Male 'valve' (gonopod) primarily undivided (20). Phallic protractor muscle originating inside gonopod (‘valve’) (21). Cerci lacking in both sexes (22). Abdominal nerve cord with at most five ganglionic masses, and unpaired connectives (23). Apyrene sperm present (24). ***Larva***: Pleurostome elongated, craniocardinal articulation far behind mandibular base. Maxillary palp with no more than 3 segments.

Absence of a dorsolongitudinal muscle on the adult's salivarium (8) has been considered an additional lepidopteran autapomorphy, but unpublished observations on nannomecopterans (R. Beutel, pers. comm.) and trichopterans render it uncertain that a presence of a formation of this kind is actually the groundplan condition in the Mecopterida.

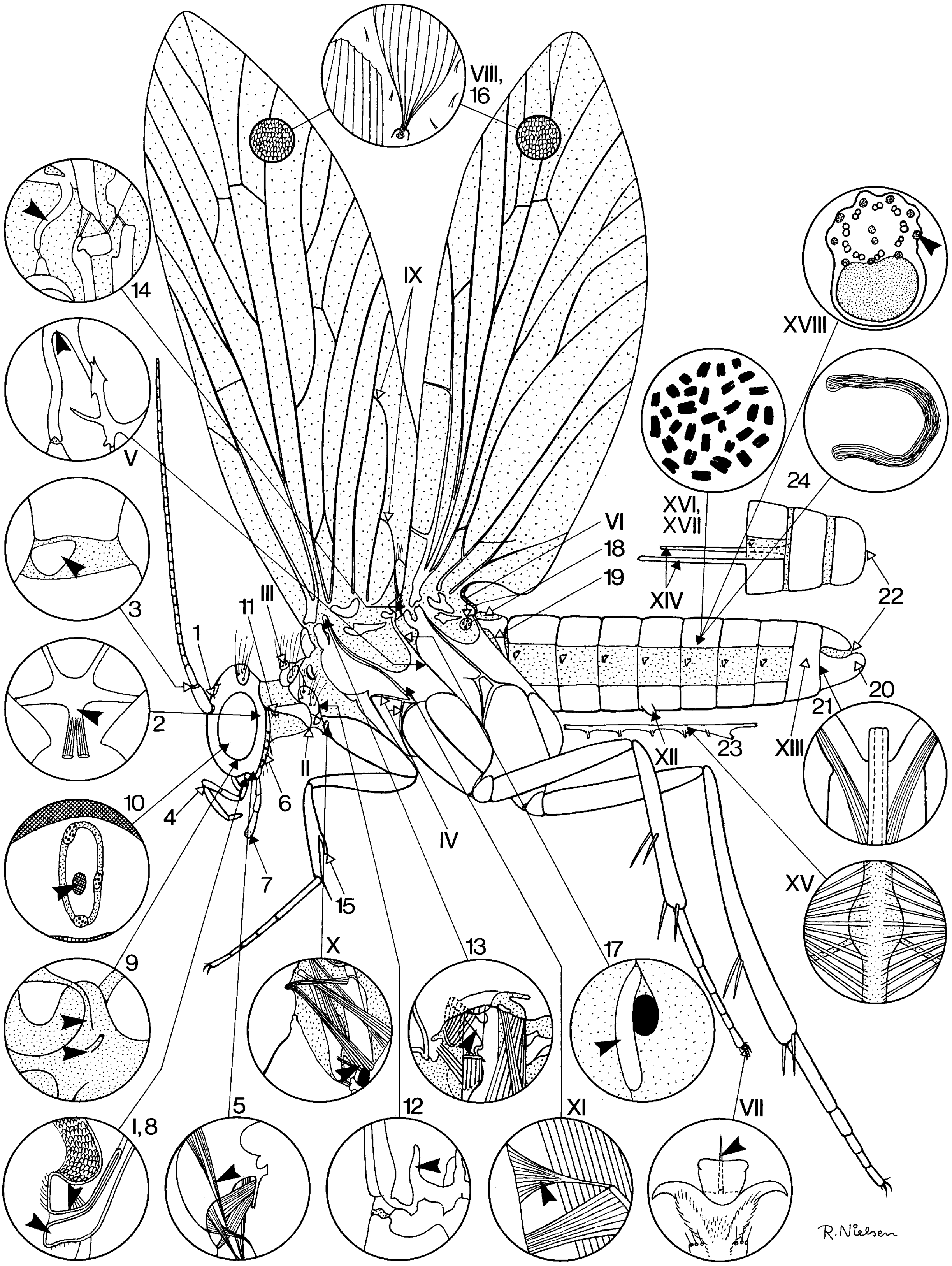


FIGURE 1. Diagram of hypothesized adult ground plan of the Lepidoptera. Roman numerals refer to putative synapomorphies of Trichoptera and Lepidoptera, hence autapomorphies of superorder Amphiesmenoptera. Arabic numerals refer to putative lepidopteran groundplan autapomorphies. The characters in question are listed in the text. After Kristensen & Skalski (1998), slightly modified.

In the light of this robust morphological support for the monophyly of the Lepidoptera, inclusive of the Micropterigoidea, the assignment (Chapman 1917, Hinton 1946, 1958) of the latter to a separate order Zeugloptera is now of historical interest only. Lepidoptera monophyly has also been supported consistently in available molecular analyses with relevant taxon sampling.

The following lepidopteran groundplan traits are apparently autapomorphic of the superorder Amphiesmenoptera. ***Adult*** (Roman numerals are details in Fig.1): Prelabium fused with hypopharynx (I). Lower posterior corner of laterocervicale produced towards the prosternum (II). Pronotum with paired setose 'warts' (III). Prothoracic episterna with unique suture pattern (IV). Secondary furcal arms of pterothorax fused with posterior margins of corresponding epimera (V). Metathorax with setose, presumably proprioceptive, sclerite in wing base membrane behind/below subalare (VI). Pretarsus above claw with 'pseudempodium' (strong seta on socket) (VII). Wings with dense vestiture of setae (forerunners of the lepidopteran scales)(VIII). Fore wing anal veins looping up into double-Y formation (IX). One ventral (tentorial) neck muscle originating on fore coxa (X). Conical furcopleural muscle in mesothorax with broad end on pleural ridge (XI). Paired glands opening on sternum V (XII). Male segment IX with tergum and sternum fused into closed ring (XIII). Anterior margin of female segments VIII and IX with long rod-like apodemes accommodating insertions of protractor and retractor muscles of extensible oviscapt (XIV). *Note*: recent work shows that the interpretation of the female postabdomen in the lowest Amphiesmenoptera is more problematical than hitherto believed, and the apodemes in question may not all be homologous (Kristensen 2003); a particularly intriguing question is whether a three-apophysis-pair configuration (with both dorsal and ventral apophyses originating on VIII) could prove ancestral in Amphiesmenoptera, since three pairs are present in *Agathiphaga* as well as in the enigmatic recently described caddisfly *Fansipangana* (Mey 1996). Ventral diaphragm muscles inserting on the nerve cord (XV). Female sex heterogametic (XVI). Chromosome number unusually high (basic number 30–31), chromosomes holocentric and oogenesis achiasmatic (XVII). Spermatozoa with outer accessory filaments thickened, filled with proteinaceous and glycogen-like material (XVIII). ***Larva***: stemmata each with one crystalline cone cell transformed into primary pigment cell, hence in transverse section the cone is seen to be only tripartite. Prelabium and hypopharynx fused into composite lobe with silk gland orifice on apex.

Evidence suggests that larvae of members of the amphiesmenopteran stem lineage were 'soil animals', living in wet conditions, like those of most extant Lepidoptera-Micropterigidae. The step from here to a truly aquatic lifestyle, which is autapotypic of immature Trichoptera, is but a small one. There is every reason to believe that these larvae were free-living, for the use of silk as part of pre-pupating larval behaviour first evolved, as far we know, in the stem lineage of the Neolepidoptera.

Lepidoptera phylogeny, and the inventory of major groupings

Some key points in the history of lepidopteran classification were given by Scoble (1992), and what follows immediately below is based on that account. The most prominent early landmark in lepidopteran classification is the 10th edition of Linnaeus’ *Systema Naturae* (Linnaeus 1758), which, other than for spiders, represents the beginning of zoological nomenclature as accepted by the *International Code of Zoological Nomenclature*. Although published work on lepidopteran natural history dates back to Aristotle (384–322 BC), and while later pre-Linnaean authors, notably Albertus Magnus, Marcel Malpighius, Jan Swammerdam, René Reaumur, and Charles De Geer, made significant contributions, it was Linnaeus who provided a classification, comprehensive for the time, in which we see the germ of subsequent systems. Linnaeus (1758) recognised three main divisions of the Lepidoptera - *Papilio*, *Sphinx*, and *Phalaena*. *Phaleana* was divided into seven subgroups. Today, all but *Phalaena* are still used for nine superfamilies. Following the Linnaean sequence these superfamilies are: Papilionoidea, Sphingoidea, Bombycoidea, Noctuoidea, Geometroidea, Tortricoidea, Pyraloidea, Tineoidea, and Alucitoidea. Linnaeus’ coverage was remarkable and his system, evidently, is embedded in our higher classification today.

Linnaeus based his classification on features of the antennae and the wings, particularly the position of the wings at rest, and on whether the insects flew by day or by night. He also took account of the mouthparts. He noted that the antennae of butterflies were clubbed, and that some members of what he called 'Bombyces' lacked a tongue. A considerable variety of features of larvae and adults is to be found in his species descriptions.

Lepidopteran classification developed from the Linnaean foundation in several ways. Numerous additional species were described, as discussed elsewhere in this paper and Linnaeus' divisions and subdivisions were further divided and formal categorical ranks were established for them. Moreover, many supraspecific taxa were added to those introduced by Linnaeus. Primary types of many Linnean Lepidoptera species survive to this day, and thus remain available for study. Linnaeus' own collection is housed in the Linnean Society of London (see http://www.linnean.org/); examples are shown in Figs 2–3.

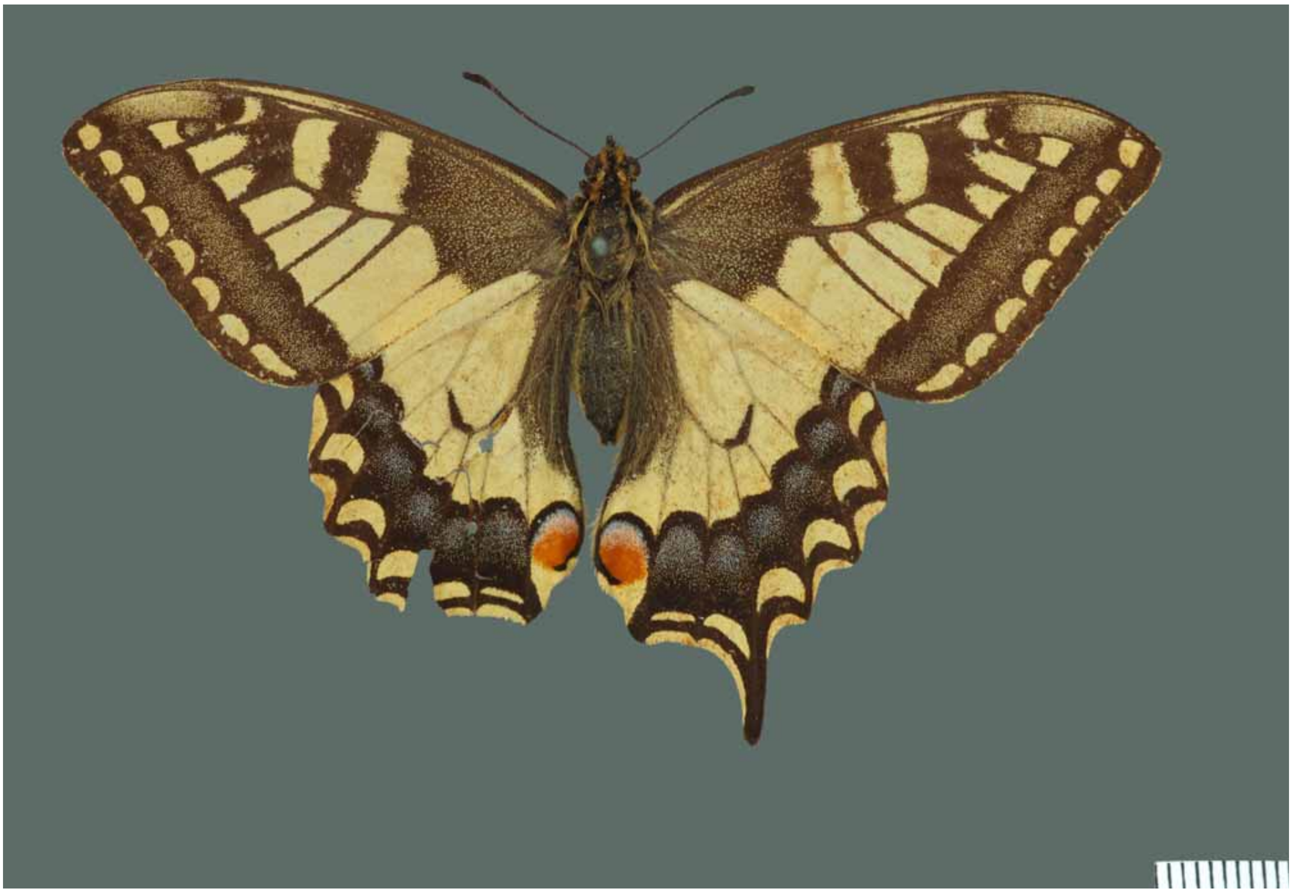
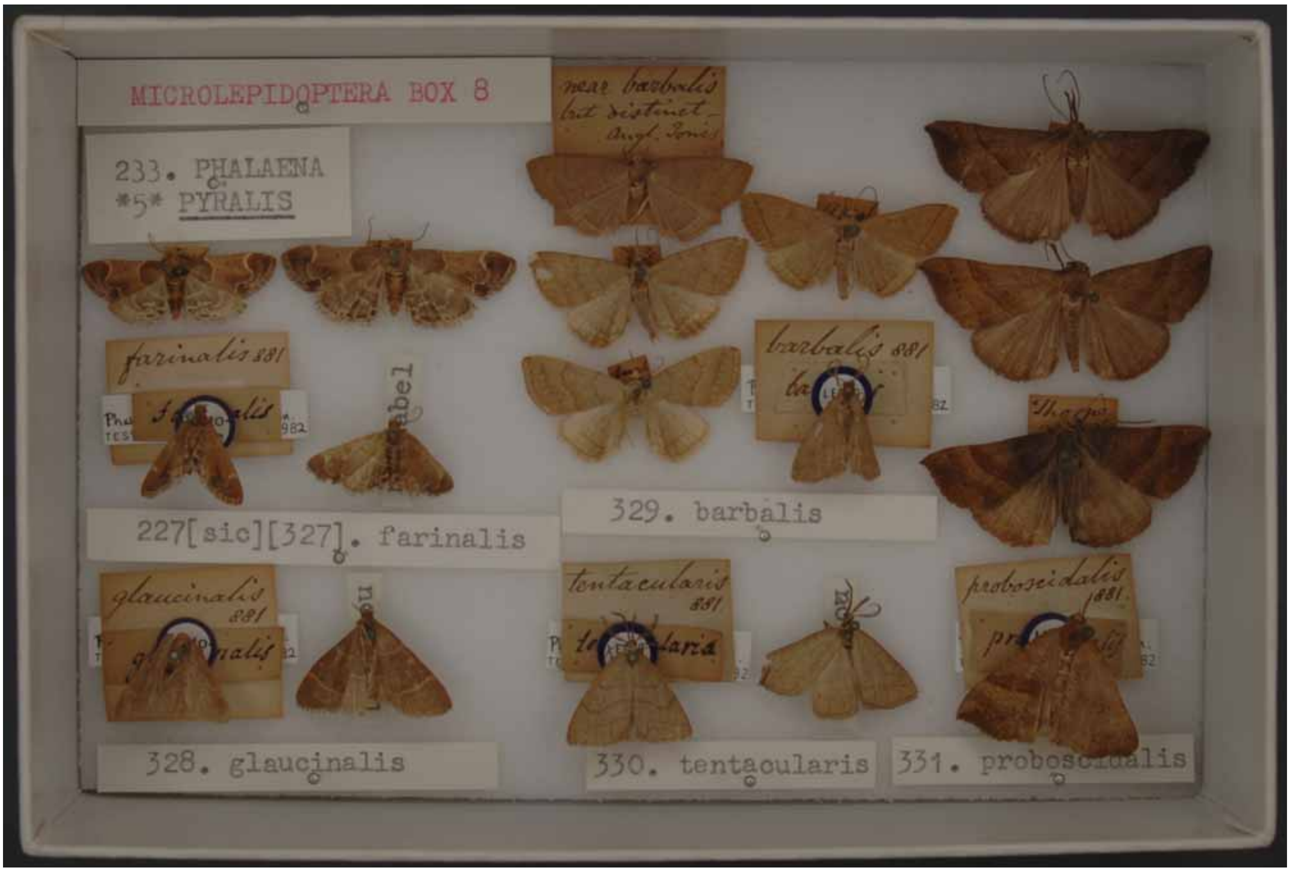


FIGURE 2. Lectotype of *Papilio machaon* Linnaeus, 1758, type species of the genus *Papiio* Linnaeus, 1758. "… *if this is not a butterfly in a nomenclatural sense, then nothing is*" (Vane-Wright 2007: 59). Courtesy of The Linnean Society of London.

Prior to Linnaeus' death, and just under twenty years after the publication of *Systema Naturae,* Denis & Schiffermüller (1775) produced a work on the Lepidoptera of the Vienna area. Their system was based on Linnaeus' classification, but they added further observations on structure and examined many additional species. They subdivided the Linnaean groups and based the names of many of the subdivisions on both larva (e.g., Larvae Punctatae) and adult (e.g., Ph[alaenae] Geometrae Unicolores). Building on these foundations, the Danish entomologist Fabricius, who was a student of Linnaeus, described many new species and named some of the Linnaean subgroups (Fabricius 1775 - and several later works). Fabricius' impact on Lepidoptera taxonomy (indeed insect taxonomy broadly) was notable. Slightly later, Latreille (1796) added further supraspecific groups, most of which represent genera in the modern sense.



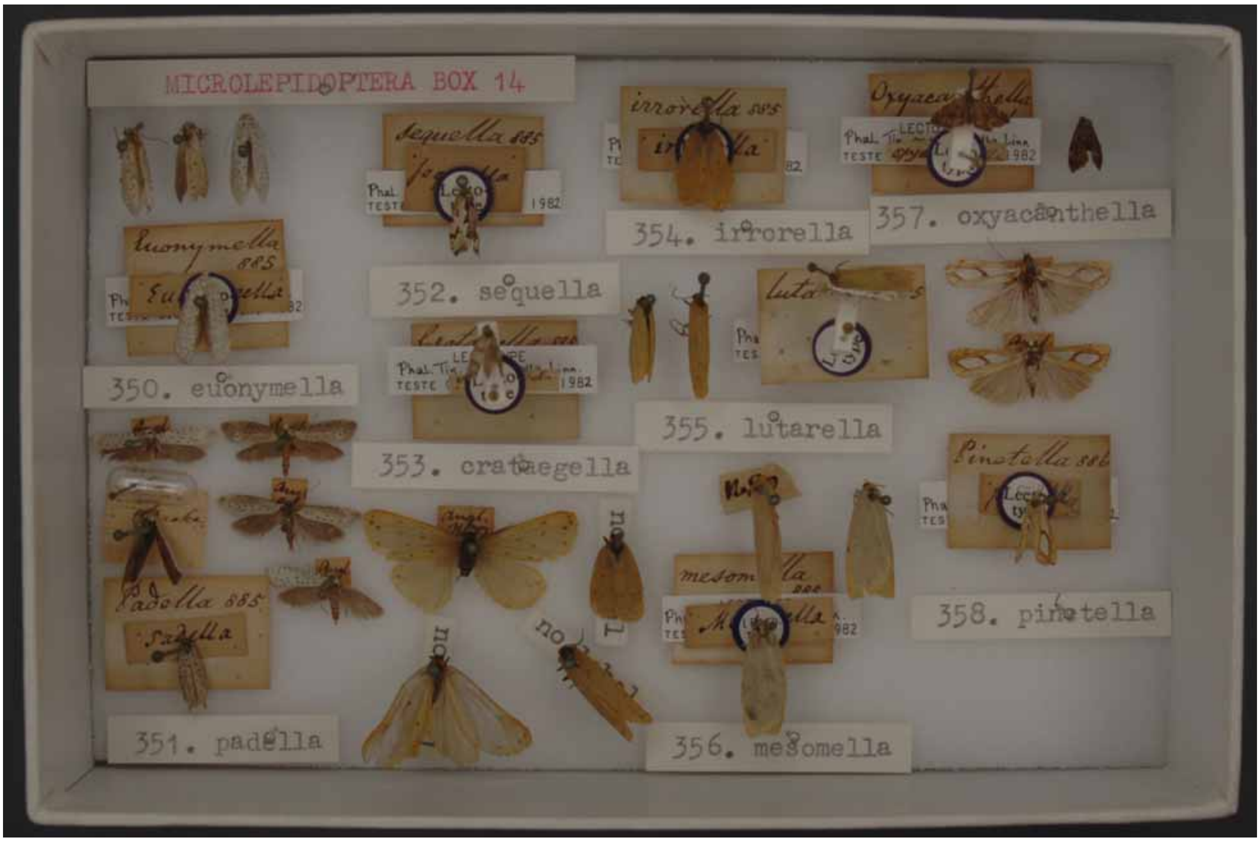


FIGURE 3. Two unit trays of moths from Linnaeus's collection. While these trays indeed contain 'Microlepidoptera' (typewritten labels in upper left corners) in the sense that the moths were described in *Pyralis* and *Tinea*, several of the species are now placed in the macrolepidopteran family Noctuidae. Courtesy of The Linnean Society of London.

A major step in the evolution of lepidopteran taxonomy was noted by Emmet (1992) who suggested that our modern concept of the genus in Lepidoptera was provided by Schrank (1801–02), who added this level between the Linnaeus' 'genus' and species. Many modern genera were established by Jacob Hübner, a designer and artist, who described and illustrated many of the genera (called *Stirpes* by him) that we recognize today (Hemming 1937). The lepidopteran genus was firmly established by Ochsenheimer (1807–1835), in a series of works completed by Treitsche, in his synthesis of the lepidopteran fauna of Europe.

Many of the higher taxa of Lepidoptera that we still accept in a recognizable form emerged from the impressive and very influential six volume study by G.A.W. Herrich-Schäffer. The work was published at regular intervals between 1843 and 1856 (Herrich-Schäffer, 1843–1856). Although, as for earlier works, this study was based on the European fauna, the implications are applicable far more widely. To a significant extent, Herrich-Schaeffer established the taxa on wing venation. He provided numerous morphological illustrations, which are remarkable in their detail and execution.

With collections being made from beyond Europe, a further dimension to the classification was added. Apart from the fact that they described numerous new genera and species, Edward Meyrick (particularly for microlepidopterans) and Sir George Hampson (particularly for macrolepidopterans) had a marked impact on the higher classification of the order. Meyrick (1895) proposed that the Lepidoptera should be divided into ten 'phyla'. Meyrick, like Herrich-Schäffer, relied to a significant extent on wing venation because he considered the pattern to be of low adaptive ('physiological') value and likely therefore to be little altered by external factors. Hampson's contribution to Lepidoptera higher classification focused mainly on Noctuoidea (see Kitching 1984 for an analysis), Pyraloidea, and Thyridoidea.

Since the mid nineteenth century many other systems have caused the earlier classifications to be modified and expanded. Some writers emphasized other character sets e.g., from larvae (Fracker 1915) or pupae (Mosher 1916). Probably the major contribution to the higher classification of the order concerns the division above the superfamily. Landmark works were written by Börner (1925, 1939) who proposed a fundamental division of the Lepidoptera into Monotrysia and Ditrysia on the basis of the structure of female genitalia. The Monotrysia (*sensu* Börner), which included only 5 percent of the Lepidoptera, are not monophyletic. But Börner's recognition of the Ditrysia as a natural group was an important step in understanding the phylogenetic structure of the order. So also was his appreciation of the systematic value of many morphological characters in the classification and diagnosis of lepidopteran families and superfamilies. Building on the works of Börner as well as of Kiriakoff (1948) and in particular Hinton (1946), Hennig (1953) outlined the relationships of the most basal lineages within the order in a benchmark article, which foreshadowed subsequent work on this subject.

One hundred and twenty-four lepidopteran families (52 of them with a subfamily classification) were recognized in the recent treatment of the order in the *Handbook of Zoology* (Kristensen ed. 1998, 2003). These families were grouped into 47 diagnosed superfamilies, and a provisional phylogeny at the superfamily level was presented. About the same time an alternative classification was presented by Heppner (1998), who later (2005) expanded it to tribal level. The two classifications are broadly similar, but some differences exist, partly because Heppner's classification expressly does not aim to reflect monophyla in the 'Hennigian' (cladistic) sense of phylogenetic systematics. Moreover, the superfamilies and higher-level entities in Heppner's work were not diagnosed. The superfamily/family/subfamily classification adopted in the *Handbook*, with some major modifications suggested in subsequent work, is given in Appendix 1. Although the superfamily cladogram printed in the *Handbook* (and see Fig. 3 in the present paper) has been referred to as representing the "consensus" position (Holloway *et al*. 2001), its provisional nature should be emphasized: its lack of resolution of major branches is conspicuous. It serves, however, as a starting point for some ongoing inquiries into Lepidoptera phylogenetic systematics (see, e.g., the http://www.tolweb.org/Lepidoptera and http://www.lepsys.eu/ websites). In Fig. 4 the approximate species numbers for superfamilies/superfamily assemblages with more than 1,000 described species is indicated by the width of the clade lines. It is immediately

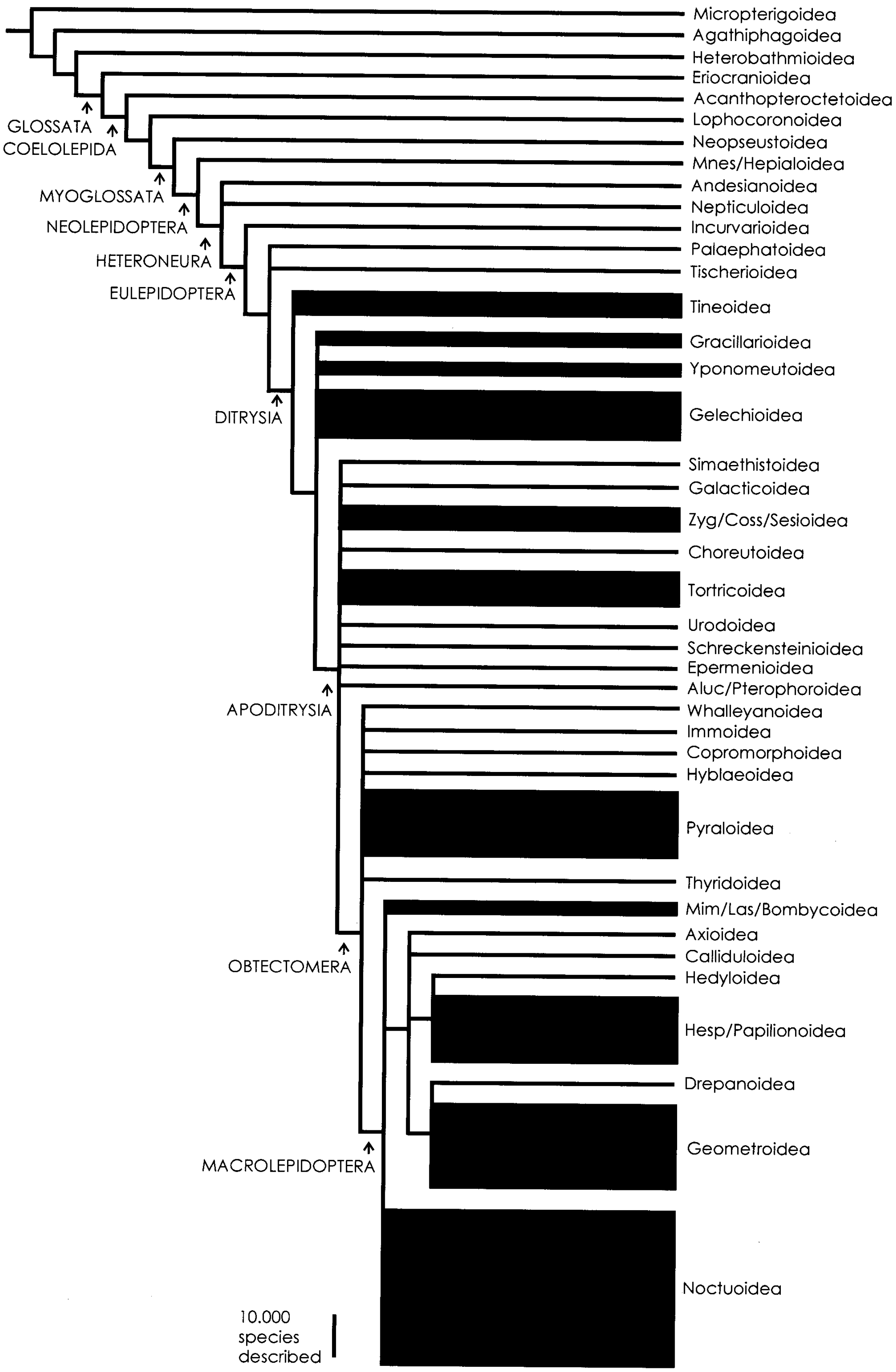


FIGURE 4. Cladogram of lepidopteran superfamilies/superfamily assemblages. Widths of clade bars pertaining to larger clades (>1.000 species) reflect estimated numbers of *described* species. Scale bar = 10,000 species. From Kristensen (ed.) (2003).

apparent, that the most species-rich lineages are cladistically quite subordinate. This particular phylogenetic pattern was ascribed considerable general significance in Hennig's writings (e.g., 1953, 1966): indeed, the basic diversification pattern within the Lepidoptera remains an unusually instructive example of what has subsequently come to be known as a 'Hennigian comb', with the first diverged extant lineages exhibiting a step-by-step acquisition of the apomorphies which characterize the most subordinate (and successful) groups. Undoubtedly the proportional representation of individual superfamilies will change markedly as descriptive Lepidoptera taxonomy approaches completion. Thus only relatively modest growth is foreseeable in the butterfly and bombycoid assemblages, while particularly strong increases are expected for the Gelechioidea and the Pyraloidea.

Inventorying the Lepidoptera: status and biases

Gaston (1991a: 286) was undoubtedly correct when writing that "The Lepidoptera are generally regarded as the best collected and studied of the four major insect orders". However, on a global scale this general belief is in itself probably incorrect. The advanced levels of butterfly and hawk/emperor moth taxonomy and of inventories of some very restricted Northern Hemisphere Lepidoptera faunas have little bearing on the overall status of systematic lepidopterology. The major tasks for delivering this more comprehensive picture lies in dealing with the world fauna of moths. The sampling of tropical moths has so far been very inadequate, and where samples have been made they have often not been worked up. This situation is significantly explained by the work of Gaston & May (1992). These authors found, on the basis of surveys of insect systematists in North America and the UK, that of the four major insect orders the Lepidoptera actually have the *smallest* taxonomic workforce. The same situation then pertained also in Australia (pers comm. from the late E.S. Nielsen). This situation is unlikely to have changed today.

From their survey, Gaston & May (1992) indicated that about 80% of present-day insect taxonomists then were based in North America and Europe, a figure unlikely to have changed much subsequently—except, probably, for some E. Asian countries. Taxonomy also has had longstanding strongholds in other industrialized countries such as Japan, Australia and New Zealand. It is therefore to be expected that the faunas will be better known in these regions than elsewhere, but it must also be noted that to several workers based here certain tropical areas (Taiwan, Borneo, Costa Rica, etc.) have recently been of focal interest.

Experience shows, that *large-scale* elucidation of life-histories of the insect fauna of a given area is feasible only for those workers who are at least largely resident in that area. The knowledge of Lepidoptera immatures is, therefore, even more geographically biased than that of the adult insects.

‘Patriotism’ has also made its mark on our knowledge of distribution in Lepidoptera, particularly in terms of the activities of non-professionals. 'Patriotism' in this context means the sum of linguistic and traditional/ cultural barriers, which restrict the activity of a worker to the study of her/his national fauna. Perhaps the most striking evidence of this mechanism is the markedly more detailed knowledge of the moth fauna, particularly of the micro-moths, of Europe compared with that of any N. American area. So many N. American lepidopterists remain 'butterfly workers', since they feel few barriers to extending their interest to the butterfly fauna of the entire Nearctic region. In contrast, the average amateur lepidopterist, at least in some European countries, having exhausted the challenges (at the collectors' level!) presented by the local butterflies, has been more likely to proceed to the study of the macro-moths, and often also the micro-moths, of the national fauna, rather than to butterflies of neighbouring countries. This explains why in some countries even the most minute micro-moths are now known in much greater detail than larger and more striking wasps, flies etc. Having said that, an increasing number of European amateur specialists in recent decades have extended their interests, and descriptive efforts, to Lepidoptera faunas outside their native regions.

A provisional survey of the described world fauna of Lepidoptera, by family-group taxa and zoogeographical regions, was published by Heppner (1991) (minor updates are given by Heppner 1998). This survey was based partly on actual counts from the literature, partly on the card indexes in the Natural History Museum (London) and the National Museum of National History (Washington), and partly on estimates (the source is uncertain in many cases). Clearly this task was a difficult one, and Heppner rightly underscored the uncertainties of the figures. Herbulot (1992) and Scoble *et al*. (1995) highlighted these uncertainties by comparisons with (near-)exact counts of Geometridae, which for some regions and/or subfamilies differed markedly; for instance the figure for Afrotropical species proved to be almost 50% higher than Heppner's. It so happens, however, that the inexactitudes in Heppner's figures largely cancel out mutually, hence his grand total for world Geometridae (20,890) is remarkably close to the figure by Scoble *et al*. (21,144), and similarly his estimated total for world Lepidoptera (146,565) is remarkably close to the estimates given about the same time by Holloway *et al*. (1987) and Hammond (1992). The number of described species is now probably some 160,000.

Table 1 shows a geographical breakdown of Heppner's global numbers of described species. Heppner noted that the Neotropical Lepidoptera fauna is considerably more species-rich than that of the Oriental, and he attempted to find explanations for this observation. He noted, for instance, that the Neotropical region covers by far the larger land area of the two. From Table 1 it is clear that when one combines Heppner's 'Oriental' and 'Australian' regions into an 'Indoaustralian' region (a concept which will be familiar to users of the monumental 'Macrolepidoptera' manuals edited by A. Seitz), the latter has a land area that is very similar to that of the Neotropical region. The two regions are also roughly comparable with respect to north-south extent, and their Lepidoptera diversities, crudely expressed as species per unit area, are then seen to be very similar indeed. The main issue, which arises from the geographical survey is, therefore, the markedly lower species-per-unit-area figure for the Afrotropical region. This pattern, which is found repeatedly in global biodiversity surveys, more than 30 years ago prompted Richards (1973) to refer to Africa as the "odd man out", and it continues to attract biogeographers' attention.

TABLE 1. Regional distribution of Lepidoptera species diversity. PAL: Palaearctic; NEA: Nearctic; NET: Neotropical; AFT: Afrotropical; INA: 'Indoaustralian'. Source: Heppner (1991).

	PAL	NEA	NET	AFT	INA
Species	22,465	11,532	44,791	20,491	47,286
Area (mio sq mi)	18,751	8,817	7,202	9,796	7,449
Sp / area	1.2	1.3	6.3	2.1	6.3

To examine patterns of species description in Lepidoptera it is worth considering separately those three major assemblages of the order with which lepidopterists are familiar. Historically, work on these groupings have followed rather different paths. These groupings are 1) The micro-moths, which embrace the more primitive lineages within the order, 'up to', and including, the 'pyraloid grade' superfamilies (mostly small (sometimes minute) moths with larvae usually feeding internally or concealed on their host plants. 2) The macro-moths, i.e., the predominantly night-flying members of the Macrolepidoptera, which may, or may not, be monophyletic. The Macrolepidoptera are medium-sized to large insects, the larvae of which are often external feeders. 3) The butterflies, a presumably monophyletic entity that may be cladistically subordinate within the Macrolepidoptera; nearly all adult butterflies are diurnal, and many have particularly colourful wing patterns.

Fig. 5 illustrates some trends in the taxonomic research on the three groupings during the latter half of the post-Linnean era, showing the numbers of new species descriptions (A) and new species synonyms (B) published during six three-years periods since the establishment of *Zoological Record* in 1864. One general trend, which is observable in all curves of new species descriptions, is a marked decline towards the fourth period (mid-twentieth century), followed by a more or less pronounced subsequent rise. However, the concordant curve shapes have different backgrounds, as has already been pointed out by Strong *et. al.* (1984) in their comments on similar statistics for a variety of phytophagous insect groups. In the case of the butterflies there can be no doubt, that the overall decrease in new species descriptions since a century ago reflects a genuine, even pronounced, drop in the number of species which still remain to be discovered/named. In the cases of the moths the drop reflects the change in the working practice of leading taxonomists, who no longer looked favourably on species descriptions "divorced from revisional or monographic work" (as expressed in Mayr, Linsley & Usinger's influential 1953 manual). Also, examination and specimen preparation procedures had become much more time-consuming, with descriptions/illustrations of genital structures eventually being considered mandatory ingredients in a worthwhile taxonomic study.

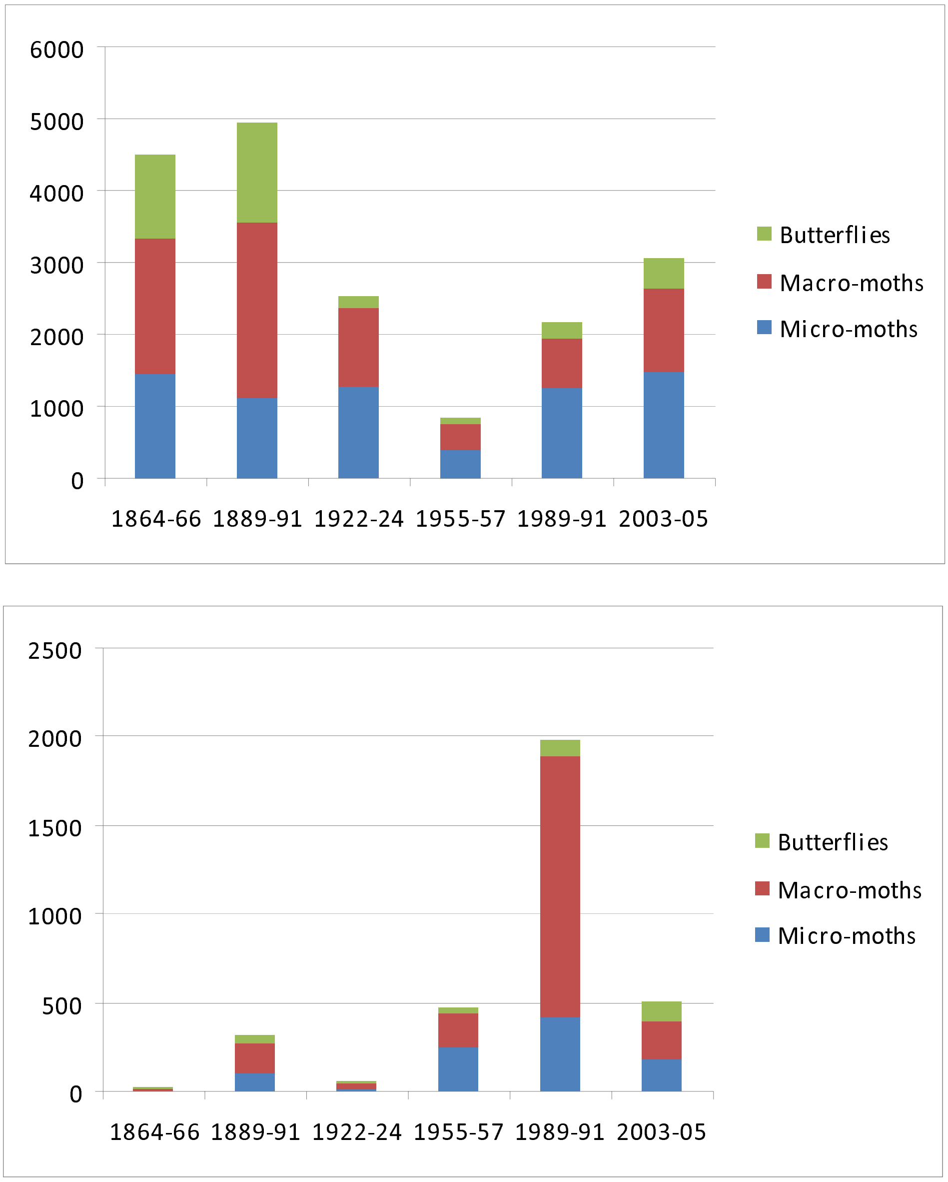


FIG.URE 5. New species described (upper) and new synonyms (lower) established for micro-moths, macro-moths and butterflies during six 3-year periods from the start of *Zoological Record*.

The preparation of permanent slide mounts of the genitalia has been a much more widespread practice among Lepidoptera taxonomists than among those working on insects of several other orders (who often are content to observe the organs at dissection microscope magnification only, with preparations stored in glycerol or even mounted dry on cards). This is undoubtedly primarily rooted in tradition, and it may in no small measure be due to the early influence exerted by F. N. Pierce on the British lepidopterists' community, including, eventually, the staff of the Natural History Museum, London. Unquestionably, this practice has enhanced appreciation of small, taxonomically significant structural details. Moreover, carefully prepared permanent mounts often are excellent objects for photomicrography and they provide maximum protection for minute dissected parts, which is an important consideration in the case of primary types particularly. On the other hand, it *is* sometimes crucially important to retain the possibility of examining the structures from different angles and/or to avoid any kind of distortion from a cover glass. Also, the time expenditure involved in consistent preparation of high-quality slide preparations (see Robinson 1976) can be difficult to justify in those cases where examination of many specimens is desirable or necessary. Here the storage of genitalia preparations in glycerol and associated with the pinned specimens, is often a satisfactory solution. (The availability in recent decades of light-weight plastic vials with silicone rubber stoppers has largely eliminated those misgivings about the vial-storage method, which were justified, when only glass vials with cork stoppers were available.)

If certain technical advances become routine requirements in taxonomy, further impositions are likely to be placed on taxonomists. Detailed microscopical observation of many skeletal features (see, e.g., Lee & Brown 2006), SEM examination of scales and antennal sensilla and, increasingly, molecular barcoding are notable examples. Even if taxonomists themselves are not involved in laboratory procedures, the removal, storage and recording of tissue samples are likely to prove to be time consuming. In contrast, other innovations (such as electronic description templates, high-quality imaging, of entire specimens and morphological details including slide mounts) may make conventional procedures less labour-intensive. The net consequences for throughput in revisionary Lepidoptera taxonomy remain to be seen.

Fig. 5 (lower graph) reveals a disconcerting observation for the abovementioned tightening of working practices, namely the legacy of synonyms created during phases of unconcerned mass-descriptions.

Species concepts. Any discussion of species diversity must in principle make reference to the species concept adopted. If asked, most taxonomists would probably say that their species are inferred to be reproductively isolated, and that morphological distinction is a surrogate measure of reproductive disjunction. In practice, most species are described on the basis of the kind of morphological differences (sometimes informed by natural history observations) traditionally used – many species being described before the biological species concept was articulated. This gives some reassuring constancy to those interested in using taxonomic data for understanding species diversity. Should, however, alternative species concepts be introduced, such as inflating subspecies to the level of species, our assessment of species numbers might change significantly.

Basal splitting events and the micro-moth grade

The basal splitting event among known extant Lepidoptera is presumed conservatively to have given rise to the Micropterigoidea (suborder Zeugloptera *auct.*) on one hand, and all other members of the order on the other. Micropterigid larvae may be characterized as 'soil animals'. Most of them feed on foliose liverworts but some (including the well known predominantly W. Palaearctic genus *Micropterix*) feed on decomposing angiosperms and/or fungus hyphae. The adults are mainly diurnal and consume fern spores or angiosperm pollen. However, all micropterigid dependence on flowering plants is likely to be secondary. Another proposal deserving serious attention is that the Agathiphagoidea (SW Pacific, with a single family and genus; two species; larvae seed miners in Kauri pines, adults nocturnal and probably non-feeding) are the sister group of all other Lepidoptera. The now widespread preference for the former solution is primarily due to fact that the suite of derived characters shared by non-micropterigoids (listed in Kristensen 1998a) in addition to a number of regressive characters includes some striking neoformations: metafurcal process, double-compartment configuration of the spermathecal duct (intermediate condition in *Agathiphaga*, Kristensen & Hünefeld unpublished), larval head-capsule with unique lateral dorsoventral muscle, hypertrophied and angularly bent pupal mandible. This solution is also supported by available molecular evidence (Wiegmann *et al*. 2002). In contrast, derived characters shared by non-agathiphagoids are all regressions/simplifications which are more likely to be homoplasious. This issue was not addressed in Shield's (1993) advocacy of the theory of the Agathiphagoidea being the sister group of all other Lepidoptera. Ivanov's subsequent (1994) arguments for the same theory based on characters in the wing base are debatable (Kristensen 2003).

The next splitting event is believed to have been between the Agathiphagoidea and the Heterobathmioidea + Glossata. Alternatively the dichotomy could be between the (Agathiphagoidea + Heterobathmioidea) and the Glossata, but the derived traits of the former assemblage seem less convincing (Kristensen 1998a) and an (Agathiphagoidea + Heterobathmioidea)-monophyly model would also require that the unique agathiphagoid plesiomorphies alluded to above would have been lost three times independently (in the Micropterigoidea, Heterobathmioidea and Glossata).). The temperate S. American Heterobathmiidae are the most basal family-group taxon in the Lepidoptera, the extant members of which are entirely dependent on angiosperms. Their larvae are miners in *Notophagus* leaves, while the adults are believed to feed on the pollen of these trees. In part, the life-style of these moths is strikingly similar to that of the most basal glossatan family, viz., the Eriocraniidae, which are mainly temperate N. Hemisphere insects. As for heterobathmiids, the larvae of eriocraniids are leaf miners in trees belonging to Fagales, they pupate in cocoons in the soil, and they have adults that are active in early spring (Kristensen & Nielsen 1983).

Basal tongue moths. The monophyly of the 'tongue-moths', Glossata, appears very strongly supported by morphology, and conflicting molecular evidence (18SrDNA data indicating a position of Acanthopteroctetidae outside a Heterobathmiidae + [other] Glossata clade) is considered spurious due to rate heterogeneity of basal glossatan lineages (Wiegmann *et al*. 2002).

The larvae of the overwhelming majority of glossatan Lepidoptera are true herbivores, as in eriocraniids and already the pre-glossatan heterobathmiids. All deviations from this pattern (fungivory, detrivory etc) in the Glossata are probably secondary (Kristensen 1997), but multiple evolution of herbivory cannot categorically be ruled out (Powell *et al*. 1998).

Glossatan autapomorphies (Kristensen 1998b) include, of course, in the first place the remarkable 'apomorphy syndrome' associated with the development of the coilable tongue, comprising 1) each galea becoming elongated, medially concave and linked to its contralateral counterpart (with the fine structure of the medial galea walls and their linking processes being themselves remarkably similar in the basal glossatan clades), 2) mandibles loosing well-formed articulations with the head-capsule and becoming non-functional (with muscles becoming histolysed) in the post-pharate stage (i.e., when they have moved the mandibles of the pupal skin during emergence from the cocoon, and the pupal skin has been shed), and 3) the epistomal sulcus disappearing as a well-formed ridge as it looses the importance it has as a strengthening device in the head capsule of a 'functionally mandibulate' insect. However, glossatan monophyly is also supported by characters not associated with mouthpart transformation, including the embedding of the adult's tritocerebral commissure in the suboesophageal ganglion, and the development of the larval spinneret.

Six basal clades are recognized within the Glossata: the Eriocranioidea, Acanthopteroctetoidea, Lophocoronoidea, Neopseustoidea (all four with just a single small family), Exoporia (Mnesarchaeoidea + Hepialoidea) and Heteroneura (all other Glossata). All Lepidoptera outside the Heteroneura are often referred to collectively as 'homoneurans'. The presently best supported topology, illustrated in Fig. 4 is Eriocraniidae + (Acanthopteroctetidae + (Lophocoronidae + (Neopseustidae + (Exoporia + Heteroneura)))). The morphological support for the respective internodes on the cladogram is surveyed in Nielsen & Kristensen (1996) and more succinctly in Kristensen (1998b). Names have been given to three of the identified high-rank taxa: Coelolepida (the non-eriocraniid Glossata), Myoglossata (Neopseustidae + (Exoporia + Heteroneura)) and Neolepidoptera (Exoporia + Heteroneura).

While the molecular analyses by Wiegmann *et al*. (2002) did retrieve a monophyletic Neolepidoptera, the basal branches of the latter were not persuasively resolved. However, the monophyly of the Heteroneura is here accepted as a reasonable working hypothesis supported by several putative morphological groundplan autapomorphies discussed in more detail by Nielsen & Kristensen (1996): Heteroneurous venation (hindwing Sc and R fused beyond a short distance from wing base, Rs with at most two branches (unbranched in all except the recently established family Andesianidae, Davis & Gentili 2003). Male with composite frenulum. Forewing jugum reduced, projecting little beyond general wing contour. Dorsal tentorial arms in adult strongly reduced. Prothoracic dorsum with median sclerotization behind principal paired 'warts', and precoxal bridge present. Mesosternum with suture-delimited 'mesoclidium', and fusion of the latter with the prospina. Two discrete bundles, with different posterior insertion sites, of mesofurco-metafurcal muscles. Metaprescutal arm and sternum I obliterated. In embryogenesis 'fault-type' formation of amnion and serosa developed, germ band immersed in yolk, and temporary epithelium-like membrane formed by peripheral yolk nuclei/vitellophages absent. This evidence arguably outweighs the morphological arguments against heteroneuran monophyly emphasized by Dugdale (1974) and Minet (1984), viz., respectively, the somewhat similar female genital systems (with separate copulatory orifice and ovipore, and with ventral bursa copulatrix) in Exoporia and Heteroneura-Ditrysia (here considered parallelisms), and the absence of musculated, crochet-bearing prolegs in Heteroneura-Nepticuloidea (here considered a secondary regression, linked to endophagy).

The basal splitting events within the Heteroneura surely remain problematical. A monophylum comprising Tischerioidea and Ditrysia is supported by putative synapomorphies in female frenulum structure (Nielsen 1985), egg shell ultrastructure (Fehrenbach 1995, 2003) and the presence of female sex chromatin (Lukhtanov 2000). Moreover, the exclusion of the Nepticuloidea from a clade comprising the Incurvarioidea, Tischerioidea and Ditrysia has been supported by their lack of a suite of apomorphies characterizing the latter, including specialized female 'calling' behaviour (oviscapt extrusion) and 'long-chain' female sex pheromones (Löfstedt & Kozlov 1997, Löfstedt *et al*. 2004), as well as bristled 'pilifers' (labrum derivatives) and a specialized proboscis morphology (secondary ventral linking processes, 'ribbed' sensilla styloconica; Krenn & Kristensen 2000). Evidence from a nuclear gene (dopa decarboxylase) support the same relationships (Friedlander *et al*. 2000), but as noted the 18S data of Wiegmann *et al*. (2002) do not. It must also be noted that there is conflicting embryological evidence for excluding the Incurvarioidea from an assemblage comprising nepticuloids and Ditrysia (Kobayashi 1997), while Davis (1986) noted some (arguably weak, Kristensen & Skalski 1998) morphological arguments for a monophyletic 'Monotrysia' comprising the nonditrysian Heteroneura then recognized (i.e., excluding the Andesianidae whose monotrysian nature was only discovered later).

The advent of the Ditrysia. The monophyly of the Ditrysia is corroborated by very notable groundplan autapomorphies including the specialized female genital apparatus (separate copulatory orifice and ovipore, and internal communication between sperm-receiving and oviduct systems), prominent internal apodemes on abdominal sternum II; moreover, the intrinsic proboscis musculature is organized as numerous short bands instead of as longitudinal fibres (Krenn & Kristensen 2004).

After the origin of the Lepidoptera many additional apomorphies were acquired during the evolution of the ditrysian stem lineage. Indeed the hypothetical ancestral ditrysian has most of the specializations one would ascribe to 'a typical lepidopteran'. Figs 6 and 7 (bottom) illustrate diagrammatically a suite of the most prominent of these specializations in, respectively, the adult and the larva, while the figure legends indicate on which internodes in 'the lepidopteran tree' the different specializations are known to have been evolved. The acquisition of this ditrysian 'morphotype' obviously enabled rapid radiation of several species-rich lineages', since above' the ditrysian ground plan few structural novelties[1] are added that are shared by sizable assemblages of superfamilies. Hence, while the clade Ditrysia perhaps comprises close to 99% of the extant lepidopteran species, structurally it is homogeneous overall. Unsurprisingly, therefore, its internal phylogeny has proved particularly difficult to unravel. The requirement that taxa should be monophyletic in the cladistic sense has led to the establishment, in recent decades, of an increased number of superfamilies comprising a single or very few families. In the classification adopted here 33 ditrysian superfamilies are recognized. The scheme of their hypothesized interrelationships shown in Fig. 4 is mainly based on Minet's (1991) benchmark study. Reference should be made to that paper and to Kristensen & Skalski (1998) for further details about the background for the large Ditrysia sector of the tree. It must be emphasized that any Ditrysia cladogram based on current morphological knowledge will contain so much homoplasy 'noise' that its value for making biological inferences is very limited.

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FIGURE 6. Diagram of hypothesized adult ground plan of the Ditrysia. Numbers refers to selected apomorphies that have evolved *within* the lepidopteran crown-group. Names in brackets refer to the stem lineages (internodes in the Lepidoptera cladogram, Fig. 4) where the individual apomorphies are believed to have originated. 1: pilifers, modified labral corners (Eulepidoptera). 2: coilable proboscis with intrinsic muscles (Myoglossata) originating also distad from base (Ditrysia), ‘double’ ventral linking (with ‘secondary ventral legulae’) and ribbed sensilla styloconica on surface (Eulepidoptera). 3: ‘Precoxal bridge’ uniting propleuron and prosternum (Heteroneura, paralleled in Neopseustoidea). 4: Mesosternal process extending to first spinasternum (Heteroneura, paralleled in Neopseustoidea). 5: Metanotum shortened, (with concave anterior margin) concomitant with enlargement of mesonotum (Heteroneura). 6: Forewing subcosta (Heteroneura) and radius (stem lineage of Lophocoronoidea + Myoglossata) unbranched. 7: Media stem strongly weakened or absent (homoplasious, some reduction present already in ground plan). 8: Hindwing with Sc and R fused into single vein (Heteroneura). 9: Rs in form of just a single branch (Heteroneura other than Andesianioidea). 10: Wing coupling comprising frenulum fold from lower anterior part of fore wing in Sc region (Eulepidoptera) (Heteroneura), and (in males) a stout frenulum bristle from hindwing costa (Heteroneura). 11: Some wing scales hollow, with perforated upper lamella and dentate apical margin (Coelolepida); wing surface without microtrichiae/acanthae (Ditrysia). 12: Metafurca with process accommodating origin of sternal trochanter depressor (stem lineage of non-micropterigids) and *two* pairs of meso-metafurcal muscles (Heteroneura). 13: Apical spur on protibia lost (homoplasious: Micropterigidae, stem lineage of Heterobathmiidae + Glossata). 14: Middle pair of mesotibial spurs lost (as 13). 15: Abdominal sternum II with distinct apodeme (accommodating insertions of a ventrolongitudinal and a tergosternal muscle) near anterior corner (Ditrysia). 16: Male segment IX ring shortened, largely/completely retracted into VIII (stem-lineage of non-incurvarioid Eulepidoptera; homoplasious in some earlier differentiated lineages).17: Female genital apparatus ditrysian with copulatory orifice on venter VIII. 18: Female abdominal apex comprising 'anal papillae' and associated posterior apophyses, separate segment IX and X components not clearly separate (stem lineage of all non-micropterigids). 19: Ductus spermathecae functionally a two-compartment structure; 'fertilization canal with narrow lumen and thickened cuticular intima (stem lineage of all non-micropterigids, condition in *Agathiphaga* intermediate) 20: Fore gut with 'stalked' stomodaeal crop (Eulepidoptera). 21: First thoracic spiracle with anterior lever, occlusor muscle and dorsal opener ligament (Coelolepida). 22: Dorsal aorta not up-curved to pulsatile diaphragm ('wing heart') in metanotum (Neolepidoptera). 23: Abdominal nerve cord with thick dorsal layer of connective tissue on which ventral diaphragm muscles attach (Neolepidoptera). 24: Testicular spermatozoa with outer covering of ‘lacinate appendages’, hence appearing flower-like in transverse section (Ditrysia – or an earlier stem lineage within the monotrysian grade of the Heteroneura?).

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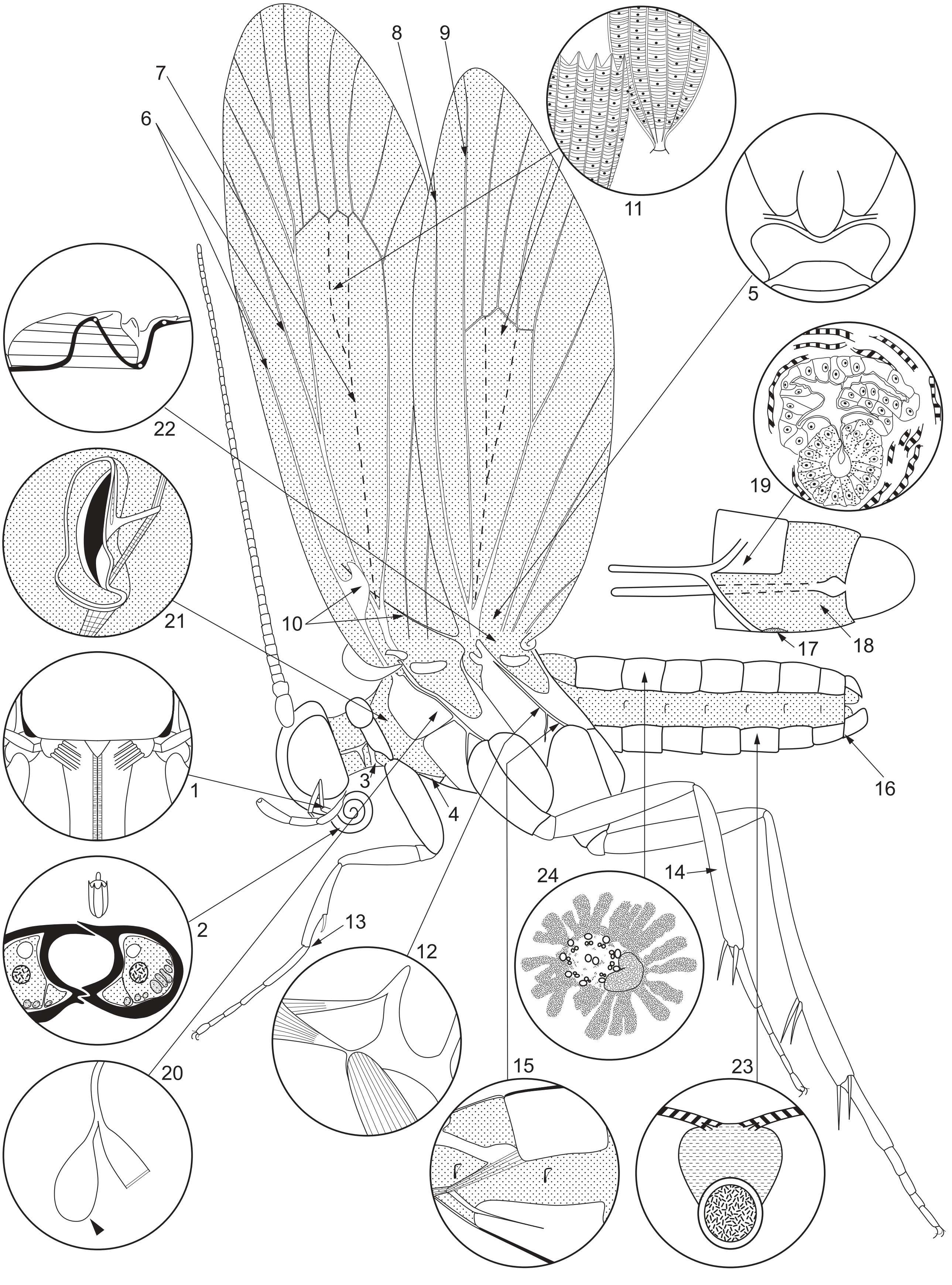
1. The complex maxillary base with an elaborate stipital 'valve' device and three very large extrinsic muscles is one example, an adult ocellus with a thickened corneal lens and unthickened corneageneous cells is another. It remains unknown what the exact distribution of these traits is within the Ditrysia, and to which degree they evolved *via* transformation series in which a number of distinctive stages in can be discerned among extant taxa.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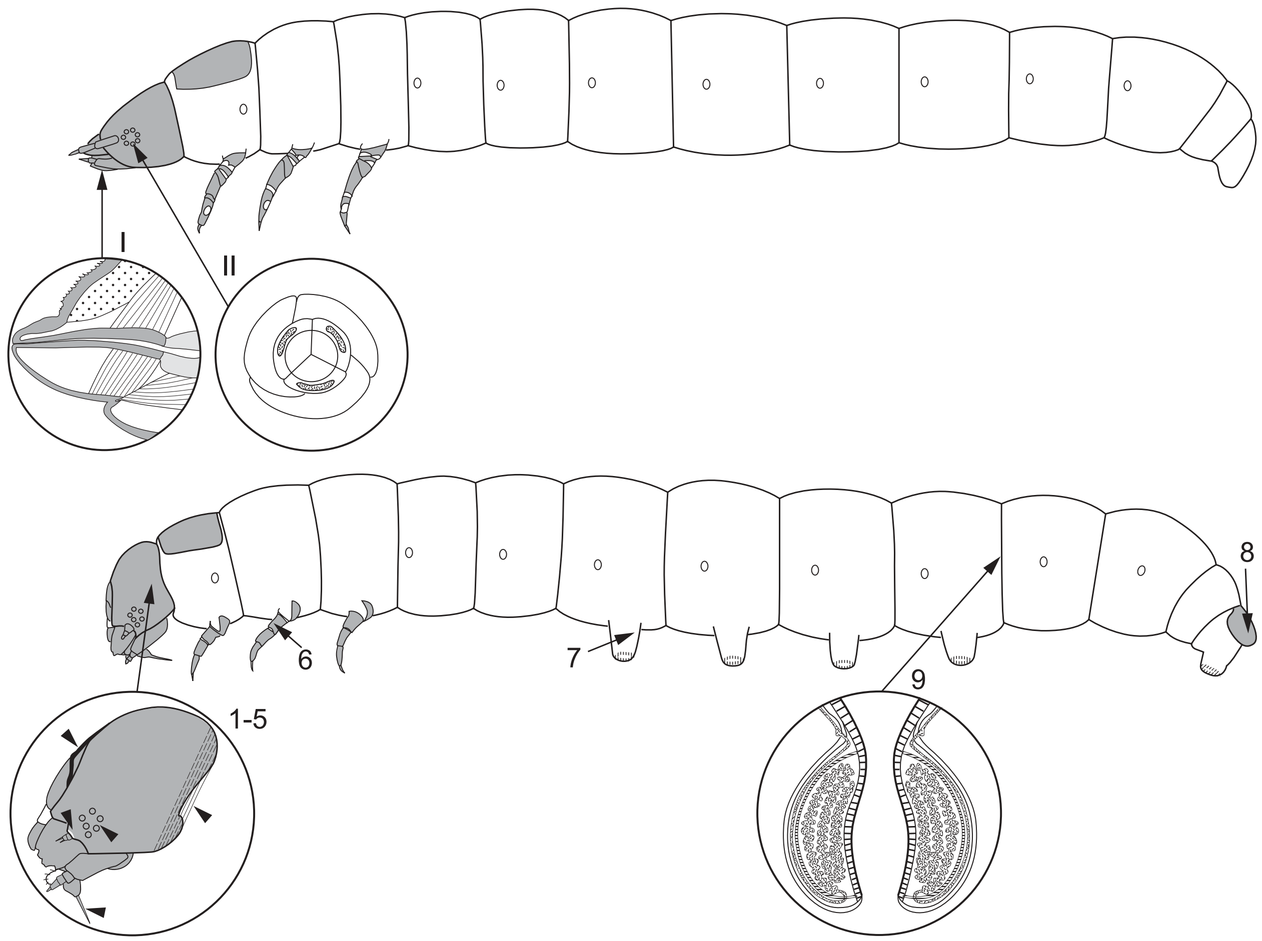

FIGURE 7. Diagrams of hypothesized larval ground plan of the Lepidoptera (above) and Ditrysia (below). Numbers refers to selected apomorphies that have evolved *within* the lepidopteran crown-group. Names in brackets refer to the stem lineages (internodes in the Lepidoptera cladogram, Fig. 4) where the individual apomorphies are believed to have originated. I: Prelabio-hypopharyngeal lobe with silk-gland orifice on apex (*note*: paralleled in Hymenoptera). II: Seven stemmata; in each stemma a Semper cell is transformed into a 'coat cell', hence crystalline cone only tripartite in transverse section. 1-5: Larval head with lateral muscle between dorsal and ventral cranial hind margins (stem lineage of all non-micropterigids), adfrontal ridges (Y- or V-shaped configuration) on anterior cranial surface (stem lineage of Heterobathmioidea + Glossata), stemmata number reduced to six (Glossata), antennal base displaced to margin of head capsule (stem lineage of Heterobathmioidea + Glossata), spinneret developed on apex of prelabio-hypopharyngeal lobe (Glossata). 6: Thoracic leg with trochanter minute, not distinctly subdivided (Glossata). 7: Musculated, crochet-bearing prolegs present on abdominal segments III–VI and X (Neolepidoptera). 8: Dorsal sclerite present on abdominal end (Neolepidoptera). 9: Malpighian tubules and posterior proctodaeum forming cryptonephridial complex (Ditrysia —or an earlier stem lineage within the monotrysian grade of the Heteroneura?).

What are the prospects for an enhanced resolution of the lepidopteran family tree? Experience has shown that examination of large morphological character sets are required to find a satisfactory number of traits, which exhibit phylogenetically informative variation at higher levels. But it must, then, also be emphasized that comparative morphology still contains vast, and largely untapped sources of information, e.g., several aspects of proboscis structure, myology, respiratory organs, internal genitalia, larval mouthparts. Also needed is a detailed cladistic reassessment of some of the morphological information that exists already (including, e.g., the wealth of data on skeleto-muscular anatomy emerging from the research programme of 'the St. Petersburg school', see, e.g., Kuznetzov & Stekolnikov 2001). In-depth morphological studies (on both integumental and internal structures) of carefully selected phylogenetic 'key' taxa throughout the order are much needed to identify those organs/body regions for which more taxonomically extensive comparative observations are likely to prove worthwhile. At this time any major breakthroughs are expected to come from analyses of molecular markers on a large scale (multiple genes, comprehensive taxon sampling), and ultimately from combined analyses of extensive molecular and morphological data sets. Projects of this kind are now in progress, notably the NSF-funded (hence USA-based) 'LepTree' (one of the 'AToL—**A**ssembling the **T**ree of **L**ife—projects) and collaborating Europe-based projects, including one headed by Lauri Kaila (Helsinki) which specifically addresses the deep nodes within the Ditrysia; for further information see http://leptree.net/ and specifically http://leptree.net/community_directory. Hence, while as recently stressed by Whitfield & Kjer (2007) the Lepidoptera-Ditrysia exemplify exactly one of those 'ancient radiations' that present particular difficulties to molecular as well as to morphological analyses, it may well be that greater resolution, and more robust support for clades above superfamily-level, will be forthcoming within the next few years.

Early ditrysian phylogeny

A large paraphyletic assemblage of ditrysian superfamilies, including the apparently first differentiated superfamilies, share some conspicuous (but plesiomorphic) traits with most non-ditrysians. They are generally small moths with a distinct CuP (at least in the hindwing; this vein, however, is repeatedly lost in subordinate clades, particularly those characterized by pronounced wing narrowing), and with larvae that are concealed feeders and usually have the proleg crochets arranged in a circle/ellipse (which may be more or less interrupted). Together with the non-ditrysians the members of this ditrysian grade are colloquially referred to as microlepidopterans or micro-moths ('micros').

The monophyly of the non-tineid Ditrysia is supported by just a few regressive traits in maxillary palp structure. The monophyly of all Ditrysia apart from the Tineoidea and Gracillarioidea has even weaker morphological support, viz., spinosity of the abdominal terga of the adult moths (Robinson & Nielsen (1993), a trait that is lost repeatedly within the Apoditrysia .

All Ditrysia, apart from the Tineoidea, Gracilliarioidea, Yponomeutoidea and Gelechioidea were united, provisionally, by Minet (1983) united in the Apoditrysia, the monophyly of which was supported by an apomorphic sternum II structure, namely that the apodemes are shortened, with enlarged bases, and do not appear as mere continuations of the 'venulae' (longitudinal costae on the sternal plate). Produced anterolateral corners are another characteristic specialization of sternum II in most Apoditrysia, but it is uncertain whether this character can be ascribed to the ground plan of the clade. The monophyly of Yponomeutoidea + Gelechioidea was suggested (Minet 1991, 1996) on the basis of a shared derived pupal type (see below) and details in labial palp structure. But significantly, Kaila's analysis (2004) of gelechioid phylogeny based on an extensive morphological data set (although with a sparse taxon sampling of outgroups) suggested a markedly different basal ditrysian phylogeny by supporting a placement of the Gelechioidea *inside* the Apoditrysia. Within the Gelechioidea level, Kaila's findings partly differ from the *Handbook* arrangement (which was based on Hodges' (1998) original morphological analysis); the same is true for the combined morphology plus molecular (mitochondrial DNA) analysis of Bucheli & Wenzel (2005), where there was a much more restricted gelechioid taxon sampling. However, a more robust gelechioid phylogeny is expected from joint collaborative efforts.

Fig. 3 reflects Minet's view that a large assemblage of apoditrysian superfamilies constitute a monophylum 'Obtectomera'. When this taxon was first proposed (1986), its monophyly was supported only by the immobility of pupal abdominal segments I–IV; related to this immobility, the pupae lost the dorsal abdominal spine-rows (which were acquired by ancestral Neolepidoptera), and they are not protruded from the pupal shelter prior to eclosion. This character complex is subject to considerable homoplasy, occurring also in the Yponomeutoidea and Gelechioidea. Among the Apoditrysia the 'obtectomeran-type' pupa also occurs in the Epermenioidea and Alucitoidea. Hence initially these two superfamilies were included in the Obtectomera, but were excluded from this taxon when it was redefined (Minet 1991) by the addition of another groundplan autapomorphy, viz., a differentiation of a dorsal lobe (sometimes merely appearing as a group of bristle-like processes) on the adult's pretarsal pulvillus.

The non-obtectomeran superfamilies in the Apoditrysia have been referred to as the 'tortricoid grade', which is the largest such assemblage by far. Interrelationships are mostly unclarified within this grade. Fig. 3 reflects Minets's tentative suggestion that Sesioidea (here delimited to include Brachodidae, Sesiidae and Castniidae), Cossoidea and Zygaenoidea may form a monophylum. The evidence for this proposal is weak, and the arrangement is not supported by Kozlov *et al*.'s analysis (1998) of a set of skeleton-muscular characters in the thorax and male genitalia (it does, though, support the monophyly of the Sesioidea in the aforementioned sense). Krenn & Kristensen (2004) identified details in proboscis musculature supporting the monophyly of Apoditrysia in the original sense (excluding gelechioids) and that one specialization shared by tortricoids and obtectomerans was absent in the examined choreutoid, alucitoid, pterophoroids, zygaenoids and sesioids. It is unsurprising that such small character sets should suggest discordant relationships; their principal value will be as contributions to more comprehensive sets for use in future analyses. The proposed monophyly of the Alucitoidea + Pterophoroidea (based on their shared specialized configuration of the meso-precoxal suture, and the resting posture with forewings markedly held out from the body) conflicts with Heppner's alternative placement of the Alucitoidea, together with the Epermenioidea, in the Copromorphoidea. Specializations shared by these superfamilies include, in addition to the pupal type (see above), a process on the larval postlabium (Heppner 1987) and a bisetose prothoracic L group. Minet rejected the monophyly of the Copromorphoidea *s. lat*. because only the Copromorphoidea s. str. (not the Epermenioidea and Alucitoidea) possess the lobed pulvillus attributed to the obtectomeran groundplan. But the relatively immobile, non-spinose and non-protruded pupa of Epermenioidea and Alucitoidea may represent a genuine synapomorphy with the Obtectomera. If the Alucitoidea + Pterophoroidea are indeed monophyletic, this would evidently require that the pupal mobility and spinosity in pterophorids be interpreted as character reversals/neoformations, and in the case of the spinosity this has already been claimed by Kuznetzov & Stekolnikov (1979) and Scott (1986). Minet (1991) noted that the Epermenioidea share with the Alucitoidea and Pterophoroidea the apparently apomorphic trait of having groups of lamellar scales in the forewing fringe. Yet obviously the acceptance of a monophyletic Epermenioidea + (Alucitoidea + Pterophoroidea) will require *ad hoc* explanations for the specializations (in immatures) shared by Epermenioidea and Alucitoidea but not Pterophoroidea.

Within the Obtectomera there is an assemblage of superfamilies (conveniently be referred to as the 'pyraloid grade') which have retained the 'microlepidopteran' characteristics. This assemblage includes the Copromorphoidea, Immoidea, Hyblaeoidea, Thyridoidea, Whalleyanoidea and the very species-rich Pyraloidea. In some previous classifications hyblaeoiods, thyrioideois and whalleyanoids (all comprising but a single family) have been formally included in the Pyraloidea but, as emphasized by Minet (1983), there is no evidence that the latter superfamily, if more broadly delimited, is monophyletic.

The inventory of micro-moths

While the micro-moth grade includes more than three quarters of the 47 presently recognized lepidopteran superfamilies, it comprises little more than one-third of the described species in the order. There will undoubtedly be general agreement, that the latter proportion is an artefact, reflecting the particularly inadequate sampling and taxonomic treatment, which the smaller moths have so far been given on a global scale. In the now thoroughly known NW European lepidopteran fauna, the micro-moths account for about sixty per cent of the total species number, and in the Holarctic as a whole they just exceed fifty per cent.

Fig. 5 shows that from the second to the third period examined here the number of new micro-moths[2] described was increasing slightly, while the corresponding numbers for macro-moths and butterflies dropped markedly. It is reasonable to assume that the proportion of the extant micro-moths named by the time that superficial mass-descriptions became unfashionable, was considerably smaller than that of the macro-moths. Not surprisingly, then, new micro-moth species are at present described at an (albeit only slightly) higher rate than macro-moths. However, the difference presumably also reflects the fact that a larger proportion of the professional taxonomic workforce is now concerned with the former. Progress is still modest, however, but it is worth noting, that while in 1989–91 the number of new species synonyms established was as high as (almost exactly) one-third of the number of new species described in the same period, the ratio of new synonyms/new species for 2003–05 has dropped to ca one-eighth. This may be due largely to a considerable ‘cleaning up’ in recent years of the names applied to the W. Palaearctic taxa which is probably where the majority of micro-moth synonyms were to be found. Since a large proportion of the more recent taxonomic changes still concerns the Holarctic fauna, it is difficult to make predictions about the magnitude of the future growth of the recognized global species number. Data from some recent global/extra-holarctic revisions of micro-moth taxa are summarized in Table 2 and show great disparity. To some extent this undoubtedly reflects a disparity in the methods by which the material examined has been procured. Most of the studies have been based on the more or less casually collected material available in the major museums, and besides the uneven coverage of different groups in collections the disparity also reflects authors’ uneven efforts in gathering the available material from the relevant collections for their revisionary work. It will be seen that several of these revisions led to less than a doubling of the number of recognized species. By contrast, the revisions of Southern S.American Palaephatidae and Gelechiidae-Gnorimoschemini, with very high percentages of new species, are based on materials of which the bulk has been obtained through large-scale specialist collecting efforts with modern methods. Similarly, the revision (with the increase factor 'infinite') of Thailand Choreutidae-Brenthiinae (small diurnal insects) and Costa Rican Glyphicoceridae were based on recent expert-collected material. It may well be argued, that these studies illustrate particularly well future trends for increase in recognized species numbers of (at least the smaller) micro-moths from tropical (and to some degree south temperate) areas.

The potential richness of south temperate regions was underscored by Platnick (1991) who suggested that the world’s terrestrial biodiversity was “probably shaped more like a pear than an egg—the preponderance of biodiversity being in the tropics *and* south temperate zones”. Among arthropods this is true of spiders, which are Platnick’s personal field of expertise, and it is also true of some lepidopteran lineages (Exoporia and Oecophoridae are further examples). However, there are contrasting patterns in other arthropod groups, with a preponderance of tropical and *north* subtropical/temperate species (aphids and sawflies are such cases of a ‘mushroom’ rather than the pear illustrating the global biodiversity pattern; Lepidoptera examples are Coleophoridae-Coleophorinae and Zygaenidae-Zygaeninae), and very probably ‘the egg’ is, after all, the overall dominant pattern. Here it may be noted that while the cited treatment of the Southern S. American pterophorids was based on the same kind of material as the above-mentioned palaephatid and gnorimoschemine revisions but had much more unexceptional increase factors, one of the treated species groups (the *Hellinsia* group) at higher latitudes in the Neotropics comprises overwhelming numbers of undescribed species (C. Gielis *in litt*. to OK).

Some very large potential increments in species numbers are documented in well sorted collection holdings rather than in printed publications; thus the estimated more-than-doubling of the number of Australian Lepidoptera (Mound & Gaston 1994) is largely based on the presence of recognized but unnamed 'morphospecies', primarily of micro-moths, in the *Australian National Insect Collection* (Canberra). For instance, while only 16 described nepticulids are listed in the recent Australian Lepidoptera checklist, the regional fauna of the family may exceed 300 species (Nielsen, Edwards & Rangsi, 1996: 27). Similarly, while the same checklist records

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2. In Fig. 2 the zygaenoid/cossoid/sesioid assemblage, which just possibly is a monophyletic entity among the non-obtectomeran Apoditrysia, is included in the 'macro-moths' although the group does not cladistically belong here. The members of these superfamilies are mostly medium-sized to large, and many are conspicuously coloured; their taxonomy has largely been dealt with by 'Macrolepidoptera' students.

19 species names for Elachistidae (s.str., = Elachistidae-Elachistinae of Hodges 1998), actually only 11 of these apply to elachistines (and they even include synonyms), but currrently 140 species are known from the region, and 300 are a conservative estimate (L. Kaila, pers comm. to OK)

TABLE 2. Total species numbers, new species and new species synonyms for a selection of micro-moth groups revised since 1970. Increase factor: Total sp./Total sp. - (N.sp. - N.syn.). References cited are either single revisionary works, or a series of interrelated publications resulting from a revisionary study. **References**. **1**: Nielsen, E.S. & Kristensen, N.P.: Monogr. aust. Lep. 1 (1989). **2**: Scoble, M.J.: J. ent. Soc. sth. Afr. 41: 81–86 (1978); Ann Transv. Mus. 31: 87–130 (1978); Ibid. 32: 35–54 (1979); J. ent. Soc. sth. Afr. 43: 139–150 (1980); Ann. Transv. Mus. 32: 197–229; Transval Museum Monograph 2 (1983). **3**: Donner, H. & Wilkinson, C.: Fauna of New Zealand 16 (1989). **4**: Davis, D.R.: Smithson. Contr. Zool. 434 (1986). **5**: Robinson, G.S.R.: Bull. Br. Mus. nat. Hist. (Ent.). 32: 253–300 (1976); Ibid. 52: 37–181 (1986). **6**: Yuan, D. & Robinson, G. R.: Bull. nat. Hist. Mus. Lond. (Ent) 62: 1–37 (1993). **7**: Duckworth, W.D.: Smithson. Contr. Zool. 106. **8**: Becker, V. O.: Bull. Br. Mus. nat. Hist. (Ent.) 45: 211–306. **9**: Povolny, D.: Steenstrupia 11: 1–36 (1985); Ibid. 12: 1–47 (1986); Ibid. 13: 1–91 (1987); Ibid. 15: 57–104, 137–160 (1989). **10**: Diakonoff, A.: *The South Asiatic Olethreutinae (Lepidoptera: Tortricidae)*. E.J.Brill. (1973). **11**: Arita, Y: Microlepidoptera of Thailand 1: 7–55 (1987). **12**: Gielis, G.: Zool. Verh. 269 (1991). **13**: Whalley, P.E.S.: Bull. Br. Mus. nat. hist. (Ent). 26: 159–179; Bull. Br. Mus. nat. Hist. (Ent.) Suppl. 17 (1971); *Tropical Leaf Moths*. British Museum (Nat.Hist)(1976). **14**: Roesler, R.U. & Küppers, P.V.: Beitr. naturk. Forsch. SüdwDtl. Beih. 3 (1979); Ibid. 4 (1981); Roesler, R.U.: Heterocera Sumatrana 3 (1983). **15**: Lewvanich, A.: Bull. Br. Mus. nat. Hist. (Ent.) 42: 185–298 (1981). **16**: Yoshiyasu, Y.: Microlepidoptera of Thailand 1: 133–184 (1987). **17**: Leraut, P.: Faune de Madagascar 72 (1989). **18**: Adamski, D.: Zootaxa 858: 1–205 (2005). **19**. Aarvik, L.: Norw. J. Ent. 51: 71–122 (2004).

Taxon / region (reference)	Total sp.	N. sp.	N. syn.	Increase factor
Hepialoidea-Hepialidae: Genus *Fraus*, Australia (1)	25	17	2	2.5
Nepticuloidea-Nepticulidae Southern Africa (2)	119	72	0	2.5
Nepticuloidea-Nepticulidae New Zealand (3)	28	14	2	1.8
Palaephatoidea-Palaephatidae New World (4)	28	25	0	9.3
Tineoidea-Tineidae: Scardiinae, World (5)	108	55	6	1.8
Gracillarioidea-Gracillariidae Genus *Caloptilia*, S.E .Asia (6)	25	9	6	1.1
Gelechioidea-Elachistidae Genus *Setiostoma*, New World (7)	17	10	0	1.7
Gelechioidea-Elachistidae Genus *Timocratia*, Neotrop. (8)	39	17	6	1.4
Gelechioidea-Glyphidoceridae Genus *Glyphidocera*, Costa Rica (18)	92	88	0	23
Gelechioidea-Gelechiidae Gnorimoschemini, southern S. America (9)	99	89	0	9.9
Tortricoidea-Tortricidae Olethreutini, S.E.Asia (10)	422	187	12	1.7

......continued

TABLE 2 (continued)

Taxon / region (reference)	Total sp.	N. sp.	N. syn.	Increase factor
Tortricoidea-Tortricidae Subtribe Neopotamiae, Afrotrop. (19)	28	19	5	2
Choreutoidea-Choreutidae *Brenthia*-group, Thailand (11)	24	24	0	'infinite'
Pterophoroidea-Pterophoridae Argentina + Chile (12)	52	30	5	1.9
Thyridoidea-Thyrididae Striglininae (13), Pantrop.	203	82	10	1.5
Pyraloidea-Pyralidae Phycitinae, Sumatra (14)	187	85	3	1.8
Pyraloidea-Crambidae Genus *Scirpophaga*, Old W (15)	35	5	12	0.8
Pyraloidea-Crambidae Nymphulinae, Thailand (16)	41	6	0	1.2
Pyraloidea-Crambidae Scopariini, Madagascar (17)	18	14	1	3.6

It must also be emphasized that some of the revisions with very low 'increase factors' exemplify a laudably cautious approach to description of new taxa. Thus the S. E. Asian *Caloptilia* revision dealt with 25 described species, but noted a further 30 species from the area, which are "probably all undescribed taxa, which are represented by just single examples, or by damaged and defective specimens, and which therefore cannot be characterized adequately". Moreover, it is likely that the bulk of the synonyms will have been discovered during the revisions cited, so that in future treatments of additional material the discovery of further species will not be counterbalanced by new synonyms to the same degree. The *Scirpophaga* revision with its negative increase factor (i.e., with new synonyms outnumbering new species) is surely a very exceptional case; the insects in question are among the largest micro-moths, some species have deceptively variable wing markings, and some are serious pests. It should be noted that some additional species have indeed been described since the 1981 revision.

A somewhat comprehensive body of knowledge of micro-moth immatures is available as far as the Holarctic is concerned, although it is probably only in N./C.Europe that the life-history is known for the majority of the *species*. However, even in the best known faunas there are few cases where groups of micro-moth immatures have been described in sufficient detail to permit reasonably reliable species identification without rearing, or to provide helpful evidence on classification immediately above the species-level. Species identification is mostly feasible, where larval monophagy/oligophagy is coupled with characteristic behavioural traits, such as leaf mining, case construction, etc. Indeed the ease of sampling, and the feasibility of species identification, has rendered leafmining micro-moths very suitable and popular subjects for the study of some fundamental questions in community ecology.

Outside the Holarctic an impressive, albeit still very incomplete, amount of information on micro-moth biology/immatures has been gathered in Australia (much of it only published in outline, see Common 1990) and New Zealand (Hudson 1928/39, Donner & Wilkinson 1989). Important progress in the study of some groups of micro-moth leafminers has been made in Southern Africa (Vari 1961, Scoble 1983), but otherwise the knowledge of micro-moth immatures/biology in the Afrotropical as well as Neotropical regions remains grossly inadequate; the same is true for the Oriental region, where the major publications by T. B. Fletcher in the early decades of the 20th century only mark a beginning.

The Macrolepidoptera

The remaining Ditrysia, which include some very species-rich superfamilies, are mostly medium-sized to large, frequently rather broad-winged insects with predominantly exophagous larvae. Most members of this assemblage have long been known to share a few structural specializations, including the arrangement of larval proleg crochets in a 'mesoseries' and presence of only two veins behind the hindwing CuA. Both traits are homoplasious, the former occurs at least in some zygaenoids, the latter is more widespread among 'microlepidopterans'. In the tree in Fig. 3 the assemblage in question is shown as constituting a monophylum, the Macrolepidoptera, which was supported (Minet 1991) by at least an apparently unique elongation of the 1st axillary sclerite in the forewing base; the validity of this putative macrolepidopteran autapomorphy is currently debated (Ivanov 1996, Minet 1998). Thus delimited, the Macrolepidoptera comprise the mimallonoid/lasiocampoid/bomycoid assemblage, Axioidea, Calliduloidea, butterflies (i.e., the hedyloid/hesperioid/papilionoid assemblage), Drepanoidea, Geometroidea (including Uraniidae) and Noctuoidea. Scott (1986) and Scott & Wright (1990) (see also Scott (1989)) listed a suite of additional putative autapomorphies of an almost identically delimited taxon Macrolepidoptera (Mimallonidae excluded). However, these specializtions either occur elsewhere among apoditrysians, or the plesiomorphic states are actually retained in scattered macrolepidopterans; hence the apomorphic state cannot be attributed to the macrolepidopteran ground plan without invoking *ad hoc* hypotheses of character reversals (Brock 1988, see also Robbins (1987). Female sex pheromones also support the monophyly of a ‘core Macrolepidoptera’, in as much as the presence of polyene and epoxide components may be a synapomorphy of a clade comprising Geometridae and Noctuidae (Millar 2000). A change in macro-moth systematics likely to attract widespread attention is the very recent formal subordination of the familiar tussock moths (formerly family Lymantriidae) and tiger moths (formerly family Arctiidae) to the family Noctuidae (Lafontaine & Fibiger 2006). That this arrangement reflects the actual phylogenetic relationships was indicated over a decade ago by the molecular work of Weller *et al*. (1994), and it has been supported by subsequent molecular (Mitchell *et al*. 2006) and morphological work (Fibiger & Lafontaine 2006, Lafontaine & Fibiger 2006). This revised arrangement seems more informative, and hence more appropriate, than the alternative of splitting Noctuidae into a host of smaller ‘families’ to avoid paraphyly. Preliminary molecular work by Abraham *et al*. (2001) indicates that some substantial changes are foreseeable also in the phylogenetic systematics of the large family Geometridae.

A much debated question has been whether a taxon Macrolepidoptera inclusive of the butterflies is a monophylum (Scott 1986, 1989; Scott & Wright 1990; Brock 1988, 1990a, b). Minet (1991) proposed that butterflies (in a broad sense, including the Hedyloidea) are subordinate in a large clade comprising also the Axioidea, Calliduloidea and Drepanoidea+Geometroidea. Probable synapomorphies of these taxa include concealment of pupal labial palps; reduction of the metapostnotal 'fenestrae laterales' (Fänger 1999); internal laminae of secondary metafurcal arms widened, their mesal edges adjacent and parallel, or posteriorly convergent. However, at least the first two of these traits are pronouncedly homoplasious, occurring also in subordinate members of other macrolepidopteran lineages. No hypothesis on the precise position of the butterflies can at present be considered well founded in spite of some effort to clarify this matter on the basis of morphological as well as molecular data; see Weller & Pashley (1995), de Jong *et al*. (1996), and Wahlberg *et al.* (2005) for further details.

The inventory of macro-moths

The macro-moths comprise the majority of the presently named Lepidoptera species, but as mentioned above this relation is expected to change markedly as both micro- and macro-moth faunas in the tropics become taxonomically more adequately known.

New macro-moth species are currently being described at a somewhat moderate rate, more than three times as many as in the 1950s, but just over the figure for the 1920s. In the penultimate three-year period surveyed in Fig. 5 the number of new species was largely overtaken by new synonyms, but this was an exceptional situation due to the publication of Poole's (1989) noctuid catalogue, in which literally generations of workers' unpublished synonyms were made available, while no new species were described. If the Poole synonyms are omitted, the number of new macro-moth synonyms in the period still amount to some seventy per cent of the figure for new species, but in 2003–05 less than twenty percent of the new species must be offset by new synonyms. A study (Gaston, Scoble and Crook 1995) using a database of taxonomic names (up to 1993) of Geometridae, based on the card index at the Natural History Museum, London, found that on a cumulative scale it was unclear as to whether or not the total number of species of the family described (ca 21,000) was reaching an asymptote. However, the number of species descriptions was certainly found to be declining markedly, and the authors concluded that on the basis of the patterns revealed by the data it seemed unlikely that the global number of geometrid species would exceed 30,000, and might be rather fewer. Unsurprisingly considerable differences were found to exist between major biogeographical regions in terms of accumulation curves of the number of species plotted against time. The pattern of species description for Geometridae (probably typical of many invertebrate taxa since 1758 - the publication date of Linnaeus's tenth edition of *Systema Naturae*), shows a slow rise for the first several decades, and then a rapid increase in the number of descriptions from the middle of the 19th Century. This is followed by an equally rapid decline from around 1900 to 1950. About 14% of valid species names across the family were recorded as having associated synonyms. Most species names were shown to have no or few synonyms, while a few had a large number of synonyms. Again, the level of synonymy was not distributed evenly across the regions. The geometrid data also showed that more than 40% of authors described only one species, while over 30% of species were described by just two authors.

For the 'macros', as for the micro-moths, much of the current taxonomic research is still concerned with the Holarctic fauna, so estimates of forthcoming additions to the described tropical fauna are difficult to make. Data from some recent global/extra-holarctic revisions of macro-moths are presented in Table 3. Few recent macro-moth revisions have increase factors approaching the highest reported for micro-moths. Unsurprisingly this is the case for the micronoctuids which are among the smallest and most inconspicuous macro-moths, but high increase factors (albeit concerning much smaller species numbers) are also reported for medium-sized and striking *Chrysartona* (Zygaenidae). A more-than-a-doubling of the species number is also reported for (Chilean) *Eupithecia* (again small moths), Afrotropical *Hypochrosis*, and the Malagasy 'fauna' treatments of epiplemine uraniids and plusiine noctuids. Overall the increase resulting from recent revisions is smaller than might have been expected *à priori*. The very low increase factor for the Bornean Noctuidae-Stictopterinae is perhaps particularly noteworthy: These moths are in no way particularly conspicuous (i.e., there is no reason to expect that they should have attracted particular attention previously), and the Bornean moth fauna is probably now among the best sampled (with modern light-trapping technology) in the Old World tropics. Comparably low increase figures were reported for the entire macro-moth fauna of the intensively investigated Santa Rosa National Park in Costa Rica (Janzen 1988), and detailed documentation is presented in two recent revisions of Geometridae (Ennominae: *Thysanopyga* group, Geometrinae: *Nemoria* group) centred on the Costa Rican biodiversity inventory. However, one may still expect to see considerably higher increase figures in many future revisions of major geometroid and noctuoid taxa, based on large-scale specialist collecting efforts in a greater variety of tropical and south temperate areas. For instance, as noted by Heppner (1991:2), "..the vast New Guinea fauna has hardly been touched". And as noted for the micro-moth revisions above it is unlikely that future discoveries of new species in the revised taxa will be counterbalanced by new synonyms to the same degree.

What has been said about micro-moth immatures is largely true for the macro-moths also. Compared with the former, macro-moth immatures are, on the plus side, mostly larger and they have attracted more attention from amateur workers. On the minus side, fewer of them have very characteristic feeding patterns, and none of the *larger* macro-moth taxa are most easily sampled as larvae, such as is the case with, e.g., the leafmining micro-moths.

TABLE 3. Total species numbers, new species and new species synonyms for a selection of macro-moth groups revised since 1970. Conventions as in Table 3. **References**. **1**: Holloway, J.D. 1976: *Moths of Borneo with special reference to Mt. Kinabalu*. Malayan Nature Society (1976). **2**: Holloway, J.D.: The Moths of Borneo 3. Southdene Sdn. Bhd. (1987). **3**: Dierl, W.: Spixiana 1: 225–268 (1978); Ibid. 2: 253–258 (1979). **4**: Dugdale, J. S.: Aust. J. Zool. 28: 301–340 (1980). **5**: Rindge, F.H.: Bull. Am. Mus. nat. Hist. 186: 271–363 (1987); Am. Mus. Novitates 3020 (1991). **6**: Poole, R.W.: U.S.Department of Agriculture, Technical Bulletin 1698 (1987). **7**: Fletcher, D.S.: Bull. Br. Mus. nat. Hist. (Ent.) Suppl. 22 (1974). **8**: Rindge, F. H.: Bull. Am. Mus. nat. Hist. 160: 193–292 (1978). **9**: Krüger, M. & Scoble, M. J.: Bull. Br. Mus. nat. Hist. (Ent). 61: 77–148 (1992). **10**: Cook, M. & Scoble, M. J.: Bull. Nat. Hist Mus (Entomology) 64: 1–115 (1995). **11**: Boudinot, J.: Faune de Madagascar 60 (1982). **12**: Holloway, J.D.: The Moths of Borneo 4. Southdene Sdn. Bhd. (1983). **13**. Holloway, J. D.: The Moths of Borneo 6. Southdene Sdn. Bhd.(1988). **14**: Griveaud, P.: Faune de Madagascar 43 (1977). **15**: Dufay, C.: Bull. mens. Soc. Linn. Lyon 37: 195–212 (1968); Faune de Madagascar 31 (1970). **16**: Kobes, L.W.R.: Heterocera Sumatrana 4 (1985). **17**:Holloway, J.D.: *The Moths of Borneo* 14. Southdene Sdn. Bhd. (1985). **18**: Efetov, K. A.: Ent. Gaz. 57: 23–50 (2006). **19**: Hausmann, A.: Spixiana 26: 97–128 (2003). **20**: Fibiger, M.: Zootaxa 1567: 1–116 (2007). **21**: Schintlmeister, A.: Quadrifina 7: 1–248 (2004).

Taxon /region (reference)	Total sp.	N. sp.	N. syn.	Increase factor
Zygaenidae-Procridinae Genus *Chrysartona*, Asia (18)	13	9	0	3.3
Lasiocampoidea-Lasiocampidae Borneo (1,2)	62	21	3	1.4
Bombycoidea-Bombycidae *Ocinara*-group, S.E.Asia (3)	23	8	6	1.2
Geometroidea-Geometridae Trichopterygini, Australia (4)	14	6	6	1.8
Geometroidea-Geometridae Genus *Eupithecia*, Chile (5)	50	36	4	2.8
Geometroidea-Geometridae Genus *Pero*, New World (6)	294	119	44	1.3
Geometroidea-Geometridae Genus *Hypochrosis*, Afrotrop. (19)	25	16	0	2.8
Geometroidea-Geometridae Genus *Zamarada*, Palaeotrop. (7)	222	120	12	1.9
Geometroidea-Geometridae Genus *Sabulodes*, New World (8)	36	15	1	1.6
Geometroidea-Geometridae *Thysanopyga*-group, Neotrop. (9)	36	19	3	1.8
Geometroidea-Geometridae Genus *Oospila*, Neotrop. (10)	74	1	48	0.6
Geometroidea-Uraniidae: Epipleminae, Madagascar (11)	23	19	0	5.8
Noctuoidea-Notodontidae Borneo (1, 12)	122	28	19	1.1

......*continued*

TABLE 3 (continued)

Taxon / region (reference)	Total sp.	N. sp.	N. syn.	Increase factor
Noctuoidea-Micronoctuidae Pollexinae, Old World (20)	74	72	0	37
Noctuoidea-Noctuidae: 'Catocalinae', Sumatra (16)	118	15	0	1.2
Noctuoidea-Noctuidae Stictopterinae, Borneo (1, 17)	89	29	22	1.1
Noctuoidea-Noctuidae non-lithosiine Arctiinae, Borneo (1, 13)	97	19	16	˜1
Noctuoidea-Noctuidae Lymantriinae, Madagascar (14)	262	80	9	1.4
Noctuoidea-Noctuidae *Lymantria*, Global (21)	167	46	17	1.2
Noctuoidea-Noctuidae Plusiinae, Madagscar (15)	39	21	0	2.2

The inventory of butterflies

As noted earlier, the modest number of new butterfly species currently being described almost certainly suggests that most of them have been discovered. So it is perhaps surprising that as many as 422 new species (offset by 116 new synonyms) were described during the last three-year period surveyed. In terms of an increase in recognized species numbers this is a doubling of the figures (246 n. sp., 93 n.syn.) for the penultimate period (1989–91).

With close to 20,000 described species, the butterflies presumably represent the largest invertebrate clade for which the species inventory is nearing completion. At the same time, the butterflies illustrate very instructively how estimates of species diversity depend on the species concept adopted. A very large number of so-called species of butterflies are polytypic, comprising numerous named subspecies distinguished on the basis of geographically correlated varability in wing pattern. At one end of the spectrum of this variability are the strikingly different local forms of many species in tropical aposematic butterfly genera such as *Heliconius* (Nympalidae-Heliconiinae, Neotropical) and *Euploea* (Nymphalidae-Danainae, Indoaustralian). At the other end is the plethora of only slightly differentiated local forms of Holarctic butterflies, identified and named by lepidopterists with, typically, a very limited taxonomic or geographical outlook. The writings by Bryk and Eisner on *Parnassius*, and those by Verity on Italian butterflies, are notorious examples of such taxonomic inflation. While the usefulness of such a formidable subspecific nomenclature is rejected by the majority of contemporary workers, there is presumably little reason to doubt that many of the named entities are indeed 'diagnosable clusters'. Were the BSC to be replaced by the 'phylogenetic species concept' (the 'smallest diagnosable cluster'), the number of recognized butterfly species would be very significantly increaseed.

While subspecies splitting is encountered frequently in butterfly taxonomy, it is, of course, not restricted to this group alone among the Lepidoptera. It may be observed, for example, just as extensively in day- flying zygaenid moths. Evidently geographical variation is most easily observable in larger insects with distinctive wing patterns, and pattern distinctiveness is obviously in turn overall particularly pronounced in diurnal taxa, which use visual signalling as part of reproductive and/or anti-predator strategies. However, it is straightforward to suggest that the genomes of most moths with habits of restricted dispersal would prove similarly variable, i.e., that they could be similarly subdivided into many smaller 'diagnosable clusters', if more resources were invested in the search (e.g., using molecular markers) for such variability.

Since there have been several butterfly workers resident in all regions, it is not surprising that the knowledge of even tropical butterfly biology and immatures is good by the standards of the order. There are still vast gaps, however, perhaps especially pronounced in the larger grass-feeding taxa such as Nymphalinae-Satyrinae and Hesperiidae-Hesperiinae, where clusters of species with not dissimilar wing patterns are to be found.

Fossil Lepidoptera

In none of the other major insect orders is the fossil record as poor as in the Lepidoptera. This is undoubtedly partly due to the special properties of their wings, which not only are particularly fragile because of the paucity (shared with caddisflies) of cross-veins and only moderate sclerotization of the principal longitudinal veins, but, and in particular, because the scale vestiture render them more un-wettable than other insect wings (Wagner *et al*. 1996)—a factor that evidently impedes their fossilisation in lacustrine (or near-shore marine) sediments. No known fossil Lepidoptera represent organisation types that differ markedly from extant ones, and fossils have so far contributed little, if anything, to the understanding of phylogenetic interrelationships within the order. Nevertheless, fossils provide the only direct means for establishing the minimum ages of individual evolutionary lineages.

The fossil record of Lepidoptera (as of other insects) was recently reviewed by Grimaldi & Engel (2005), whose excellent account is recommended strongly. The oldest fossil currently believed to belong to the Lepidoptera is *Archaeolepis manae* from the Lower Jurassic (ca 190 MYO) and according to Grimaldi & Engel a recent re-examination of the specimen has given additional support to its ordinal placement. A small number of moths are known from younger Jurassic strata, but the first lepidopteran fossil that can with any certainty be assigned to a known family lineage (viz., Micropterigidae) is from the Lower Cretaceous. The existence of Glossata also in the lower Cretaceous is documented by a larval fossil with a distinct spinneret, while re-examination of an alleged adult glossatan moth from the upper Jurassic failed to confirm the presence of a proboscis. Indeed the presence of glossatans of this age would be unexpected, if angiosperm feeding evolved in the stem lineage of Heterobathmiidae + Glossata. Following Labandeira *et al.* (1994), leaf mines from the Mid Cretaceous Dakota formation attributed to a member of Gracillariidae-Phyllocnistinae have been considered to demarcate the known minimum age of the Ditrysia. Nevertheless, Grimaldi & Engel rightly caution about the uncertainty inherent in identifying leaf miners. In any case there is little doubt that the main radiation of the Lepidoptera followed the main radiation of angiosperms in the Cretaceous. The point has repeatedly been made that since bat predation is probably the principal selective force behind the evolution of tympanal organs in nocturnal Lepidoptera, all the tympanate moths lineages (including such species-rich lineages as pyraloids, geometroids and noctuoids) cannot have predated the origin of bats whose currently known minimum age is Early Tertiary. The minimum age for the butterfly families Pieridae and Nymphalidae as estimated from molecular evolution is more than 70 MYO, hence the butterflies as a whole must be somewhat older (Braby *et al.* 2006, Wahlberg 2006).

How many extant species of Lepidoptera exist?

Heppner's (1991, 1998) above-mentioned compilations of numbers of described Lepidoptera species were accompanied by an estimate of the total species number, which in 1991 was given as 255,000. It was reached by roughly doubling the estimated numbers of described species from tropical regions, while the numbers for the Palaearctic and Nearctic regions were increased by somewhat under one-tenth and just above one-fifth, respectively. By 1998 Heppner considered it likely that the figure "may be even higher", which is almost certainly a conservative statement.

Erwin's (1982) article on tropical forest beetles and arthropod species richness led to an upsurge of interest in methods of estimating the total species diversity of insects (and indeed all living organisms). Introductions to the literature in this field were given by Gaston (1991a,b) and Hammond (1992). These authors found little support for assumptions of the existence of 30 million insect species, or more. Their conclusions, expressly stated to be conservative, converge on figures between five and ten millions. How many of these, then, are Lepidoptera? Gaston's approach was to solicit the views of practicing taxonomists about the proportions of species in 'their' groups, which still remain to be described. In the case of the Lepidoptera the views obtained "suggest that an upper bound to the overall size of the order of 500,000 species is reasonable, and that a figure somewhat lower is quite probable". Hammond (1992, fig. 4.6) summarized his 'conservative estimates' of total organismic diversity in a pie-chart, wherein the Lepidoptera constitute 3.2% of 12.5 millions species, i.e., 400,000 species, a figure compatible with Gaston's conclusion.

Erwin (1991) strongly criticised Gaston's specialists'-opinions-approach to estimating insect diversity. It is true, that the figures arrived at are beset with great uncertainties, but so are figures obtained from other current approaches (Gaston 1991a, b). As far as the Lepidoptera are concerned, We believe that a near-half-million species estimate indeed appears likely on the basis of available knowledge. If the micro-moth/macro-moth ratio on a global scale is similar to that in the thoroughly known NW European fauna (which seems a reasonable *à priori* assumption), then a figure of 500,000 Lepidoptera would require an approximate 5.5 times increase in the number of recognized species of micro-moths and 2.5 times increase of macro-moths (the increase for butterflies is considered negligible in this context). Heppner's (1991) abovementioned modest estimate of 255,000 lepidopteran species would require figures as low as ca 2.5 and 1.3 respectively. From the above (Tables 3 and 4, with comments) it would appear that the true number is somewhere in-between, and we submit that it is likely to be closest to the upper figure. Even careful collection-based taxonomic revisions are unlikely to unravel the existence of numerous sibling species, which will turn out to be quite distinct after the elucidation of their habitat and food plant requirements, phenology, pheromone composition etc.

One of the approaches, mentioned in Hammond's article, for crudely estimating global insect diversity, is to extrapolate from the ratio between the relatively reliably known figures for British butterflies (there stated to be 67 species), World butterflies (17.500) and British Insects (22,000); this calculation yields a world total of some 5.75 millions insect species. Of course, the same principle may be applied for estimating total Lepidoptera diversity. Using the figures in Karsholt & Razowski (1996) for British species (butterflies: 71; total Lepidoptera: 2,386) and Heppner's (1998) for World butterflies (19,238) one arrives at a World total of close to 647,000 species.

The uncertainties inherent in this approach are well illustrated by the fact, that one arrives at a total around 418,000 species, if instead of butterflies one uses the only other larger lepidopteran lineage for which the World total is reasonably well known, viz., the bombycoid assemblage *s.lat.* (including the lasiocampoids and shingids), with British and World figures of 31 and 5,437 respectively. Interestingly, the disparity between extrapolations from butterfly and bombycoid figures are markedly smaller if instead of the British lepidopteran fauna the slightly larger, and probably almost equally well investigated Swedish and Austrian faunas are used as bases. The relevant figures (again taken from Karsholt & Razowski 1996) are for Sweden 121 (butterflies), 34 (bombycoids) and 2.296 (total), and for Austria 202 (butterflies), 53 (bombycoids) and 3948 (total). The extrapolated world totals are, then, with butterfly data ca 376, 000(Au)–432,000(Sw), with bombycoid data ca 405,000(Au)–431,000(Sw). For whatever these calculations are worth, it is noticeable, that their results support the general conclusions reached above: *There are considerably more than a quater-million Lepidoptera species, probably in the order of magnitude of half a million, but there are not a million - let alone several millions.*

An intriguing feature in Hammond's aforementioned chart is the drastic reduction, compared with the figures for currently recognized species, of the percentage of the Lepidoptera relative to that of the other major insect orders. In the chart of the currently described organisms (Hammond's fig 4.5) the contributions of these orders are, resepectively, Coleoptera 23.8%, Lepidoptera 8.9%, Hymenoptera 7.7% and Diptera 7.1%; in the estimated total the beetles remain almost constant, at 24.9%, the Hymenoptera and flies increase markedly, to 19.3% and 12.9%, whereas the Lepidoptera as noted *decrease* to a mere 3.2%. While a shift in the species-number ratio of this magnitude was not supported by the 'specialists' opinions' reported by Gaston (1991a), it does remain likely, that the Lepidoptera will turn out to be clearly the smallest order of the four on a global scale, as they are in NW Europe, and also in the Nearctic (Kosztareb & Schaefer 1990).

What may new discoveries say about Lepidoptera evolution?

Given that so many Lepidoptera evidently remain to be discovered, examined and described the question arises as to what extent we may anticipate our current understanding of Lepidoptera evolution being enhanced by future discoveries. Some recent case-studies will illustrate the issue.While it is true that representatives of most of the higher taxa of Lepidoptera had been described by the end of the 19th century, and that the vast majority of the new species currently being described are essentially ‘variations on known themes’, it must be emphasized that the present insights into the evolution (particularly the early phases) of the order are in no small measure due to examination of taxa described after 1950. Among the most significant discoveries in systematic lepidopterology in the 20th century are those of the non-glossatan lineages represented by *Agathiphaga* (Fig. 8, described in 1952) and *Heterobathmia* (Fig. 9, described in 1979), and the first representatives of the homoneuran glossatan families Lophocoronidae and Neotheoridae were not described until the 1970s.

FIGURES 8–9. Representatives of the two non-glossatan moth lineages that were described in the second half of the 20th century. 8: an agathiphagid: *Agathiphaga vitiensis* Dumbleton, 1952; wing span 27 mm. 9: a heterobathmiid: *Heterobathmia pseuderiocrania* Kristensen & Nielsen, 1979; wing span 10 mm. Paintings by Roland Johansson.

But exciting innovations in Lepidoptera phylogenetic systematics are not due only to the discovery of new taxa. Indeed, in recent decades only a single new lepidopteran family has been established on the basis of a species newly described in the same publication, namely the Catapterigidae[3] (Zagulajev & Sinev 1988). More often such innovations come after close re-examination of already described ones the significance of which have not previously been fully recognized or, indeed, recognised at all. Thus the recently established South American non-ditrysian heteroneuran families Andesianidae (Fig. 10, Davis & Gentili 2003) and Palaephatidae (Fig. 11, Davis 1986) both include previously described species that had been assigned to families in the Ditrysia (Cossidae and Tineidae, respectively). These two families are of exceptional interest: andesianids (as noted above) for being heteroneurans which have retained what seems to be two Rs branches, palaephatids for having proved surprisingly species-rich and having an amphi-Pacific distribution (occurring also in Australia). In a similar way, a number of small ditrysian families that have been established within the last quarter-century are based on taxa which had previously been assigned to other families, but were found upon re-examination to lack apomorphies supporting these placements. This situation applies to Prodidactidae (Epstein & Brown 2003), Lacturidae (Heppner 1995), Simaethistidae and Whalleyanidae (Minet 1991), Oenosandridae (Miller 1991) and Urodidae (Kyrki 1988). A remarkable finding is the species-rich pantropical moth assemblage now classified as a family Micronoctuidae (Fibiger & Lafontaine 2005, Lafontaine & Fibiger 2006) and comprising the smallest known Macrolepidoptera (Fig. 13) with a wing span down to 5.7 mm (fringes excluded). Preliminary molecular work does support the assignment of these moths to the Noctuoidea, but a convincing placement of them within the superfamily remains to be substantiated (Fibiger pers. comm. to NPK). While it may come as no surprise if the *Micronoctua* group will prove to be quite subordinate noctuids, this does not detract from the excitement of the discovery of the taxon, which comprises few described and hundreds of undescribed species, many discovered in unsorted museum accessions of both micro- and macromoths (Fibiger 2007).

One recent discovery that attracted particular attention was that a small Neotropical moth group previously placed in Geometridae-Oenochrominae actually deserves the status of a separate family Hedylidae (Fig. 12) and may prove to be the closest relatives of the butterflies (Scoble 1986, Ackery *et al.* 1998, Wahlberg *et al.* 2005).

Forthcoming new insights will with certainty come also from discoveries of immature stages of high-rank taxa from which such stages are unknown. The non-neolepidopteran families Lophocoronidae and Neopseustidae remain particular challenges in this respect. Importantly, future discoveries are likely also to expand significantly the knowledge of the geographical ranges of certain taxa, particularly in the case of moths with cryptic life-styles. For instance, recent findings (Don Davis, David Lees & George Gibbs, pers. comm. to NPK) in the Neotropical, Afrotropical and Australian regions indicate that the range and diversity of Micropterigidae in the tropics is greater than believed a few decades ago, and they call for caution in interpreting distribution patterns that probably are still very incompletely known.

In sum: experience from recent decades suggests that significant new insights about the evolutionary history of Lepidoptera are still in store for us—in nature as well as in the treasure-houses of museum collections.

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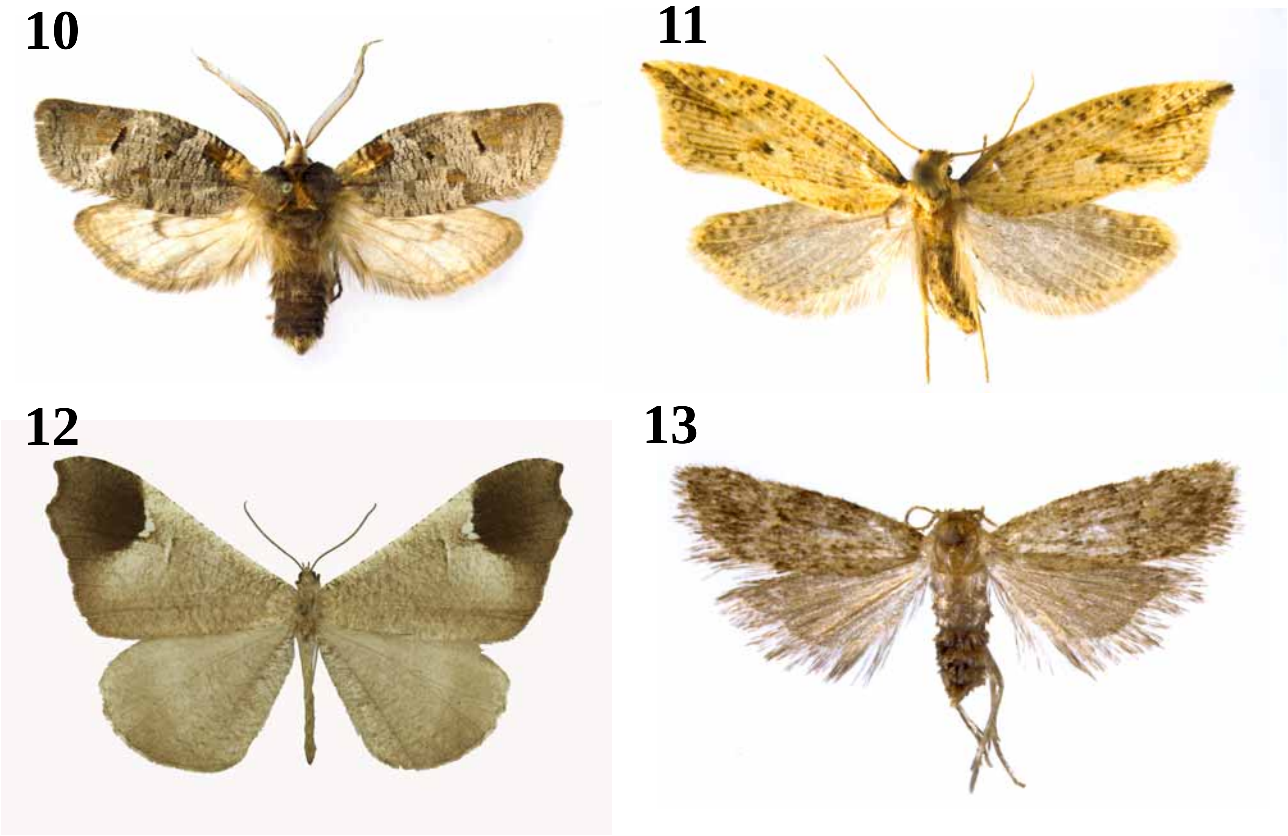
[3] *Catapterix* is indeed an interesting moth which should be examined in more detail when fixed material suited for study of 'soft anatomy' becomes available. However, on the basis of present knowledge its placement within the Acanthopteroctetidae, as the sister group to (or subordinate in?) *Acanthopteroctetes* seems reasonably well founded.



FIGURES 10–13. Representatives of some notable taxa in the Lepidoptera-Heteroneura which have been described, or whose significance has become clear, in the second half of the 20th century. 10: *Andesiana lamellata* Gentili, 1985 (Andesianidae); wing span 45 mm. 11: *Palaephatus striatus* Davis, 1986 (Palaephatidae); wing span 24 mm. 12: *Macrosoma coscoja* (Dognin, 1900) (Hedylidae); wing span 37 mm. 13: *Micronoctua karsholti* Fibiger, 1990 (Micronoctuidae); wing span 7 mm.

Lepidoptera systematics: information sources

The Lepidoptera counterpart of Junk's monumental '*Coleopterorum Catalogus*' was still quite incomplete when its publication ceased by the time of World War II. By now, of course, the published parts are very outdated. The series was later revived in 1980s (J.Heppner ed.) and has served the publication of Poole's aforementioned noctuid catalogue, which represents a notable step forward in Lepidoptera stocktaking; treatments of several smaller families have since been forthcoming. Other useful modern global-scope reference works are Bridges' butterfly catalogues (1989a–e; Nymphalidae are not covered) and the ' World Catalogue of Insects' series in which so far treatments of Pterophoroidea & Alucitidae (Gielis 2003), Tortricidae (Brown 2005), Gracillariidae (de Prins & de Prins 2005) and Coleophoridae (*s.str.*) (Baldizzone *et al*.2006) have appeared. As noted above, the large family Geometridae was catalogued by Scoble et al. (1995) and the hawkmoths (Sphingidae) were catalogued by Kitching & Cadiou (2000), both outside a serial framework.

Of special note are the six volumes constituting the 'Catalogue of the Generic Names of the Moths of the World' compiled by I.W.B.Nye and his colleagues at the Natural History Museum, London. These Generic Names catalogues were built from the comprehensive collection of index cards to Lepidoptera. The archive is composed of over 290,000 cards to all categories down to species and infraspecific names. It provides names, their associated bibliographical information and taxonomic status. Two digital products have emerged from this remarkable resource - one direct one indirect. *LepIndex*, the Global Lepidoptera Names Index, (Beccaloni et al., http://www.nhm.ac.uk/research-curation/projects/lepindex/index.html) provides users with searchable web-access to images of all the cards of Lepidoptera (indexing ceased for most taxa in 1981). The Butterflies and Moths of the World website (Pitkin & Jenkins, http://www.nhm.ac.uk/research-curation/projects/butmoth/) is a web-based interactive catalogue to the genus-group names of Lepidoptera from Linnaeus (1758) to July 2004. The compilation was derived from several published sources (notably, of course, the Generic Names volumes), with many of these sources themselves being based on the card archive.

Regional/local checklists come in many forms. The only major zoogeographical region for which complete, modern Lepidoptera checklists are available are North America (Hodges et al., 1983) and Australia (Nielsen *et al.* 1996); a checklist of Neotropical Lepidoptera is in the course of publication since 1984 (Heppner ed.). Important sub-regional checklists include, e.g., those by Karsholt & Razowski (1996) on Europe (and a more recent electronic list is available on http://www.faunaeur.org/), Heppner (1992) on Taiwan and Vári *et al.* (2002) on Southern Africa.

As for other insect orders a useful survey of identification works, including primary research articles, was given by Hollis (1980). Works of regional scope that proved invaluable tools for Lepidoptera systematists worldwide include the accounts of Nearctic Lepidoptera immatures in 'Immature Insects' (F.Stehr ed, 1987), the book by Common (1990) on Australian moths, and Holloway *et al*. 2001 on Malesian Lepidoptera. The somewhat detailed account of Lepidoptera systematics on a global basis presented in the multi-author treatment of the order in the '*Handbuch der Zoologie/Handbook of Zoology*' series (Kristensen ed. 1998) also gives many references to identification literature.

Many important internet resources for systematic Lepidopterology can be found at http://www.lepsoc.org/lepidoptera_websites_both.php. Of particular note are also the principal websites that give access to important classical descriptive literature, thereby greatly facilitating revisionary studies to workers who have no easy access to comprehensive libraries: ‘Biodiversity Heritage Library’ (http://www.biodiversitylibrary.org/) and ‘Animal Base’ (http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/search#about); both are still in development

Lepidoptera systematics: current and future research priorities

It will require very considerable resource investments on the part of the systematic lepidopterists' community to cope with the predicted doubling-to-quadrupling of the recognized species numbers. Not only will the descriptive/analytical phase itself be demanding, so will also the initial phases, viz., specialist collecting in all parts of the world (evidently prioritizing species-rich ecosystems vulnerable to, or even acutely endangered by, accelerating human activities) and the intermediate phase of specimen processing that can render the procured material accessible to practising taxonomists. Exactly because of the easily damageable scale vestiture which is the hallmark of Lepidoptera, a suite of otherwise useful automated entomological collecting devices (such as Malaise and interception traps) are of limited usefulness for these insects; also, time-consuming preparation procedures already during the field work are near-mandatory for truly satisfactory results, a least in the case of the smaller micro-moths. Moreover, as already mentioned, this vestiture obscures many of the traits that are useful for assigning specimens to family-group taxon, and it thereby impedes non-specialist sorting of museum accessions to the level at which most taxonomists are working.

It is difficult to estimate the number of entomologists presently engaged in research on Lepidoptera systematics. Most professional workers who make contributions in this field have demanding commitments of other kinds as well (teaching, curatorial, managerial) as have, of course, the amateur taxonomists. The figure for full-time research equivalents of the contemporary Lepidoptera systematics workforce is, therefore, *very* much lower than the number of authors of publications on the subject. The specialist coverage of lepidopteran subgroups is somewhat uneven, and the exceedingly low number of taxonomists working on the most species-rich families, such as Pyralidae, Crambidae, Geometridae and Noctuidae (Holarctic faunas excepted), is a particular problem. Lepidopterists make no exception to the gloomy picture of the age-structure in the taxonomists' community as a whole, as underscored in the afore-mentioned Gaston & May survey: to our knowledge there are at present disturbingly few Ph.D. students in Lepidoptera systematics worldwide.

With so much ground still to be covered, and so few workers to cover it, contemporary systematists working on the largest insect orders should pay considerable attention to the criteria on which research priorities should be set. To those systematists who are employed by primarily non-taxonomically orientated institutions (and they constitute a considerable proportion of the grand total), priorities naturally come in the form of taxa which contain economically important species, or which prove to be convenient target taxa for sampling and monitoring in biodiversity assessment/nature management contexts. Moreover, of course, workers in such institutions are usually supposed to deal with geographically restricted faunas.

But what are the guidelines for the few systematists in those universities or major research museums, where *licentia academica* is still supposed to prevail? Arguably phylogeny-based generic/genus group classifications of higher taxa (family/subfamily level) should be among the highest contemporary priorities. Good examples of such classifications *of a global scope* of genus-rich taxa are Kitching's (1987) treatment of Noctuidae-Plusiinae and Miller's (1991) of Notodontidae. A number of studies of this kind have been restricted to regional faunas; examples are the treatments of Holarctic sesiids (Naumann 1971/1977) and Australian tineids (Robinson & Nielsen 1993), oecophorids (Common 1994, 1997, 2000) and olethreutine tortricids (Horak 2006). In spite of their limitations such regionally based phylogenies may prove useful platforms for developing global classifications. Similarly, purely descriptive, but comprehensive and well-illustrated generic accounts, whether global (e.g., that of Pitkin *et al*. 2007 on Geometrinae-Pseudoterpini) or regional (e.g., that of Pitkin 2002 on Neotropical Geometridae-Ennominae) are invaluable stepping stones on the way towards the desirable phylogeny-based classifications.

Classificatory 'skeletons' of the said kinds are essential for providing appropriate frameworks for species-level revisionary taxonomy. Opinions are divided about priority setting in the latter approach, but few biologists will contest that describing *all* species and classifying them in accordance with their position on "the one true tree of life" is the ultimate goal of systematics. Genuine progress will depend on a balanced partition of resource investments in bottom up projects in the form of species-level revisions, and top down projects in the form of generic/genus group classifications of higher taxa (family/subfamily level). In this respect contemporary systematic lepidopterology is no different from contemporary systematization of other groups of organisms. What *is* special about systematization of Lepidoptera as well as the other 'megadiverse' insect orders is the sheer magnitude of the task. Development of the afore-mentioned classificatory 'skeletons' of the largest family-group taxa will be undertakings which will require time investment (material gathering, preparations and descriptive/pictorial documentation of morphological characters, gene sequencing, phylogenetic analyses, etc) beyond the capacity of individual researchers, and they will be practicable only to research teams with access to major institutions with truly comprehensive collections. If, therefore, we are to have the much needed *globa*l classificatory 'skeletons' for e.g., the 'catocaline' or 'hadenine' noctuids, ennomine or larentiine geometrids, phycitine or pyraustine pyraloids etc., etc., then we shall need initiatives to this effect being supported at the *managerial level* in major research museums, or perhaps more realistically in consortia thereof. Such initiatives would expectedly come in the form of funded projects with X principal investigators, Y post-docs, Z research students, A technicians and B operation money. Projects of this kind have so far not been commonplace in systematic entomology, but they are what progress in several other scientific disciplines is currently dependent on.

There is, currently, considerable interest in the role of the internet in taxonomy, although the diversity of approaches suggests an area in a state of rapid evolution and exploration. The semi-structured and formalised nature of taxonomic content lends itself to being transposed into database format, rendering it potentially far more accessible and flexible. But the landscape of taxonomic cyberspace is complex. Taxonomic data on the web fall into a few main categories. Ever more descriptive taxonomy is becoming available online as pdf files through electronic journals or journals, like this one, that are largely electronic. Although digital, the medium here remains, like paper, a fixed one. Fixed medium has the benefit of being archivable and helps protect nomenclatural stability. Contributions can also be quality controlled by the traditional review process. But like paper publications, those in pdf format lack the capacity to be updated other than by further and separate publication of results. By contrast, web-pages posted as HTML are capable of being updated, but the ease by which they can be created and posted on the internet means that quality is both highly variable and typically not indicated to readers. Many such websites for Lepidoptera are accessible on the web. An experiment to provide comprehensive web-based taxonomic revisions in a more controlled environment is the aim of the CATE project (www.cate-project.org), which is being developed currently. One of the two taxa used to trial and demonstrate the CATE method and principles is the Sphingidae (ca 1400 species). Revisions created through the CATE system (see Godfray et al., in press; Scoble et al., in press) are updatable: anyone with access to the web can submit a proposal to a CATE website. Proposals may range from simple geographical records to descriptions of new taxa. However, peer-review and editorial procedures are built into the workflow so that quality control can be maintained. Less structured, but highly updatable, mechanisms for taxonomy are 'scratchpads' (V. Smith, pers. comm.; www.editwebrevisions.info/scratchpadSiteList). These are based on a content management system and are intended to encourage web-based collaboration between taxonomists. The most recent large scale and highly ambitious international project called the *Encyclopedia of Life* (see www.eol.org) is aimed at building a web-page for each of the *ca* 1.8 million species. Aggregation ('mashup') technology will be used to source taxonomic information from across the web with the intention of encouraging taxonomists to structure and edit the resulting content.

The future of taxonomy looks increasingly as if the internet will eventually predominate as the platform for providing access to information about biodiversity, including all kinds of relevant taxonomic and other data. Software is ever more able to provide users with the data they require in a customised form, such as global or regional checklists, maps of species distributions based on point data, and descriptions of species. The main challenges in this endeavour are generating collaboration among a scattered and variable community, developing the capacity to atomise data to structure underlying databases, and quality control. There is an increasing expectation that information of all kinds should be available on the web. The taxonomic impediment shows little sign of being resolved by more conventional means and the best chance of integrating the effort of all Lepidoptera taxonomists, be they professional or not, is likely to be through collaboration in cyberspace. It will take a new generation of taxonomists and technology (that of the semantic web particularly) for this vision to be realised, but it is more likely to bear fruit than a more dirigist approach, which has largely failed to produce an organised and structured way of doing taxonomy. Information and Communication Technologies (ICTs) do not merely provide a more accessible and flexible medium for posting data. Rather they provide a highly accessible (virtual) environment for community involvement by anyone with an internet connection. ICTs profoundly change the collaborative and managerial landscape for improving taxonomic coverage. Optimizing the outcome of this innovation will require a judicious balance between initiatives coming through bottom up engagement by practising taxonomists (of whatever status) and from top down priority setting by management within the systematists' community.

Two final points concerning taxonomic research strategy should be mentioned as particularly pertinent to lepidopterology because of its sizeable amateur contingent. The role non-professionals play and continue to play in Lepidoptera taxonomy cannot be overstated. Duckworth, Genoways and Rose (1993) estimated that there were around 2.5 billion specimens (of all taxa) in natural history collections across the world. (L. Speers *in* Scoble 2003 suggested a range of 1.5 to 3 billion.) Being such a popular group, the Lepidoptera component of this huge estimate is surely significant. Amateurs have contributed to this collective resource in two ways. First, they have supplied institutions with specimens to such an extent that many great holdings would be bereft without the material contributions they have made over more than two and a half centuries. And amateurs follow the tradition and continue to gift material. Second, many specimens continue to be held in private collections to this day—some such holdings competing in terms of importance with collections in state-owned collections. Furthermore, most amateur lepidopterists are not just collectors, but also knowledge creators through their records and publications—publications that are often written in collaboration with professional workers. Amateurs form, then, a significant component of our collective taxonomic knowledge base. Given the popularity of Lepidoptera, their contributions are conspicuously high when we look across all taxa.

Two concerns deserve attention. One is that institutions need to be prepared to cope with substantial amounts of material when they are gifted or bequeathed. Storage space and curatorial effort to deal with large amounts of material need careful planning. Such planning includes the capacity to finance the requirements. A second problem arises when provision has not been made for a private collection when the owner dies. Beneficiaries may not share the same concern for such a collection or may fail to understand its scientific value. It is by no means unknown for collections to be broken up and sold on the open market to maximise their financial returns. The issue of stewardship is a responsibility for the lepidopterist community at large—amateur, professional and institutional.

As noted above, the rate of description of new taxa by professional taxonomists broadly has decreased as the result of adoption of stricter working standards and the emphasis on revisionary taxonomy. However, new species continue to be described without peer-review and without being placed in a revisionary context. It is a major challenge to professional lepidopterists in leading institutions, which are comparatively well-resourced, to establish close links with the communities of amateur lepidopterists, and less privileged professionals, to optimize the utilization of the considerable labour potential in these communities. If we are to understand and describe, to effect, the diversity of the Lepidoptera, all lepidopterists need to unite in a common effort. Given the number of enthusiasts, these goals are likely to be within our reach.

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Appendix 1

The Lepidoptera system (to subfamily-level) adopted in the Lepidoptera treatment in the *Handbook of Zoology* (Kristensen ed. 1998, 2003), with a few annotated changes adopted from subsequent publications. This list does not make use of the sequencing, *incertae sedis* and *sedis mutabilis* conventions, hence it is not intended to represent a detailed phylogenetic systematization of the order. Also, as noted in the main text the understanding of the phylogenetic relationships within most of the larger ditrysian superfamilies and families is still very incomplete.

- MICROPTERIGOIDEA
    - Micropterigidae
- AGATHIPHAGOIDEA
    - Agathiphagidae
- HETEROBATHMIOIDEA
    - Heterobathmiidae
- **All following: Clade GLOSSATA**
- ERIOCRANIOIDEA
    - Eriocraniidae
- **All following: Clade COELOLEPIDA**
- ACANTHOPTEROCTETOIDEA
    - Acanthopterocteidae
- LOPHOCORONOIDEA
    - Lophocoronidae
- **All following: Clade MYOGLOSSATA**
- NEOPSEUSTOIDEA
    - Neopseustidae
- **All following: Clade NEOLEPIDOPTERA**
- **EXOPORIA**-MNESARCHAEOIDEA
    - Mnesarchaeidae
- **EXOPORIA**-HEPIALOIDEA
    - Palaeosetidae
    - Prototheoridae
    - Neotheoridae
    - Anomosetidae
    - Hepialidae
- **All following: Clade HETERONEURA**
- ANDESIANOIDEA
    - Andsianidae[a]
- NEPTICULOIDEA
    - Nepticulidae
        - Pectinivalvinae
        - Nepticulinae
    - Opostegidae
        - Opostegoidinae
        - Oposteginae
- **All following: Clade EULEPIDOPTERA**
- INCURVARIOIDEA
    - Heliozelidae
    - Adelidae
        - Adelinae
        - Nematopogoninae
    - Prodoxidae
        - Lamproniinae
        - Prodoxinae
    - Cecidosidae
    - Incurvariidae
    - Crinopterygidae
- PALAEPHATOIDEA
    - Palaephatidae
- TISCHERIOIDEA
    - Tischeriidae
- **All following: Clade DITRYSIA**
- TINEOIDEA
    - Tineidae
        - Myrmecozelinae
        - Harmacloninae
        - Meesiinae
        - Dryadaulinae
        - Scardiinae
        - Nemapogoninae
        - Tineinae
        - Setomorphinae
        - Perissomasticinae
        - Hapsiferinae
        - Hieroxestinae
        - Erechtiinae
        - Siloscinae
        - Euplocaminae
        - Stathmopolitinae
        - Teichobiinae
        - Eriocottidae
        - Eriocottinae
        - Compsocteninae
    - Arrhenophanidae
    - Acrolophidae
    - Lypusidae
    - Psychidae[b]
        - Naryciinae
        - Taleporiinae
        - Placodominae
        - Typhoniinae
        - Psychinae
        - Epichnopteryginae

        - Oiketicinae
        - Psedarbelinae
- GRACILLARIOIDEA
    - Roeslerstamiidae
    - Douglasiidae
    - Bucculatricidae
    - Gracillariidae
        - Gracillariinae
        - Lithocolletinae
        - Phyllocnistinae
- YPONOMEUTOIDEA
    - Yponomeutidae
        - Scythropiinae
        - Yponomeutinae
        - Saridoscelinae
        - Attevinae
        - Praydinae
        - Argyresthiinae
    - Ypsolophidae
        - Ypsolophinae
        - Ochsenheimeriinae
    - Plutellidae
    - Acrolepiidae
    - Glyphipterigidae
        - Orthoteliinae
        - Glyphipteriginae
    - Heliodinidae
    - Bedeliidae
    - Lyonetiidae
        - Cemiostominae
        - Lyonetiinae
- GELECHIOIDEA[c]
    - Elachistidae
        - Stenomatinae
        - Ethmiinae
        - Depressariinae
        - Elachistinae
        - Agonoxeninae
        - Hypertrophinae
        - Deuterogoniinae
        - Aeolanthinae
    - Xyloryctidae
        - Xyloryctinae
        - Scythridinae
    - Chimabachidae
    - Glyphidoceridae
    - Schistonoeidae
        - Oeciinae
        - Schistonoeinae
    - Oecophoridae
        - Oecophorinae
        - Stathmopodinae
    - Lecithoceridae
    - Batrachedridae
        - Epimarptinae
        - Batrachedrinae
    - Deoclonidae
        - Deocloninae
        - Syringopainae
    - Coleophoridae
        - Coleophorinae
        - Momphinae
        - Blastobasinae
        - Pterolonchinae
    - Autostichidae
        - Autostichinae
        - Symmocinae
        - Holcopogoninae
    - Peleopodidae
    - Amphisbatidae
    - Cosmopterigidae
        - Chrysopeleiinae
        - Antequerinae
        - Cosmopteriginae
    - Gelechiidae
        - Physoptilinae
        - Gelechiinae
        - Dicgomeridinae
        - Pexicopiinae

All following: Clade APODITRYSIA[d]

- *UNASSIGNED TO SUPERFAMILY*
    - Prodidactidae [e]
- SIMAETHISTOIDEA
    - Simaethistidae
- GALACTICOIDEA
    - Galacticidae
- ZYGAENOIDEA
    - Epipyropidae
    - Cyclotornidae
    - Himantopteridae
    - Anomoeotidae
    - Megalopygidae
    - Somabrachyidae
    - Aididae
    - Limacodidae
        - Limacodinae
        - Chrysopolominae

  - Dalceridae
  - Lacturidae
  - Heterogynidae
  - Zygaenidae
    - Procridinae
    - Callizygaeninae
    - Phaudinae
    - Chalcosiinae
    - Zygaeninae
- SESIOIDEA
  - Brachodidae
  - Sesiidae
    - Tinthiinae
    - Sesiinae
  - Castniidae
    - Tascininae
    - Castniinae
- COSSOIDEA
  - Cossidae
    - Cossinae
    - Zeuzerinae
    - Cossulinae
    - Metarbelinae
    - Ratardinae
    - Hypoptinae
  - Dudgeonidae
- TORTRICOIDEA
  - Tortricidae
    - Tortricinae
    - Chlidanotinae
    - Olethreutinae
- CHOREUTOIDEA
  - Choreutidae
    - Millieriinae
    - Choreutinae
- URODOIDEA
  - Urodidae
- SCHRECKENSTEINIOIDEA
  - Schreckensteiniidae
- EPERMENIOIDEA
  - Epermeniidae
- ALUCITOIDEA
  - Tineodidae
  - Alucitidae
- PTEROPHOROIDEA
  - Pterophoridae
    - Macropiratinae
    - Agdistinae
    - Ochyroticinae
    - Deuterocopinae
    - Pterophorinae

All following: Clade OBTECTOMERA

- WHALLEYANOIDEA
  - Whalleyanidae
- IMMOIDEA
  - Immidae
- COPROMORPHOIDEA
  - Copromorphidae
  - Carposinidae
- HYBLAEOIDEA
  - Hyblaeidae
- THYRIDOIDEA
  - Thyrididae
    - Striglininae
    - Thyridinae
    - Siculodinae
    - Charideinae
- PYRALOIDEA
  - Pyralidae
    - Galleriinae
    - Chrysauginae
    - Pyralinae
    - Epipaschiinae
    - Phycitinae
  - Crambidae
    - Scopariinae
    - Crambinae
    - Schoenobiinae
    - Cybalomiinae
    - Linostinae
    - Midilinae
    - Musotiminae
    - Nymphulinae
    - Noordinae
    - Odontiinae
    - Wurthiinae
    - Evergestinae
    - Glaphyriinae
    - Cathariinae
    - Pyraustinae

All following: Clade MACROLEPIDOPTERA

- MIMALLONOIDEA

  - Mimallonidae
- LASIOCAMPOIDEA
  - Anthelidae
    - Munychryiinae
    - Anthelinae
  - Lasiocampidae
    - Chionopsychinae
    - Chondrosteginae
    - Poecilocampinae
    - Macromphaliinae
    - Lasiocampinae
- BOMBYCOIDEA
  - Eupterotidae
    - Tissanginae
    - Hibrildinae
    - Janinae
    - Panacelinae
    - Eupterotinae
  - Bombycidae
    - Apatelodinae
    - Phiditiinae
    - Prismostictinae
    - Bombycinae
  - Endromidae
  - Mirinidae
  - Saturniidae
    - Oxyteninae
    - Cercophaninae
    - Arsenurinae
    - Ceratocampinae
    - Hemileucinae
    - Agliinae
    - Salassinae
    - Ludiinae
    - Saturniinae
  - Carthaeidae
  - Lemoniidae
  - Brahmaeidae
  - Sphingidae
    - Smerinthinae
    - Sphinginae
    - Macroglossinae
- AXIOIDEA
  - Axiidae
- CALLIDULOIDEA
  - Callidulidae
    - Pterothysaninae
    - Grivaudiinae
    - Callidulinae
- HEDYLOIDEA
  - Hedylidae
- HESPERIOIDEA
  - Hesperiidae
    - Coeliadinae
    - Pyrrhopyginae
    - Pyrginae
    - Heteropterinae
    - Trapezitinae
    - Hesperiinae
- PAPILIONOIDEA
  - Papilionidae
    - Baroniinae
    - Parnassiinae
    - Papilioninae
  - Pieridae
    - Dismorphiinae
    - Pseudopontiinae
    - Pierinae
    - Coliadinae
  - Riodinidae[f]
  - Lycaenidae
    - Poritiinae
    - Miletinae
    - Curetinae
    - Lycaeninae
  - Nymphalidae
    - Libytheinae
    - Heliconiinae
    - Nymphalinae
    - Limenitinae
    - Charaxinae
    - Apaturinae
    - Morphinae
    - Satyrinae
    - Calinaginae
    - Danainae
- DREPANOIDEA
  - Epicopeiidae
  - Drepanidae
    - Thyatirinae
    - Cyclidiinae
    - Drepaninae

- GEOMETROIDEA
  - Sematuridae
    - Apoprogoninae
    - Sematurinae
  - Uraniidae
    - Auzeinae
    - Epipleminae
    - Microniinae
    - Uraniinae
  - Geometridae
    - Archiearinae
    - Ennominae
    - Oenochrominae
    - Alsophilinae
    - Desmobathrinae
    - Geometrinae
    - Sterrhinae
    - Larentiinae
- NOCTUOIDEA[g]
  - Oenosandridae
  - Doidae
  - Notodontidae
    - Thaumetopoeinae
    - Pygaerinae
    - Platychasmatinae
    - Notodontinae
    - Phalerinae
    - Dudusiinae
    - Heterocampinae
    - Nystaleinae
    - Dioptinae
  - Micronoctuidae
  - Noctuidae
    - Rivulinae
    - Boletobiinae
    - Hypenodinae
    - Araeopterinae
    - Eublemminae
    - Herminiinae
    - Scolecocampinae
    - Hypeninae
    - Phytometrinae
    - Aventiinae
    - Erebinae
    - Calpinae
    - Cocytiinae
    - Stictopterinae
    - Euteliinae
    - Nolinae
    - Aganinae
    - Arctiinae
    - Lymantriinae
    - Strepsimaninae
    - Plusiinae
    - Eustrotiinae
    - Bagisarinae
    - Acontiinae
    - Pantheinae
    - Diphtherinae
    - Dilobinae
    - Raphiinae
    - Balsinae
    - Acronictinae
    - Metoponiinae
    - Sinocharinae
    - Lophonyctinae
    - Agaristinae
    - Eucocytiinae
    - Cuculliinae
    - Oncocnemidinae
    - Amphipyrinae
    - Psaphidinae
    - Stiriinae
    - Heliothinae
    - Eriopinae
    - Bryophilinae
    - Xyleninae
    - Hadeninae
    - Noctuinae

a. Family established by Davis & Gentili (2003) for *Andesiana* Gentili, 1989, previously assigned to Cossidae.

b. The psychid subfamilies listed in the *Handbook* account are those proposed by Sauter & Hättenschwiler (1991) on the basis of the Palaearctic fauna; formal diagnoses for all still remain to be worked out.

c. In the *Handbook of Zoology* account the classification within this superfamily was based on an original morphology-based phylogenetic analysis by R. W. Hodges. Subsequent analyses based on a more extensive morphological data set (Kaila 2004) and on mitochondrial DNA plus morphology (Bucheli & Wenzel 2005), yielded somewhat different results, but no formal reclassifications were yet proposed in these studies, which both emphasized the need for additional data. Hence, while the gelechioid classification shown here is still the Hodges *Handbook* arrangement, it must be emphasized that considerable rearrangements are foreseeable.

d. Kaila (2004) found the Gelechioidea to be subordinate in the Apoditrysia.

e. Family established by Epstein & Brown (2003) for *Prodidactis mystica* (Meyrick, 1918), previously assigned to Tortricidae, Yponomeutidae and Limacodidae.

f. In the *Handbook of Zoology* account this taxon was treated as subordinate in Lycaenidae. Its status as a distinct family follows suggestions from a number of butterfly workers (see Vane-Wright 2003) and is tentatively followed here.

g. Arrangement within this superfamily here modified in accordance with Lafontaine & Fibiger (2006). A more detailed account of the diagnostic traits of individual family-group taxa was given in a previous publication by Fibiger & Lafontaine (2006) where, however, a more extensive family splitting was adopted.