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Phylogeny and Evolution of Lepidoptera

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Abstract

Until recently, deep-level phylogeny in Lepidoptera, the largest single radiation of plant-feeding insects, was very poorly understood. Over the past two decades, building on a preceding era of morphological cladistic studies, molecular data have yielded robust initial estimates of relationships both within and among the ~43 superfamilies, with unsolved problems now yielding to much larger data sets from high-throughput sequencing. Here we summarize progress on lepidopteran phylogeny since 1975, emphasizing the superfamily level, and discuss some resulting advances in our understanding of lepidopteran evolution.

INTRODUCTION

Lepidoptera, arguably the largest single radiation of plant-feeding insects, also function ecologically as pollinators and prey. In addition, they have substantial impact on humans and many other species. Lepidoptera also provide important model systems for studies of genetics, physiology, development, ecology, and evolutionary biology.

A robust phylogenetic framework is essential for all attempts to understand the diversity, adaptations, and ecological roles of Lepidoptera. Until recently, however, deep-level lepidopteran phylogeny remained poorly known, and relationships within the ~43 superfamilies had only begun to receive concerted study. Following an era of morphological cladistic studies, molecular data since the 1990s have yielded robust initial estimates of relationships both within and among superfamilies. Using still larger data sets from high-throughput sequencing, researchers are now addressing previously unsolved problems. Here we summarize progress on lepidopteran phylogeny since 1975, focusing on the superfamily level (18).

OVERVIEW OF APPROACHES IN LEPIDOPTERAN PHYLOGENETICS FROM 1975 TO 2016

Modern lepidopteran phylogenetic research began in the 1970s and 1980s with detailed studies of anatomy coupled with early application of Hennigian phylogenetics (65, 66). This now-classic work focused mostly on the earliest-diverging lineages, the so-called nonditrysians, yielding a well-resolved hypothesis on the major subdivisions of the order (65, 66). Morphological-phylogenetic works then followed on later-originating major clades (83, 84) and subgroups therein (3, 4, 47, 58, 61, 69, 90, 101, 124). An edited volume (63) summarized progress as of 1998 and presented the first comprehensive working hypothesis of phylogeny within and among superfamilies.

Early molecular phylogenetic studies on Lepidoptera in the 1990s used the highly abundant sequences of the mitochondrial genome and nuclear ribosomal DNA (12, 14, 125, 134). Nuclear protein-coding genes were introduced several years later (13, 16, 38, 138), and their number expanded over the next 15 years (17, 93, 106, 130), with up to 19–26 in some recent studies (17, 111, 151). Much of the progress described below stems from this multigene approach based on the polymerase chain reaction. Although these methods remain useful, others are increasingly supplementing or superseding them. For deeper divergences, transcriptomes and genomes yielding hundreds to thousands of genes show strong resolving potential (8, 9, 11, 53). Whole mitochondrial genomes are also providing strong signals at multiple levels (57, 126, 140). The newest methods capture target DNA regions using conserved hybridization probes (37, 73), followed by high-throughput sequencing. In forthcoming lepidopteran studies, the anchored hybridization (73) approach has yielded hundreds of loci and strong resolution at modest per-taxon cost (10). This method seems likely to become widely applied for large-scale phylogenetic studies.

Morphological studies continue (100), and the first morphological character matrix across the Ditrysia (45) now permits quantitative comparisons of morphological versus molecular phylogenetic signal. In the next section, we attempt to synthesize all lines of evidence in summarizing the current understanding of relationships among lepidopteran superfamilies. We exclude species currently unplaced to superfamily or family as well as the little-known superfamilies Simaethistoidea and Whalleyanoidea (127). **Figure 1** summarizes our conclusions and provides representative live-specimen images for the major lineages.

SYSTEMATIC POSITION AND MAJOR SUBDIVISIONS OF THE LEPIDOPTERA

The well-established sister group to Lepidoptera is Trichoptera (caddis flies), most of whose larvae are aquatic. Numerous synapomorphies support the monophyly of Lepidoptera (66). The most recent authoritative summary of lepidopteran diversity (127), our source for all such numbers except where otherwise specified, recognizes 157,424 extant species in 43 superfamilies and 133 families. The most securely established large subgroup of Lepidoptera is the clade Ditrysia, which contains 29 superfamilies and 98% of lepidopteran species (127).

Early-Diverging Lineages: The Nonditrysians

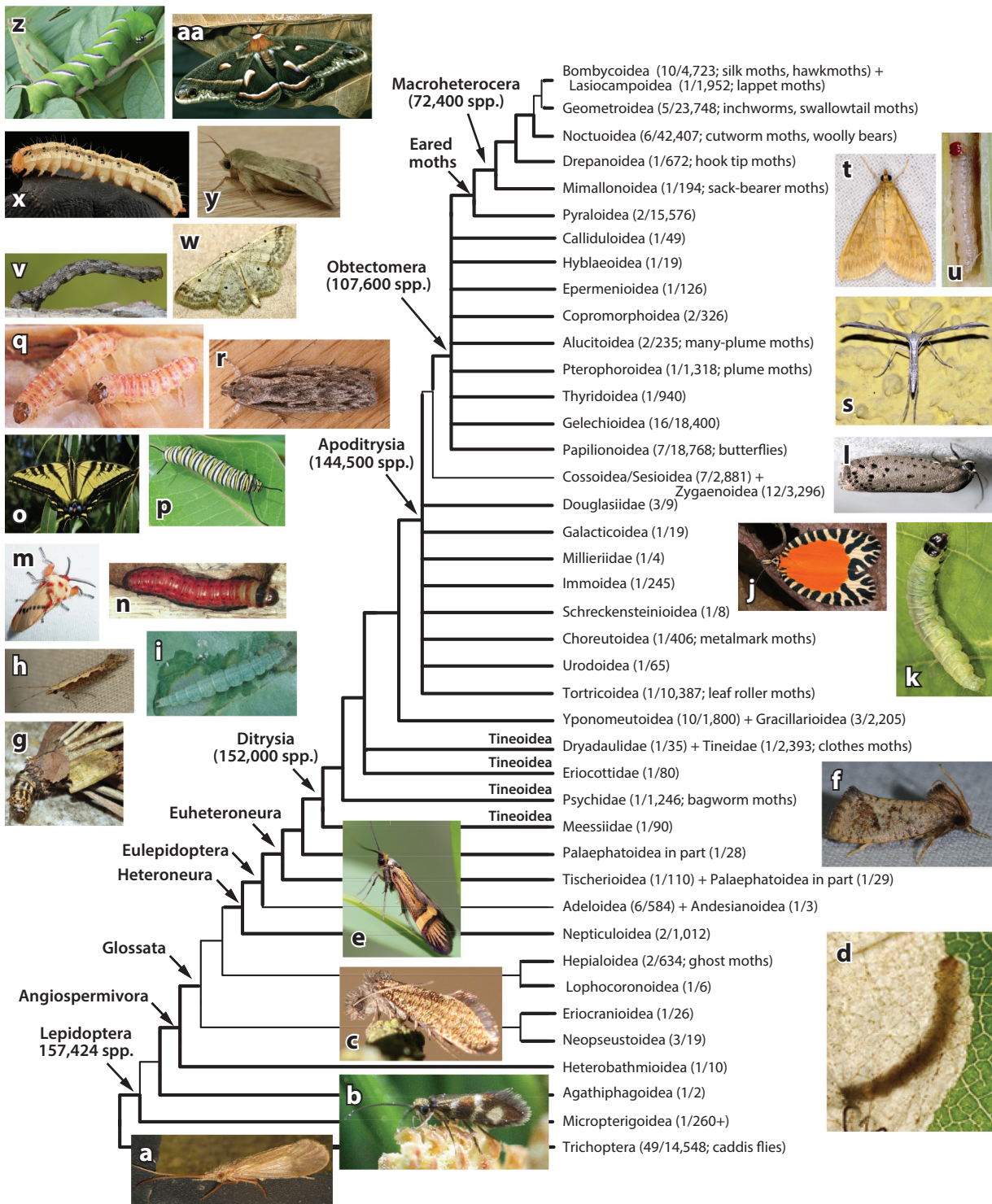
Nonditrysian Lepidoptera are a paraphyletic group of 14 superfamilies and ~21 families, most of which are species poor (23, 64, 109). The adults are mostly small (wingspan <10 mm), and most larvae are internal feeding. The morphological hypothesis (65, 66) features a nested series of clades corresponding to stepwise acquisition of traits characterizing most Lepidoptera. Molecular evidence strongly supports most of these clades, strongly contradicts several, and remains ambiguous about a few. The largest securely established clade is the newly named Angiospermivora (109), comprising all lepidopterans except Micropterigidae and Agathiphagidae and feeding in the larval stage almost always on angiosperms.

Micropterigidae, unlike most other Lepidoptera, retain functional mandibles in the adult, which feeds on pollen and fern spores. The larvae are also unusual: They dwell on or in the ground and feed mainly on liverworts or detritus. Agathiphagidae include just two Australo-Pacific species. The adult mandibles are apparently nonfunctional. The larvae feed on seeds of the conifer *Agathis*. According to morphology, Micropterigidae branch off first, and Agathiphagidae branch off second, from the remaining Lepidoptera. This phylogeny is compatible with stepwise progression from an ancestral ground-dwelling, nonphytophagous larva, to arboreal feeding on gymnosperms, and from thence onto angiosperms (62). An early molecular study strongly agreed (138), but multigene studies sometimes group micropterigids with agathiphagids, complicating the ecological interpretation (63, 109, 111). Transcriptomics strongly reasserts the hypothesis of a basal divergence between Micropterigidae and all others, but the question is not fully settled.

Within Angiospermivora, there is strong evidence for a clade Glossata, characterized by acquisition of the typical adult proboscis, that excludes only Heterobathmiidae. The morphological hypothesis (65, 66) postulates three nested basal divergences within Glossata, giving rise to Coelolepida (hollow wing scales), Myoglossata (proboscis with intrinsic musculature), and Neolepidoptera (musculate, crochet-bearing larval abdominal prolegs). These putative clades, however, are strongly contradicted by molecular evidence, implying homoplasy in the early history of their defining traits (9, 64, 109). In contrast, two other nested subclades within Glossata have strong molecular support: Heteroneura (differing venation in forewings versus hindwings, frenular wing coupling) and Eulepidoptera (origin of the pilifers, bristle-bearing organs at the proboscis base, and an advanced mechanism locking the proboscis halves). Molecular evidence further supports a clade Euheteroneura (109), containing Ditrysia plus Tischerioidea and Palaephatoidea. Finally, phylogenomic analysis resolves a subset of South American Palaephatidae as the sister group to Ditrysia, rendering palaephatoids paraphyletic (9).

Overview of Ditrysia

Delimiting subgroups is more difficult in Ditrysia than in nonditrysians. Three nested major subdivisions are now recognized (**Figure 1**). The group Apoditrysia was proposed for all Ditrysia



except Tineoidea, Yponomeutoidea, Gracillarioidea, and Gelechioidea (83, 84). Subsequently, Gelechioidea were shown to belong within Apoditrysia (8, 49, 53, 93, 111). Within Apoditrysia, Minet (83) proposed a group Obtectomera, defined initially by a pupa with fused abdominal segments but later modified to accommodate other partially conflicting characters (84). Molecular evidence strongly supports a revised Obtectomera that includes Gelechioidea (8, 53, 93, 111). Finally, within Obtectomera there is robust molecular support (8, 53, 93, 111) for a group Macroheterocera (big moths) that includes such familiar taxa as Geometroidea, Noctuoidea, and Bombycoidea.

Early-Diverging Ditrysia: The Nonapoditrysians

Molecular data (8, 53, 93, 108, 111) now strongly confirm the proposed monophyly of Ditrysia apart from Tineoidea (84) but argue strongly against monophyly of Tineoidea, which is defended by a single putative synapomorphy (24). Morphology analyzed alone and in combination with multigene data supports tineoid monophyly, but very weakly (45). In contrast, in multigene and transcriptomic analyses excluding all or most synonymous change, tineoids are paraphyletic with respect to the remaining Ditrysia (93, 108, 111). Tineoid monophyly, seen when synonymous change is included (108, 111), is an artifact of base composition convergence (111). The strong molecular evidence appears to outweigh the morphological evidence, and the superfamily classification will probably need to change. The newly recognized family Meessiidae (108), formerly included in Tineidae, appears to be the earliest-branching ditrysiian lineage known (but see below), followed by Psychidae (bagworm moths). Either Tineidae *sensu stricto* + Dryadaulidae or these families plus Eriocottidae appear to be sister group to the remaining Ditrysia. Finally, there is strong molecular evidence that the earliest-diverging lineage of nontineoid ditrysiians is Yponomeutoidea + Gracillarioidea (93, 111), which in turn are sister group to Apoditrysia. A majority of tineoid species feed on detritus and/or fungi, rather than on living plants. Given that

Figure 1

Estimated phylogeny of superfamilies of Lepidoptera, synthesized from multiple sources. Thicker lines denote more securely established groupings, and parentheses enclose number of families/species. Classification and species counts follow data from Reference 127 except as noted in the text. Panels provide representative images for major lepidopteran clades. Format for panel legends: major group name (and common name if available); approximate (forewing) length where available; image author and/or source; license code. (a) Trichoptera (caddis fly); D. Hobern, Wikipedia (W); CCA 2.0G. (b) Micropterigoidea (micropterigid moth); 3.5 mm; M. Kurz, W; CCA 2.0G. (c) Eriocranioidea (ericiroaniid moth); 5 mm; Svdmlen; CCA 2.5G. (d) Eriocranioidea (ericiroaniid larva); <5 mm; Charley Eisman. (e) Adeloidea (adelid moth); 10 mm; Svdmlen; CCA 2.5G. (f) Tineoidea (grass tubeworm moth); 10 mm; A. Reago and C. McClarrine; CCA 2.0G. (g) Tineoidea (bagworm moth); B. Dupont; CCA 2.0G. (h) Yponomeutoidea (plutellid moth); 7 mm; D. Hobern; CCA 2.0G. (i) Yponomeutoidea (diamondback moth larva); M. Shepard, G.R. Carner, and P.A.C. Ooi, Insects and their Natural Enemies Associated with Vegetables and Soybean in S.E. Asia, Bugwood Network (BW); CCA 3.0. (j) Galacticoidea (mimosa webworm); 10 mm; Ash, W; CCA 2.0G. (k) Tortricioidea (tortricid moth); 14 mm; G. Wise, W; CCA 2.0G. (l) Tortricioidea (tortricid larva); 7 mm; G. Csoka, Hungary Forest Research Institute, BW. (m) Zygaenoidea (flannel moth); 13 mm; gailhampshire; CCA 2.0G. (n) Cossioidea (carpenter worm); 30 mm; J. Solomon, USDA Forest Service, BW; CCA 3.0. (o) Papilionoidea (western tiger swallowtail); Calibas; public domain (PD). (p) Papilionoidea (monarch butterfly); USDA Forest Service; PD. (q) Gelechioidea (pink bollworm); P. Greb, USDA Agricultural Research Service; BW; CCA 3.0. (r) Gelechioidea (gelechiid moth); D. Hobern, W; CCA 2.0G. (s) Pterophoroidea (plume moth); F. Welter-Schultes, W; CC0 1.0 PD. (t) Pyraloidea (European corn borer); 13 mm; © entomart; PD. (u) Pyraloidea (European corn borer); Clemson University USDA Cooperative Extension Slide Series, BW; CCA 3.0. (v) Geometroidea (inchworm); 20 mm; Svdmlen, W; CCA 2.5G. (w) Geometroidea (inchworm moth); 12 mm; © entomart; PD. (x) Noctuoidea (corn earworm); 25 mm; USGS Bee Inventory and Monitoring Lab; CCA 2.0G. (y) Noctuoidea (Old World bollworm); 20 mm; D. Hobern; CCA 2.0G. (z) Bombycoidea (privet hawkmoth); 85 mm; © entomart; PD. (aa) Bombycoidea (cecropia moth); 80 mm; E.L. Manigault, Clemson University Donated Collection, BW; CCA 3.0. Key to license codes: CC = Creative Commons; A = Attribution (only); number (e.g., 2.0) = version; G = generic.

tineoids appear to represent several successive basal divergences in Ditrysia, the latter may have gone through an initial evolutionary phase in which saprophagy/mycophagy were dominant, prior to reradiating on living angiosperms (108).

Early-Diverging Apoditrysia: The Nonobtectomerans

The boundary between obtectomeran and nonobtectomeran Apoditrysia is still being clarified, primarily by molecular data. Several groups not traditionally considered Obectomera appear to belong there, including Gelechioidea, Alucitoidea, and Epermeniidae. In contrast, some presumptive obtectomerans, such as Immidae (66), no longer appear to belong to that clade (8, 53).

The paraphyletic nonobtectomeran Apoditrysia, approximately nine superfamilies and 25 families (~16,500 species), have proven exceptionally difficult to resolve. From morphology, only two groupings of superfamilies have been postulated: (*a*) the pairing of Cossioidea + Sesioidea (sometimes treated as a single superfamily) (127) and (*b*) the grouping of Cossioidea/Sesioidea together with Zygaenoidea (84, 117) to form what we informally term the CSZ complex. Monophyly of the CSZ complex has been difficult to assess in molecular studies, in part because the two highly divergent ectoparasitic families of Zygaenoidea are so unstable in position (8, 111). If these are excluded, however, the grouping has strong molecular support (53, 111). In contrast, morphological analyses (45) do not support monophyly. The CSZ complex is probably the sister group to Obectomera (53, 111), though more evidence is needed. Essentially no other relationships among lower apoditrysian superfamilies have been definitively established, though transcriptomic data are showing promise (8, 53).

Relationships within Obectomera

The most securely established large clade (~88,000 species) within Obectomera, supported by all molecular studies to date, consists of Pyraloidea plus Macroheterocera (here taken to include Mimallonidae) (8, 53). We refer to these informally as the eared moths, because adults of most macroheterocerans, and nearly all pyraloids, bear a pair of lateral tympanic organs somewhere near the boundary between the metathorax and abdomen. Similar structures are rare elsewhere in Lepidoptera, although other types of ultrasound detectors may be widespread (22, 87). Butterflies, formerly placed with big moths in Macrolepidoptera (65, 66), are now decisively excluded from this clade.

Phylogenomics is gradually clarifying macroheteroceran relationships. Mimallonidae (the sack-bearers) appear to be sister group to the remaining macroheterocerans (8, 53, 126). The next split is between Drepanoidea *sensu lato* (127) and Geometroidea + Noctuoidea + Bombycoidea (8, 126). Within the latter triplet, one study supported Geometroidea + Noctuoidea (53), but another favored Geometroidea + Bombycoidea (8). Morphological characters may favor the latter pairing (104), which is also consistently found in mitogenomic studies (57, 60, 140).

Relationships among the other nine obtectomeran superfamilies remain problematic (93, 111). Initial transcriptomic analyses appeared to provide strong resolution but included few superfamilies (8, 53) and were sometimes in conflict. In the absence of more complete taxon sampling, strong conclusions cannot be drawn.

PROGRESS ON THE MAJOR LEPIDOPTERAN SUPERFAMILIES

Each of the superfamilies containing $\geq 1,500$ species (as well as several smaller ones) (114) has now been subject to one or more molecular studies that attempt to span its diversity. We here

summarize advances on these major superfamilies, focusing mainly on the family level. Progress is also rapid, however, at the subfamily level and below.

Tineoidea: Clothes Moths, Bagworm Moths, and Relatives

Recent studies (93, 108, 111) have altered the previous classification of tineoid families (24). Tineidae have proven strongly monophyletic, but only after inclusion of Acrolophidae plus removal of three aberrant genera (93, 108). Psychidae (1,350 species) are securely monophyletic, but only after inclusion of Arrhenophanidae (93, 108, 111). Relationships among the 11 psychid subfamilies are incompletely studied, but results so far (108, 113) support a basal divergence between psychine and arrhenophanine lineages. Tineidae *sensu stricto* are split basally into an acrolophine versus a tineine lineage, but as yet, there is almost no further resolution (108). Approximately 13% of the ~2,200 described species of Tineidae are unplaced to subfamily, and two of the largest previous subfamilies (24) are demonstrably polyphyletic (108). Multiple new deep ditrysian lineages may await discovery.

Yponomeutoidea: Ermine Moths and Relatives

Yponomeutoidea, which include approximately 1,800 species of small- to medium-sized moths, have long been problematic. Building on the work of Kyrki and others (29, 67, 68), a molecular study (122) provided moderate to strong support for yponomeutoid monophyly and recognized 10 families. Some relationships among families were strongly supported but not all, and further work is needed. Yponomeutoidea are one of the earliest lepidopteran groups to include both internal and external feeders and to extensively colonize herbaceous as well as woody plants. The diamondback moth (Yponomeutoidea: Plutellidae) is the first genome-sequenced nonobtectomeran (143).

Gracillarioidea: Leaf-Mining Moths

Gracillarioidea formerly included Bucculatricidae, Douglassiidae, Gracillariidae, and Roeslerstammiidae (24). Molecular evidence now removes Douglassiidae to the nonobtectomeran Apoditrysa (55, 93, 111, 122). The remaining families plus Yponomeutoidea form a robust monophyletic group, but Gracillarioidea are probably paraphyletic with respect to Yponomeutoidea. Gracillariidae (~1,900 species, wingspan 4–20 mm), mostly arboreal feeders, are the largest predominantly leaf-mining lepidopteran clade (71). Nearly all species undergo larval hypermetamorphosis (i.e., a dramatic shift in morphology upon switching from fluid feeding to tissue feeding) (21). Recent multigene studies (55, 56) robustly support eight subfamilies comprising three larger clades.

Tortricoidea: Leaf-Roller Moths and Relatives

The larvae of Tortricoidea (>10,800 species, all in Tortricidae) (41, 48) are mostly either external-feeding leaf tiers or borers in various plant parts. There are three subfamilies and 20 tribes (41, 48). A multigene study (105) strongly supported both individual monophyly of and a sister-group relationship between the two large subfamilies Tortricinae and Olethreutinae. Most tribes and relationships among them were well supported, although two tribes proved paraphyletic. Tribes vary markedly in diet breadth, correlated with internal versus external feeding and with deposition of eggs singly versus in large clusters (105).

Zygaenoidea

The definition and internal phylogeny of Zygaenoidea (currently ~3,300 species in 12 families) remain in flux (34, 35, 83, 127, 142). Zygaenoid larvae are mostly exposed external folivores, which are rare outside Obtectomera, but the small families Cyclotornidae and Epipyropidae are at least initially ectoparasites on auchenorrhynchan Hemiptera. Zygaenoid larvae are typically slow growing and heavily defended and are often aposematic, as are the adults of some zygaenoid groups (35).

A morphological analysis treating five families (34) supported a limacodid group consisting of Limacodidae, Dalceridae, Aididae, and Megalopygidae, but excluding Zygaenidae. Molecular studies with additional taxa have begun to fill out the picture (8, 93, 111). Molecular evidence strongly supports a core Zygaenoidea including all except the two ectoparasitic families, basally divided into limacodid-group versus zygaenid-group families. Most but not all family definitions and relationships within these two groups are strongly supported. In molecular analyses, the ectoparasitic families are long branched and unstably placed, never grouping with other zygaenoids. In analyses including morphology (45), however, weak support joins them with the limacodid group. Overall the evidence favors the molecular result because of its very strong support, but the conflict appears genuine.

Cossoidea + Sesiioidea (Cossoidea *Sensu Lato*)

Monophyly for this putative clade, defended by two potential synapomorphies (32, 84), is uncertain. It is supported by some but not all multigene analyses (17, 93, 111), sometimes with inclusion of the parasitic zygaenoids, and usually with low support except when the latter are omitted. It was also supported, weakly, in analyses including morphology (45). Larvae in these groups are typically stem borers. Monophyly of each superfamily individually also remains uncertain. Four synapomorphies have been proposed for Sesiioidea (32, 83, 84) but only one, variably expressed, for Cossoidea (32, 83), and none for Cossidae (32). Analyses including morphology weakly support monophyly for each superfamily (45). In contrast, in molecules-only analyses, the two are invariably intermingled (93, 111), sometimes with strong support (8), and even the family Cossidae is not monophyletic. Further work is needed.

Gelechioidea

Gelechioidea (~18,400 species, plus many undescribed; wingspan typically <10 mm) remain poorly known and may eventually prove to be the most species-rich superfamily. Gelechioid larvae are mostly host specific on living plants and are typically concealed external feeders, though some are leaf miners or borers (50). There have also been unusually numerous shifts to saprophagy/fungivory (50, 123).

Both morphological and molecular data (43, 45, 123) support monophyly of Gelechioidea, but the circumscription of and relationships among families remain problematic. Two morphological studies (46, 49) reached very different conclusions. The first multigene analyses (50, 111) differed substantially from both of these results, in part owing to very low support values. Somewhat stronger groupings were seen in a combined morphological/molecular analysis by Heikkilä et al. (43), who recognized 16 families. An independent molecular analysis (123) found a different rooting but otherwise similar branching structure. If the former tree (43) is rerooted following the latter (123), the two studies both support tentative division of the superfamily into three large assemblages, with similar internal relationships. Larval ecologies show strongly clumped

distributions on this phylogeny. Saprophagy is mostly limited to one subclade of the depressariid assemblage, whereas internal feeding is almost entirely restricted to the other two assemblages. Although progress has been made, a robust phylogeny of the families will require much further work.

Papilionoidea: Butterflies

Papilionoidea (18,768 species) are the largest clade of Lepidoptera in which adults are almost always diurnal (though diurnality has arisen repeatedly in other superfamilies). Most butterfly larvae are exposed external folivores, though some are leaf rollers or stem borers. Molecular evidence has markedly changed our understanding of butterfly relationships. There is now strong support for inclusion here of Hedyliidae (2, 116), formerly placed in Geometridae. Papilionoidea as formerly defined (2), excluding Hesperiiidae (skippers) and Hedyliidae, are paraphyletic, because the Papilionidae are sister group to all remaining butterflies *sensu lato* (44, 53, 93, 111). Intensive study of among-family relationships supports the following phylogeny, expressed in standard parenthetical notation in which each pair of left and right parentheses at the same level of nesting encloses a monophyletic group: (Papilionidae, ((Hedyliidae, Hesperiiidae), (Pieridae, ((Lycaenidae, Riodinidae), Nymphalidae)))). There are now multiple phylogenetic studies on the individual families as well (36, 51, 119, 128, 129, 132); Lycaenidae are probably least well understood. A recently funded project (75) seeks to produce a molecular phylogeny for all butterfly species. Butterflies, in which phylogenetics is especially advanced, have been the model group for most recent applications of phylogeny to broader questions in lepidopteran evolution (see below).

Pyraloidea: Snout Moths, Grass Moths, and Relatives

Pyraloidea (15,576 species, with many more undescribed) (96, 127) are typically small- to medium-sized moths. Most feed as larvae on living plants, as concealed external folivores, or as stem borers. However, pyraloids are exceptionally ecologically diverse and also include detritivores, coprophages, predators, and parasites as well as aquatic herbivores.

Monophyly for Pyraloidea *sensu stricto* (81, 82) is supported by morphological analyses (45) and by all molecular studies to date (93, 110, 112). The chief synapomorphy, seen in nearly all species, is a pair of unique ventral tympanal organs on the second abdominal segment (92). Minet (81, 82) divided pyraloids into two families, Pyralidae and Crambidae, citing differences in their tympanal organs. Molecular evidence strongly supports the monophyly of each (110). Relationships among the five subfamilies of Pyralidae (5,921 species) are strongly resolved by molecular and morphological analyses (110, 124), except that Chrysauginae are poorly understood and might even include the earliest-diverging lineages in the family (110). In Crambidae, an initial molecular study (110) strongly resolved many relationships among the 21 subfamilies, including a clade associated with mustard oil plants and another associated with wet habitats. A smaller mitogenomic study on pyraloids yielded concordant results (141). Multiple nodes remain problematic, however, and further work is needed.

Geometroidea: Inchworms and Allies

Geometroidea previously included Geometridae, Uraniidae, and Sematuridae (86). Molecular evidence (8, 111) strongly favors addition of both Epicopeiidae, previously in Drepanoidea (86), and the new family Pseudobistonidae (104). Geometroids are typically medium-sized to large moths (wingspans 12–120 mm). The larvae are exposed leaf feeders, typically on woody plants.

Within geometroids, the preponderance of recent evidence (8, 104, 111) favors the following relationships: ((Uraniidae, Geometridae), (Sematuridae, (Epicopeiidae, Pseudobistonidae))). Owing to sparse sampling and conflicting results, however (53, 118), this arrangement is not definitive. The provisional phylogeny parallels the distribution of paired tympanic organs. Geometridae bear unique tympanic organs on the base of the abdomen. Uraniidae possess another unique form of this organ, differing in morphology and location between the sexes. The other families lack tympanic organs. Molecular evidence has now strongly resolved most relationships among the eight subfamilies of Geometridae (24,000 species) (1, 111, 118, 139, 144). Multigene studies also strongly resolve relationships among the three subfamilies of Uraniidae (111, 118), concordant with an earlier morphological hypothesis (72).

Bombycoide Complex: Silkworms and Allies

Minet (85) recognized a bombycoide complex consisting of Bombycoidea, Lasiocampoidea, and Mimallonoidea. Subsequent analyses, cited above, now place Mimallonoidea at or near the base of Macroheterocera, but multigene and especially transcriptomic data strongly group Lasiocampoidea (Lasiocampidae) with Bombycoidea (8, 45, 111). Within this clade, molecular evidence strongly resolves most relationships among the ten bombycoide families (11, 106, 150, 151), which include Anthelidae, formerly placed in Lasiocampoidea (85). Extensive phylogenetic information now exists on the two largest families, Saturniidae (wild silk moths) and Sphingidae (hawkmoths) (7, 52, 54, 107).

Noctuoidea: Cutworms and Allies

Noctuoidea (~42,000 species) is by far the largest lepidopteran superfamily. The adults are typically medium to large in size. Noctuid monophyly is strongly supported by molecular evidence (93, 111, 112, 146), though (surprisingly) not by morphological analysis alone (45). Unexpectedly, molecular evidence very strongly assigns the formerly noctuid family Doidae (59) to Drepanoidea (8, 93, 111), implying a dual origin for the characteristic noctuid pair of tympanic organs on the last thoracic segment. Noctuid larvae are typically exposed leaf feeders, though some groups bore in stems, flowers, or fruits, and some live on or below the soil.

Understanding of the relationships within Noctuoidea has changed substantially in recent years. Molecular data strongly establish that Noctuidae in the former broad sense (59) are paraphyletic with respect to the former Arctiidae and Lymantriidae (89, 133, 146). There is now general agreement on a system of six monophyletic families (146) consisting of the earlier-diverging Oenosandridae (8 species) and Notodontidae (3,800 species) plus a clade comprising Erebiidae (24,569 species), subsuming lymantriids and arctiids; Noctuidae *sensu stricto* (11,772 species; the trifine noctuids) (59); Nolidae (1,738 species); and Euteliidae (520 species). Oenosandridae were argued on morphological grounds to be sister group to the remaining noctuids (79), but molecular evidence remains inconsistent, sometimes strongly grouping oenosandrids with Notodontidae (80, 93, 111, 140, 146). Relationships among the remaining families are also unclear. The strongest evidence to date, from mitogenomics (140), favors the hypothesis (Erebiidae, (Nolidae, (Euteliidae, Noctuidae))), contradicting the most robust multigene result (148). Initial phylogenetic analyses have been carried out on all families except Euteliidae (70, 80, 102, 145, 147–149), but countless questions remain.

THE TIMESCALE OF LEPIDOPTERAN PHYLOGENY

The fossil record provides only the barest outline of lepidopteran history, much of which must therefore be inferred by comparison among extant species. The oldest unambiguously

lepidopteran fossil (136) is from the early Jurassic (193 Mya) and is approximately as old as the earliest trichopteran fossil (42). The earliest evidence for any subdivision of extant Lepidoptera is a much younger, lower Cretaceous fossil belonging to Glossata (125 Mya) (42). Therefore, Micropterigoidea, Agathiphagoidea, and Heterobathmioidea must have already diverged by then, though the earliest fossil micropterigid is somewhat younger (111 Mya) (135). The first reported fossil of Ditrysia is a leaf mine from the mid-Cretaceous (103 Mya) (69), assigned to a modern subfamily of Gracillariidae, though reservations about this interpretation have been expressed (42). No further securely identified fossils of Ditrysia occur until extant families start to appear in the late Paleocene (56 Mya) (42).

The lepidopteran fossil record is very poorly studied and appears to be much sparser than that of other comparably diverse insect orders (18, 42, 66, 120). The fragility and buoyancy of the scale-covered bodies and wings of Lepidoptera probably impede their preservation in lake-bed deposits (30), making compression fossils rarer than amber inclusions and trace fossils such as leaf mines. Scales and wings often obscure diagnostic features in fossils, and diagnostic features themselves are scarce even for extant lineages of Ditrysia (45). Very few lepidopteran fossils have explicitly synapomorphy-based identifications, and almost no molecular datings for lepidopteran groups have adhered strictly to the best practice (98) of using only such fossils as calibration points (25). Fortunately, lepidopteran fossils have now been extensively cataloged (27, 121), and many are being critically reexamined (26).

Despite limited fossil evidence, there have now been many molecular datings within Lepidoptera that use one or more fossils and/or other calibrations based on geography or host-plant age. Moreover, multiple dating studies have tied the origin or diversification of particular lepidopteran clades to specific Earth-history events, a potentially important advance (20, 99, 131). Most though not all divergence datings (52, 114, 139) have focused on butterflies (36, 40, 44, 94, 119). Results have varied, but the inferred ages for Papilionoidea and constituent families have typically been 140–80 Mya (lower to middle Cretaceous), two to three times older than their oldest fossils (Cenozoic; ~56–30 Mya) (42).

Several authors have examined broader divergences, with somewhat conflicting results. A multi-gene study across Lepidoptera (131) dated the first split between extant lineages at 215 Mya (late Triassic), the origin of Ditrysia at ~160 Mya (late Jurassic), and the origin of Apoditrysia at ~140 Mya (early Cretaceous), approximately twice as old, on average, as the corresponding oldest fossils. In contrast, a phylogenomic analysis across all insect orders (88) that included seven extant and three fossil lepidopterans yielded much younger ages of ~140 Mya, ~100 Mya, and ~80 Mya, respectively. This study (88) also estimated the origin of Lepidoptera at ~245 Mya, whereas a multigene analysis across hexapods (19) placed that origin at 270 Mya. Given the multi-causal variability in divergence-time estimates (28, 40, 137) and the paucity of secure calibrations (25, 120), some caution is warranted about the conclusions drawn thus far. As the array of rigorously identified fossils expands, however, and dating methods become more sophisticated and better understood, divergence datings in Lepidoptera should become increasingly accurate and precise.

TOWARD UNDERSTANDING LEPIDOPTERAN EVOLUTION

Progress on phylogenetics is helping to answer long-standing questions about lepidopteran evolution. Space permits only a brief sketch of some promising directions. Phylogenetic studies of host-plant use have shown an overall trend across Lepidoptera (with numerous exceptions) from internal feeding (most nonditrysians) to concealed external feeding (most nonmacroheteroceran ditrysians) to fully exposed folivory (butterflies and macro-moths) (77, 103), associated with

increase in body size. The reasons for this and other trends, such as the repeated switch to detritivory/fungivory, remain unexplored. Conserved association with particular plant lineages, the basis for coevolution sensu Ehrlich & Raven (33), has proven to be pervasive though not universal across surprisingly broad plant and lepidopteran taxonomic scales (77). Strong phylogenetic and genetic/biochemical evidence is emerging for escape and radiation coevolution in some groups of butterflies (31, 39). How widely it may apply elsewhere is unclear, and some studies in other groups appear to rule it out (76). Attention has also begun to focus on the evolutionary causes and consequences of phylogenetic change in host range (15, 97). Although the emphasis on herbivory still dominates studies of lepidopteran evolution, phylogenies are starting to elucidate evolutionary patterns in several modes of defense against predators, which may be equally important and complex (7, 52, 149).

Phylogenies are also helping to trace the evolution of key lepidopteran traits that have been previously studied mainly from genetic/developmental and biochemical perspectives. Analysis of the evolution of wing-pattern formation in butterflies, a prominent model system in evo-devo (91), is being extended to other major lineages (6, 115). Similarly, phylogenies are also helping to reconstruct the biochemical diversification of lepidopteran long-distance mating pheromones (74). For example, the use of type I pheromones (long straight-chain alcohols and their mainly acetate and aldehyde derivatives) versus type II pheromones (long-chain polyunsaturated hydrocarbons and their epoxy derivatives), variable among subfamilies of the former Noctuidae sensu lato (5, 78), is more conserved than had previously appeared. Type I subfamilies belong to Noctuidae sensu stricto, whereas type II subfamilies are now placed in Erebiidae (146). The latter subsumes the former Arctiidae and Lymantriidae, the only other noctuoids in which type II pheromones are known (78). Countless other lines of investigation could also be cited. Phylogeny-enabled study of lepidopteran evolution is a limitless enterprise for the future.

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