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Diversity and Significance of Lepidoptera: A Phylogenetic Perspective

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The Lepidoptera – moths, butterflies, and skippers – represent one of the three most species-rich insect orders and the largest evolutionary radiation of herbivorous animals (Scoble 1992, Wahlberg et al. 2013). The Jurassic origins of the Lepidoptera make it the youngest of the five mega-diverse insect orders, the others being Coleoptera, Diptera, Hymenoptera and Hemiptera – all except the last united within the Holometabola. Although most lepidopterans are confined to vegetative substrates and display perhaps the narrowest collective diet breadth of these groups, most of the higher phylogenetic diversity arose in association with the diversification of flowering plants during the Cretaceous (Powell et al. 1999, Grimaldi and Engel 2005), paralleled by the diversification and spread of mammalian predators and insect parasitoids. Their morphological, physiological, and behavioral innovations for capitalizing on chemically defended food plants and for avoiding and deterring predators have made Lepidoptera major components of the evolutionary landscape, and they represent an important nexus for studying the history of life. Lepidopteran larvae, whether exposed feeders that graze externally or concealed as leaf miners, leaf rollers, and stem borers, stand out among the holometabolous insects as conspicuous participants in the evolutionary dynamics of defensive behaviors, crypsis, and aggressive mimicry. Ecologically, butterflies and moths constitute a primary food source for diurnal and nocturnal vertebrate insectivores, serve as hosts for innumerable specialist insect parasitoids, and have important roles as pests and pollinators, acting as both agents and objects of natural selection. Having coevolved with predators and host plants, butterflies, moths, and their larvae represent a significant component of terrestrial biodiversity, and their herbivory has influenced the evolution of plant defensive mechanisms. They are an important forum for exploring ecological and evolutionary questions surrounding the mechanics of speciation, natural selection, and mimicry, and the roles of chemistry and climate shifts in the evolution of life histories.

From the societal standpoint, lepidopterans provide obvious resources, silk being perhaps the most obvious of these, but they also number among the most destructive and economically important forest and agricultural pests. Many species are candidates for combating invasive plants and, along with beetles, moths represent one of the most commonly tapped orders for biocontrol agents (Weed and Casagrande 2011). Because they respond quickly to environmental change, including climatic and atmospheric shifts and landscape alteration, Lepidoptera serve as a means of detecting systemic threats to

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biological resources and as an early-warning system for ecological degradation. They include some of the more well-known threatened and endangered species. Butterflies and moths also include some of the most conspicuous and beautiful insects, and represent a common gateway group through which children and young adults develop an understanding of natural history and of entomology in particular. More broadly, butterflies and moths have figured prominently in religious and spiritual frameworks and as symbols of beauty, frailty, and spirit in the works of artists and writers for millennia (Nazari 2014).

Yet there is a duality in how Lepidoptera are perceived. The charisma of butterflies is perhaps matched by a more mundane and darker mystique surrounding their nocturnal relatives. Beyond their banal use in metaphor ("moths to a flame") and their association with closet and wardrobe pests, moths are often used to represent agents of the macabre in popular culture, as in films such as *Silence of the Lambs* or *The Mothman Prophecies*. Lepidopterists have embraced this mythos, generating common names and taxonomic appellations associated with darkness and death, as in "death's-head hawkmoth." Reflecting the duality of popular perception is an asymmetry in the popular understanding of lepidopteran taxonomy and diversity: butterflies are rarely understood as simply a derived subset of moths, nested within more than 40 other superfamilies. The common question "What's the difference between butterflies and moths?" brings shudders to zoologists in the same way as asking the difference between rabbits and mammals. But most importantly for present purposes, the relationships among many of these groups, including butterflies, remain poorly understood and are often controversial.

I first briefly outline the more conspicuous ways in which Lepidoptera intersect with human society via culture, agriculture, and natural resource conservation, and particularly the roles they play in the scientific study of evolutionary and ecological phenomena. Next, I review some of the current directions and challenges, epitomized in the study of Lepidoptera, when it comes to documenting and understanding species diversity. In the chapter's remaining core, I review current understanding of how species diversity is distributed across major lepidopteran groups and some of the more conspicuous biological innovations with which evolutionary bursts of diversification might have been associated – the various groups' evolutionary highlights, so to speak, from within the context of their phylogeny as we understand it. Because lepidopteran classification remains in flux, I also highlight the more significant recent changes in classification, reflecting advances in the inference of lepidopteran phylogeny. Although the emphasis of this discussion is phylogenetic, I also stress the geographic distribution of lepidopteran species richness, and the research directions, challenges, and opportunities that a better understanding of that richness presents.

13.1 Relevance of Lepidoptera: Science

Lepidoptera have provided signature examples of numerous biological phenomena and, in many cases, the impetus for the development of inquiry, including the physiology of metamorphosis and diapause, the existence of mimicry and aposematism, chemical ecology and coevolution, mutualisms and tri-trophic interactions, the chemical mediation of diet breadth and dietary specialization, and the mechanics of speciation and sexual selection. Early demonstrations of natural selection were grounded in empirical research of butterflies and moths, and in many of these arenas, Lepidoptera have enjoyed sustained pre-eminence. The discovery of lock and key mechanisms in moth genitalia (Eberhard 1985, Shapiro and Porter 1989, Mikkola 2008, reviewed by Masly 2012) and of sphragides ("chastity belts"), which are widely distributed in butterflies (Ehrlich and Ehrlich 1978), have illuminated the mechanisms of sexual selection and sperm competition, respectively. The respective roles of pheromone chemistry, phenology, and diurnality promise to be equally valuable in the study of disruptive selection and allochronic speciation.

Lepidoptera have provided some of the most high-profile examples of both diffuse and strict coevolution. The more well-studied examples include the mimicry complex among *Heliconius* butterflies (Nymphalidae; Gilbert 1984, Brower 1996), dioptine prominent moths (Notodontidae; Miller 1996, 2009), and other winged insects, many of which share passion flowers (Passifloraceae) as larval hosts. Yucca and yucca moths (Prodoxidae) include some of the few demonstrable examples of strict coevolution, if not cospeciation (reviewed by Pellmyr 2003). The study of Lepidoptera has illuminated the chemical mediation of diet breadth and dietary specialization over evolutionary time, and the role of chemistry in the origins of aposematism mimetic systems. Some of these studies have in turn led to advances in our understanding of insect vision and bioacoustics in larval and adult insects. Genes responsible for butterfly vision have been shown to be under positive selection where wing patterns are involved in both Müllerian mimicry and kin recognition (Briscoe et al. 2010, Bybee et al. 2012). So-called "singing caterpillars" (DeVries 1991) communicate with ants by means of acoustic signaling as a defense against parasitoids, and acoustic aposematism seems to have evolved independently in multiple lepidopteran groups (Brown et al. 2007). Adult sphingid and saturniid moths have evolved means of foiling bat sonar to avoid bat predation (Barber and Kawahara 2013, Barber et al. 2015), and adults of the most diverse lepidopteran groups (Noctuoidea and Pyraloidea) are not only equipped with sonar-detection but also, in some cases, have themselves evolved acoustic aposematism (Barber and Connor 2007, Conner and Corcoran 2012, Corcoran et al. 2009), warding off their would-be predators with sound instead of, or in addition to, bright colors. Because they can be sampled readily, butterflies and moths are common foci of community ecology and faunistic studies. Likewise, as they have been well-collected and documented in many regions (especially North America and Europe), Lepidoptera from these areas are among the most readily identified and vouchered, and have a unique role in the development of genomic collections and phylogenomic studies. In North America, DNA barcodes have been obtained for more than 95% of the macrolepidopteran fauna (Zahiri et al. 2014). To the extent that fresh specimens can be determined reliably in the field, genome-grade tissues may be amassed more efficiently than for many invertebrate groups, and phylogenomic progress is likely to be rapid in Lepidoptera.

Perhaps more than any insect group, Lepidoptera feature prominently among species under legal protection and in various conservation programs and habitat restoration projects. Although a great deal of effort and research has focused on the conservation of particular species or assemblages of butterflies and moths, Lepidoptera have an important role in highlighting systemic threats to natural areas and aiding the assessment of conservation priorities. Growing recognition of the sheer magnitude of biological diversity has necessitated a more refined approach to conservation than focusing exclusively on individual species, and Lepidoptera present themselves as useful tools, rather than simply targets, of conservation efforts. The utility of Lepidoptera in evaluating the stability of biological communities derives, in many areas, from how well known the faunas are and from the availability of comparative data to assess rarity and uniqueness. But more generally, butterflies and moths have long been recognized to respond rapidly to climate and landscape-level changes, anthropogenic and otherwise. In the past decade, observers have noted the northward spread of species, an increase in the number of generations per year, and the contraction of species restricted to high-altitude or montane habitats, apparently in response to climatic temperature shifts and prolongation of growing seasons (reviewed by Parmesan 2006).

13.2 Relevance of Lepidoptera: Society

Lepidoptera account for some of the most economically and agriculturally significant examples

of forest, agricultural, and stored-product pests, many of them outbreak and invasive species. The accidental introduction of forest pests and our responses to them have had repercussions for native faunas. The introductions of the gypsy moth *Lymantria dispar* and the browntail moth *Euproctis chrysorrhoea* (both Erebidae), and more recently the winter moth *Operophtera brumata* (Geometridae), have incurred enormous costs to North American forests. The systemic non-target impacts of pesticide deployment (e.g, of dichlorodiphenyltrichloroethane (DDT) and carbaryl (Sevin)) and of parasitoids introduced as biocontrol agents, such as the fly *Compsilura concinnata* (Tachinidae; Boettner et al. 2000), have likewise been immeasurable.

Caterpillars, especially those of Noctuidae, Tortricidae, and Pyraloidea, are some the most frequently intercepted agricultural pests and elicit quarantine actions on fresh produce and stored products entering the United States from abroad. Specialist lepidopteran herbivores are frequently screened in the development of biocontrol programs to target invasive plants, such as the Brazilian pepper tree *Schinus terebinthifolius* (Manrique et al. 2012) and black swallow-wort *Vincetoxicum* spp. (Hazelhurst et al. 2012), the latter of which has been implicated in declines of monarch butterflies by acting as a potential oviposition sink (Casagrande and Dacey 2007). The unchecked, transcontinental spread of the pyralid moth *Cactoblastis cactorum*, originally employed as a biocontrol agent for prickly pear *Opuntia* in Australia, now threatens numerous cactus species (Stiling 2002).

13.3 Diversity and Diversification: A Clarification of Numbers and Challenges

This chapter is devoted largely to documenting the state of our understanding of species diversity. "Biodiversity" is a term that gained popularity after Wilson (1988) used it to refer to the panoply of taxonomic, biological, and behavioral richness, but its definition has since grown somewhat vague. As Wilson himself decried in a different context while championing the use of a more rarely used word (consilience), loss of precision accompanies popularity of usage, and words often see their intended meaning diluted through overuse. Biodiversity may have become such a word, in that its meaning – and relevance – are at risk of being overshadowed by its caché. Nevertheless, the quantification of biological diversity has been the subject of many empirical and theoretical works from faunistic, ecological, genetic, and phylogenetic perspectives. In view of its varied usage, I use the term biodiversity sparingly but embrace its vagueness to convey meaning that transcends raw numbers of species and includes as wide a breadth as possible of behavioral, ecological, and genetic richness.

That said, and with full recognition that the meaning of biodiversity defies simple quantification, I stress that any interpretation of species richness rests ultimately on some criterion for what constitutes a species in the first place and, as is the case elsewhere in biology, such issues abound in entomology generally and in Lepidoptera particularly. The centuries-old debate over the ontology of species has been largely metaphysical and often semantic, focused on how best to define entities assumed to have some essentialist nature beyond or independent of our detection. And as with all metaphysical debates, this one has led nowhere except to demonstrate that scientists operating under different premises inevitably reach different conclusions. Rather than perpetuate or recapitulate such discussions here, I will for the sake of clarity (and, from this point forward, brevity) presume a certain fundamental consensus on the idea that at least broadly consistent criteria for diagnosing species enable our ability to explore them scientifically and classify them efficiently.

Whatever their essence, species occupy unique roles in the taxonomic hierarchy as benchmarks that differentiate the empirical, phylogenetic framework of classification from the study of microevolutionary change within populations. This distinction, while easily blurred by the increasingly routine use of molecular genetic

tools in taxonomic and phylogenetic studies, bears directly on our appreciation of species richness in Lepidoptera, nowhere more apparently than in the use of mitochondrial DNA barcodes to identify cryptic species. In perhaps no order of insects has the use of DNA barcodes been more extensively applied than in the Lepidoptera (Hajibabaei et al. 2006, Rougerie et al. 2014). As has been the case in other insect groups, such studies have uncovered species diversity far exceeding that already described. The focus below is confined to assessing how species diversity is distributed among recognized higher lepidopteran taxa, and how these components of lepidopteran biodiversity are associated with behavioral and morphological innovations.

13.4 State of Lepidopteran Systematics and Phylogenetics

Biological species richness defies one-dimensional abstraction. Our tendency as biologists is to equate evolutionary "success" with species richness, as if it reflects longevity or endurance – we often equate a net increase in speciation with some notion of collective fitness, and not simply with a propensity for rapid reproductive isolation that generates many species, but short-lived ones. Species-rich groups are commonly attributed to one or more evolutionary novelties or key innovations, but these are rarely tested empirically. A complementary view is that each extant species represents a historically unique entity, not only a unique collection of behaviors and adaptations but a genome that has evolved and survived the filter of extinction events and bears clues for deciphering biological and evolutionary history through its relationships with other organisms. This is the essence of comparative biology: that biological classification represents not simply a collection of unique identifiers used for determining specimens, nor simply a mnemonic system of categorization and information storage, but a set of testable hypotheses of relationships reflecting historical events. Comparative analysis of shared behavioral, anatomical, and physiological features enables us to understand their mechanics and to disentangle independent origins of superficially similar attributes from those attributable to singular ancestral events.

The historical dimension of taxonomy and classification underlies its power not only to arrange, but also to explain biological diversity, but there lingers a more one-dimensional view of systematics as a technical discipline confined to the formulaic business of describing and naming species. As growing threats to biological diversity have been accompanied by dwindling resources available to document it, so too has concern that the pace of taxonomic progress is inadequate to document biological diversity before most of it disappears. Often, such arguments involve the so-called taxonomic impediment as an obstruction to scientific progress. For better or worse, Lepidoptera are among those taxa at the forefront of lively discussions and debates over ways to overcome the taxonomic impediment – commonly misinterpreted as a shortcoming in the field of systematics, as opposed to an indication of the sheer magnitude of biological diversity remaining to be described. The past decade has seen proposals to amend or upend the Linnaean system of hierarchical classification in favor of molecular taxonomy, to bypass nomenclatural codes in favor of democratized registries, and to replace rigorous diagnoses with heuristic distance-based measures that impede comparative analysis. Some have even used the rate of species and subspecies descriptions to argue that taxonomy is flourishing (Costello et al. 2013), again as if the endeavor of systematics is a one-dimensional descriptive exercise devoid of empirical strength.

As in other groups with conspicuously patterned organisms, butterflies and some of the more showy moth groups have received a great deal of taxonomic attention at the species level, which perhaps has diverted attention from higher-level phylogenetic research toward what is seen as the taxonomic impediment. Although most practicing systematists have come to eschew

the description of subspecies, historical proliferation of subspecific and infrasubspecific epithets in Lepidoptera has been conspicuous and these efforts have been viewed by some as having drained attention and potential expertise from comparative higher-level studies. Kristensen et al. (2007) suggested that the study of higher-level lepidopteran relationships (among superfamilies, for example) has been compromised by the group's charisma. He articulated two mutually reinforcing tendencies in which (i) lepidopteran wing scales – the feature responsible for the beautiful but distracting color patterns – obscure important structures relevant to deciphering phylogenetic relationships except at the species level, and (ii) the more promising entomologists most likely to overcome this hurdle are discouraged from working on Lepidoptera because of the anti-intellectual stigma associated with aesthetically pleasing insects.

Notwithstanding the observations of Kristensen et al. (2007), it should be acknowledged that the difficulty encountered in generating robustly supported hypotheses of relationship among lepidopteran superfamilies has likely been amplified by the fact that much of lepidopteran evolution took place rapidly; many of the primary events were compressed, and major groups might have arisen rapidly and diversified simultaneously. Most lepidopteran superfamilies are thought to have originated in the Cretaceous, well before the extinction event that triggered the end of the Mesozoic Era roughly 66 mya. However, many of the major macroheteroceran (macrolepidopteran) superfamilies are thought to have arisen close to this mark, either in the upper stages of the Cretaceous Period or in the lower Tertiary, and most have undergone radiations in the past 60 million years, paralleling those of major flowering plant groups. Latitudinal migration of land masses, changes in atmospheric gas concentrations, and periodic ice ages are likely to have brought about shifts in lepidopteran diapause that coincided with changes in the availability of food plants, creating phenological filters. Certain species radiations might not have been simply precipitated by evolutionary novelties in their ancestral food plants, but accelerated by changes in dominant vegetation responding to climatic change (Goldstein and Fibiger 2005), such as the origin of C4 grasses and the spread of grasslands during the Miocene (Toussaint et al. 2012).

It is interesting to observe parallel debates over which side of the Cretaceous–Paleogene boundary major groups of Lepidoptera and other organisms (bats, for example) evolved. But in some cases the question is currently untestable, either because lepidopteran fossils are rare (Sohn et al. 2015) or because we cannot differentiate whether mass extinctions, the causes of mass extinctions, or the biological vacuum resulting from mass extinctions enabled the fixture of major evolutionary innovations to which species radiations are commonly attributed. We also do not know how such extinctions may have set the stage for rapid diversification within groups already equipped with the underlying mechanics for adaptation. Regardless of our ability to pinpoint such origins, it is possible to identify the relative order of events, even if rapid diversification of many dominant life forms occurred simultaneously. For this reason, molecular data have been looked to as potential saviors of lepidopteran phylogeny re-construction. And although they remain promising, methods of temporal dating has proven frustrating, and classifications based exclusively on molecular phylogenetic evidence remain suspect as long as clear morphological characters cannot be adduced to support them.

13.5 General Overview

The considerable progress in elucidating higher-level relationships – establishing robust support for some of the major clades and identifying problematic "wild card" taxa as priorities for future research – has also incurred equally considerable taxonomic flux within and among superfamilies. This flux is likely to continue as the higher-level phylogenetic arrangement remains unstable in several key areas. Few major groups of Lepidoptera have enjoyed simultaneous

stability in rank, composition, and higher-level assignment (e.g., to a superfamily or infraorder). Most lepidopteran families and superfamilies described in the past 25 years, as well as major changes in rank, are scattered throughout the order. The composition and rank of groups within the Gelechioidea have been the least stable of all the superfamilies. Notwithstanding the composition of the Papilionoidea (butterflies and their relatives), flux in the recognition of family rank within the Macroheterocera has been most pronounced within the Noctuoidea.

To summarize matters effectively, it is necessary first to clarify some terminology surrounding the classification of large and small moths, butterflies, and skippers. Primary divisions in traditional, pre-Hennigian classification schemes differentiated butterflies from everything else, recognizing Rhopalocera (butterflies and skippers, bearing clubbed antennae) and paraphyletic Heterocera (moths, bearing varied antennal morphologies). These reflect popular conventions used to tell brightly colored day-flying animals from more drab, nocturnal ones. Most of these shortcuts have numerous exceptions and oversimplify the fundamental diversity in each of these groupings. Within Heterocera, a cascade of additional groupings existed based on important but imperfect characters such as wing coupling (Jugatae versus Frenatae), wing venation (Homoneura versus Heteroneura), separation of the gonopore from the copulatory orifice (Monotrysia versus Ditrysia), and, most loosely, size (Microlepidoptera versus Macrolepidoptera). Such classifications persisted long after they were recognized as unnatural. By convention, "Microlepidoptera" refers to roughly 75% of the moth families, including all the primitive superfamilies. The prefixes "macro" and "micro" are especially confusing misnomers, given the existence of large (e.g., Hepialoidea) moths within the primitive superfamilies traditionally thought of as micros and the diversity of small moths (e.g., Micronoctuinae) in multiple superfamilies of higher Ditrysia. Because the placement of butterflies has remained unstable, the term "Macrolepidoptera" has gradually fallen out of usage and been replaced by "Macroheterocera," reflecting the removal of butterflies. One large superfamily, the Pyraloidea, remains terminologically or colloquially orphaned in this scheme, considered neither macrolepidopteran (except by some microlepidopterists) nor microlepidopteran (except by some macrolepidopterists). Although the composition of Macroheterocera has been ambiguous with respect to other groups (e.g., Drepanoidea, Doidae, and Mimallonidae), it seems to have stabilized (Regier et al. 2013; Table 13.1).

The more well-supported traditional groupings of Lepidoptera have corresponded to conspicuous but not necessarily unreversed morphological features. To the extent that our understanding of these features has been refined, they continued to form the foundation for lepidopteran classification. Major morphological innovations that we interpret as uniquely derived correspond to synapomorphies for a series of subordinal, infraordinal, and rankless clade names applied to nested, progressively less-inclusive groups of one or more superfamilies (Fig. 13.1, Table 13.1). Many of the major morphological innovations are associated with adult and larval feeding habits (morphology of the haustellum or proboscis, and endophytophagy versus external feeding in larvae); wing venation (primitively homoneurous, or identical in configuration between fore- and hindwings versus the more derived heteroneurous condition); wing-coupling mechanisms (e.g., the presence of forewing jugum in homoneurous moths versus retinaculo-frenate mechanisms in higher Lepidoptera); the mechanics of the reproductive system; and, within higher Lepidoptera, the configuration of tympanal ears. Many of the gross anatomical novelties occurred early in the evolution of the order: the evolution of the haustellum in the glossatan superfamilies from mandibulate ancestors; of modified wing scales in the ancestral Coelolepida and the musculated haustellum preceding innovations associated with differentiated flight mechanics and wing-coupling mechanisms in the Heteroneura; and the massive radiation accompanying the origin of the

Table 13.1 Classification of the Lepidoptera.

Order LEPIDOPTERA Linnaeus, 1758			No. of genera	No. of spp.
Suborder ZEUGLOPTERA Chapman, 1917 (1 superfamily)				
	1	**Micropterigoidea** Herrich-Schäffer, 1855 (265 spp.)		
	1	Micropterigidae Herrich-Schäffer, 1855	21	265
Suborder AGLOSSATA Speidel, 1977 (1 superfamily)				
	2	**Agathiphagoidea** Kristensen, 1967 (2 spp.)		
	2	Agathiphagidae Kristensen, 1967	1	2
Clade ANGIOSPERMIVORA Regier et al., 2015				
Suborder HETEROBATHMIINA Kristensen & Nielsen, 1983 (1 superfamily)				
	3	**Heterobathmioidea** Kristensen & Nielsen, 1979 (10 spp.)		
	3	Heterobathmiidae Kristensen & Nielsen, 1979	1	10
Suborder GLOSSATA Fabricius, 1775 (6 infraorders, all following)				
Infraorder DACNONYPHA Hinton, 1946 (1 superfamily)				
	4	**Eriocranioidea** Rebel, 1901 (30 spp.)		
	4	Eriocraniidae Rebel, 1901	5	30
Clade COELOLEPIDA Nielsen & Kristensen, 1996 (5 infraorders, all following)				
	—	Superfamily unassigned (1 spp.)		
	5	Aenigmatineidae Kristensen & Edwards, 2015	1	1
Infraorder ACANTHOCTESIA Minet, 2002 (1 superfamily)				
	5	**Acanthopteroctetoidea*** Davis, 1978 (5 spp.)		
	6	Acanthopteroctetidae Davis, 1978	2	5
Infraorder LOPHOCORONINA Common, 1990 (1 superfamily)				
	6	**Lophocoronoidea*** Common, 1973 (6 spp.)		
	7	Lophocoronidae Common, 1973	1	6
Clade MYOGLOSSATA* Kristensen & Nielsen, 1981 (3 infraorders, all following)				
Infraorder NEOPSEUSTINA Davis & Nielsen, 1980 (1 superfamily)				
	7	**Neopseustoidea** Hering, 1925 (14 spp.)		
	8	Neopseustidae Hering, 1925	4	14
Clade NEOLEPIDOPTERA* Packard, 1895 (2 infraorders, all following)				
Infraorder EXOPORIA Common, 1975 (2 superfamilies) 11				
	8	**Hepialoidea** Stephens, 1829 (666 spp.)		
	9	Mnesarchaeidae Eyer, 1924	1	14
	10	Hepialidae Stephens, 1829	69	652

Table 13.1 (Continued)

Order LEPIDOPTERA Linnaeus, 1758			No. of genera	No. of spp.
Infraorder HETERONEURA Tillyard, 1918 (34 superfamilies, all following)				
Clade NEPTICULINA Meyrick, 1928				
9	**Nepticuloidea** Stainton, 1854 (1,046 spp.)			
	11	Nepticulidae Stainton, 1854	13	852
	12	Opostegidae Meyrick, 1893	7	194
Clade EULEPIDOPTERA Kiriakoff, 1948				
Clade INCURVARIINA Börner, 1939				
10	**Andesianoidea** Davis & Gentili, 2003 (3 spp.)			
	13	Andesianidae Davis & Gentili, 2003	1	3
11	**Adeloidea** Bruand, 1850 (583 spp.)			
	14	Heliozelidae Heinemann & Wocke, 1876	12	124
	15	Adelidae Bruand, 1850	5	294
	16	Incurvariidae Spuler, 1898	11	51
	17	Cecidosidae Bréthes, 1916	5	16
	18	Prodoxidae Riley, 1881	9	97
	19	Tridentaformidae Davis, 2015	1	1
Clade EUHETERONEURA Regier et al., 2015				
Clade ETIMONOTRYSIA* Minet, 1984				
12	**Palaephatoidea** Davis, 1986 (57 spp.)			
	20	Palaephatidae Davis, 1986	7	57
13	**Tischerioidea** Spuler, 1898 (112 spp.)			
	21	Tischeriidae Spuler, 1898	3	112
Clade DITRYSIA Börner 1925				
—	Superfamily unassigned (104 spp.)			
	—	Family unassigned (25 genera, 100 spp.)	25	100
	22	Millieriidae Heppner, 1982	3	4
14	**Tineoidea** Latreille, 1810 (3,719 spp.)			
	23	Eriocottidae Spuler, 1898	6	80
	24	Psychidae Boisduval, 1829	211	1,246
	25	Tineidae Latreille, 1810	321	2,110
	26	Meessiidae (Capuse, 1966)	35	248
	27	Dryadaulidae Bradley, 1966	1	35
15	**Gracillarioidea** Stainton, 1854 (2205 spp.)			
	28	Roeslerstammiidae Bruand, 1850	13	53

(Continued)

Table 13.1 (Continued)

Order LEPIDOPTERA Linnaeus, 1758			No. of genera	No. of spp.
	29	Bucculatricidae Fracker, 1915	4	297
	30	Gracillariidae Stainton, 1854	100	1,855
16	**Yponomeutoidea** Stephens, 1829 (1756 spp.)			
	31	Yponomeutidae Stephens, 1829	94	362
	32	Ypsolophidae Guenée, 1845	7	163
	33	Plutellidae Guenée, 1845	48	150
	34	Glyphipterigidae Stainton, 1854	28	535
	35	Argyresthiidae Bruand, 1850	1	157
	36	Lyonetiidae Stainton, 1854	32	204
	37	Attevidae Mosher, 1916	1	52
	38	Praydidae Moriuti, 1977	3	47
	39	Heliodinidae Heinemann & Wocke, 1876	13	69
	40	Bedelliidae Meyrick, 1880	1	16
	41	Scythropiidae Friese, 1966	1	1
Clade APODITRYSIA Minet, 1983				
—	Superfamily unassigned (1 family, 29 spp.)			
	42	Douglasiidae Heinemann & Wocke, 1876	2	29
17	**Simaethistoidea** Minet, 1991 (4 spp.)			
	43	Simaethistidae Minet, 1991	2	4
18	**Gelechioidea** Stainton, 1854 (18769 spp.)			
	44	Autostichidae Le Marchand, 1947	72	650
	45	Lecithoceridae Le Marchand, 1947	100	1,200
	46	Xyloryctidae Meyrick, 1890	60	524
	47	Oecophoridae Bruand, 1850	313	3,400
	48	Depressariidae (Meyrick, 1883)	114	2,300
	49	Cosmopterigidae Heinemann & Wocke, 1876	135	1,792
	50	Gelechiidae Stainton, 1854	507	4,700
	51	Elachistidae Bruand, 1850	47	901
	52	Coleophoridae Bruand, 1850	5	1,400
	53	Batrachedridae Heinemann & Wocke, 1876	10	99
	54	Scythrididae Rebel, 1901	30	669
	55	Blastobasidae Meyrick, 1894	24	430
	56	Stathmopodidae Janse, 1917	44	408
	57	Momphidae Herrich-Schäffer, 1857	6	115
	58	Pterolonchidae Meyrick, 1918	2	30
	59	Lypusidae Herrich-Schäffer, 1857	3	150
	60	Schistonoeidae Hodges, 1998	1	1

Table 13.1 (Continued)

Order LEPIDOPTERA Linnaeus, 1758		No. of genera	No. of spp.
19	**Alucitoidea** Leach, 1815 (235 spp.)		
61	Tineodidae Meyrick, 1885	12	19
62	Alucitidae Leach, 1815	9	216
20	**Pterophoroidea** Latreille, 1802 (1,318 spp.)		
63	Pterophoridae Latreille, 1802	90	1,318
21	**Carposinoidea** Walsingham, 1897 (326 spp.)		
64	Copromorphidae Meyrick, 1905	9	43
65	Carposinidae Walsingham, 1897	19	283
22	**Schreckensteinioidea** Fletcher, 1929 (8 spp.)		
66	Schreckensteiniidae Fletcher, 1929	2	8
23	**Epermenioidea** Spuler, 1910 (126 spp.)		
67	Epermeniidae Spuler, 1910	10	126
24	**Urodoidea** Kyrki, 1988 (66 spp.)		
68	Urodidae Kyrki, 1988	3	66
25	**Immoidea** Common, 1979 (245 spp.)		
69	Immidae Common, 1979	6	245
26	**Choreutoidea** Stainton, 1858 (406 spp.)		
70	Choreutidae Stainton, 1858	18	406
27	**Galacticoidea** Minet, 1986 (19 spp.)		
71	Galacticidae Minet, 1986	3	19
28	**Tortricoidea** Latreille, 1802 (10,387 spp.)		
72	Family Tortricidae Latreille, 1802	1,071	10,387
29	**Cossoidea** Leach, 1815 (2,881 spp.)		
73	Brachodidae Agenjo, 1966	14	137
74	Cossidae Leach, 1815	151	971
75	Dudgeoneidae Berger, 1958	6	57
76	Metarbelidae Strand, 1909	18	196
77	Ratardidae Hampson, 1898	3	10
78	Castniidae Boisduval, 1828	34	113
79	Sesiidae Boisduval, 1828	154	1,397
30	**Zygaenoidea** Latreille, 1809 (3,296 spp.)		
80	Epipyropidae Dyar, 1903	9	32
81	Cyclotornidae Meyrick, 1912	1	5
82	Heterogynidae Rambur, 1866	1	10
83	Lacturidae Heppner, 1995	8	120
84	Phaudidae Kirby, 1892	3	15
85	Dalceridae Dyar, 1898	11	80

(Continued)

Table 13.1 (Continued)

Order LEPIDOPTERA Linnaeus, 1758			No. of genera	No. of spp.
	86	Limacodidae Duponchel, 1845	301	1,672
	87	Megalopygidae Herrich-Schäffer, 1855	23	232
	88	Aididae Schaus, 1906	2	6
	89	Somabrachyidae Hampson, 1920	4	8
	90	Himantopteridae Rogenhofer, 1884	11	80
	91	Zygaenidae Latreille, 1809	170	1,036
Clade OBTECTOMERA Minet, 1986				
31	**Whalleyanoidea** Minet, 1991 (2 spp.)			
	92	Whalleyanidae Minet, 1991	1	2
32	**Thyridoidea** Herrich-Schäffer, 1846 (940 spp.)			
	93	Thyrididae Herrich-Schäffer, 1846	93	940
33	**Hyblaeoidea** Hampson, 1903 (18 spp.)			
	94	Hyblaeidae Hampson, 1903	2	18
	95	Prodidactidae Epstein & Brown, 2003	1	1
34	**Calliduloidea** Moore, 1877 (49 spp.)			
	96	Callidulidae Moore, 1877	7	49
35	**Papilionoidea** Latreille, 1802 (18,768 spp.)			
	97	Papilionidae Latreille, 1802	32	570
	98	Hedylidae Guenée, 1858	1	36
	99	Hesperiidae Latreille, 1809	570	4,113
	100	Pieridae Swainson, 1820	91	1,164
	101	Riodinidae Grote, 1895 (1827)	146	1,532
	102	Lycaenidae Leach, 1815	416	5,201
	103	Nymphalidae Rafinesque, 1815	559	6,152
36	**Pyraloidea** Latreille, 1809 (15,587 spp.)			
	104	Pyralidae Latreille, 1809	1,056	5,921
	105	Crambidae Latreille, 1810	1,018	9,666
Clade MACROHETEROCERA Chapman, 1893				
37	**Mimallonoidea** Burmeister, 1878 (194 spp.)			
	106	Mimallonidae Burmeister, 1878	27	194
38	**Drepanoidea** Boisduval, 1828 (672 spp.)			
	107	Cimeliidae Chrétien, 1916	2	6
	108	Doidae Donahue & Brown, 1987	2	6
	109	Drepanidae Boisduval, 1828	122	660
39	**Lasiocampoidea** Harris, 1841 (1,952 spp.)			
	110	Lasiocampidae Harris, 1841	224	1,952

Table 13.1 (Continued)

Order LEPIDOPTERA Linnaeus, 1758		No. of genera	No. of spp.
40	**Bombycoidea** Latreille, 1802 (4,723 spp.)		
111	Apatelodidae Neumoegen & Dyar, 1894	10	145
112	Eupterotidae Swinhoe, 1892	53	339
113	Brahmaeidae Swinhoe, 1892	7	65
114	Phiditiidae Minet, 1994	4	23
115	Anthelidae Turner, 1904	9	94
116	Carthaeidae Common, 1966	1	1
117	Endromidae Boisduval, 1828	12	59
118	Bombycidae Latreille, 1802	26	185
119	Saturniidae Boisduval, 1837	169	2,349
120	Sphingidae Latreille, 1802	206	1,463
41	**Geometroidea** Leach, 1815 (23,749 spp.)		
121	Epicopeiidae Swinhoe, 1892	9	20
122	Sematuridae Guenée,1858	6	40
123	Uraniidae Leach, 1815	90	686
124	Geometridae Leach, 1815	2,002	23,002
125	Pseudobistonidae Minet, Rajaei & Stüning 2015	1	1
42	**Noctuoidea** Latreille, 1809 (42,407 spp.)		
126	Oenosandridae Miller, 1991	4	8
127	Notodontidae Stephens, 1829	704	3,800
128	Erebidae Leach, 1815	1,760	24,569
129	Euteliidae Grote, 1882	29	520
130	Nolidae Bruand, 1847	186	1,738
131	Noctuidae Latreille, 1809	1,089	11,772
Total		**15,414**	**157,761**

Superfamilies (**42**) and families (*131*) are numbered in bold and shaded italics, respectively. Estimates of described species and genera follow those of Nieukerken et al. (2011), variously updated from Sohn et al. (2013, Yponomeutoidea), Heikkilä et al. (2014, Gelechioidea), and Regier et al. (2012, Pyraloidea; 2013, Ditrysia; 2014, Tineoidea; 2015, non-ditrysian superfamilies). The classification presented herein follows that of Nieukerken et al. (2011), excepting the addition of the Angiospermivora as well as certain higher-level additions and status changes (families newly described, elevated, or synonymized) published more recently. These include the addition of the homoneurous family Aenigmotineidae (Kristensen et al. 2015) and, in the Tineoidea, of Meessiidae and Dryadaulidae, both elevated in Regier et al. 2015); in the Gelechioidea (addition of Depressariidae, redefined by Heikkilä et al. 2014); Adeloidea (addition of Tridentaformidae; Regier et al. 2015); Mnesarchaeoidea (synonymized with Hepialoidea by Regier et al. 2015); Yponomeutoidea (addition of Scythropiidae, elevated by Sohn et al. 2013); and Geometroidea (addition of Pseudobistonidae; Rajaei et al. 2015). Neither the Myoglossata nor the Neolepidoptera are recovered in the analyses of Regier et al. (2015) due to the removal of the Lophocoronoidea from a position basal to each of these groups to one adjacent to the Exoporia (Hepialoidea) and the relocation of Acanthopteroctetidae (Acanthopteroctetoidea) to within the Neopseustoidea, but we retain their arrangement in this table per Nieukerken et al. (2011) for reference. Asterisks (*) refer specifically to these departures from Regier et al. (2015) and Fig. 13.1, where the placement of Lophocoronoidea reflects Regier et al. (2015) and Acanthopteroctetoidea is retained as a superfamily and sister to the Neopseustoidea. Significant questions remain regarding superfamily assignments of certain

(Continued)

Table 13.1 (Continued)

ditrysian families (e.g., of Millieriidae) and family-level classification, particularly within the Gelechioidea (Heikkilä et al. 2014), and with respect to the composition of Tineoidea, which seems to be paraphyletic with respect to the remaining Ditrysia in recent analyses (Regier et al. 2013, 2015). The composition of the Macroheterocera follows that of Nieukerken et al. (2011) with the addition of the Mimallonoidea, following the results of Mutanen et al. (2010) and Regier et al. (2013). The Prodidactidae were reassigned to the Hyblaeoidea by Kaila et al. (2013), and the placement of this family remains problematic. Classification problems for the Doidae are even more acute: this family was described and treated as a noctuoid but placed within the Drepanoidea by Nieukerken et al. (2011), and was united with the Mimallonidae by Regier et al. (2013). Nonetheless, the Doidae are retained as a family in the Macroheterocera.

ditrysian reproductive system followed by the appearance of exophytophagous larvae and adult tympanal organs that enabled avoidance and deterrence of predators.

At this writing (November 2015), 42 superfamilies and 131 families are recognized, including eight families unassigned to superfamily (five early lepidopterans, one early Ditrysian, and two Apoditrysian; Table 13.1) and a smattering of unassigned genera. The most recent global compilation of described lepidopteran genera and species, included in the classification of Nieukerken et al. (2011), is used as the basis for discussion below and for the numbers in Table 13.1. These do not necessarily reflect species and genera described or synonymized since 2011. Certain family- and superfamily-level rearrangements published subsequently to Nieukerken et al. (2011) have been incorporated, but not all recently published hypotheses of relationships are accommodated. Those with the most far-reaching impacts are discussed, including the ongoing rearrangement of the Noctuoidea and the most recent discussions over the placement of butterflies (Mutanen et al. 2010, Kawahara and Breinholdt 2014). Although a detailed treatment of each superfamily is not attempted here, a perfunctory treatment of the most diverse or conspicuous superfamilies is accompanied by selected family accounts.

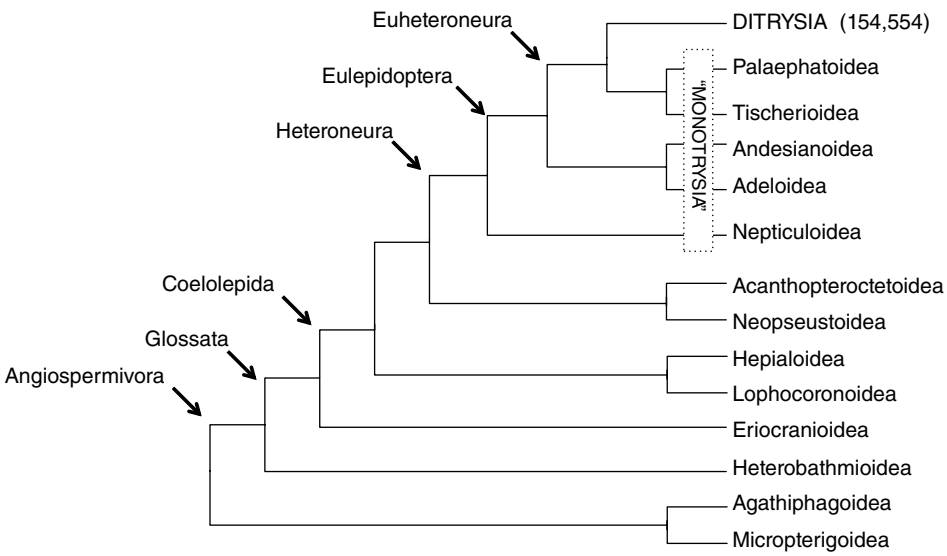

Figure 13.1 Phylogenetic skeleton of basal lepidopteran superfamilies, revised in part following Regier et al. (2015) but retaining Acanthopteroctetoidea and not specifying paraphyly of Palaephatoidea. (Table 13.1 provides further elaboration).

13.5.1 Primitive Lepidoptera

The most phylogenetically basal of the extant lepidopteran superfamilies (Fig. 13.1) retains several primitive features, including well-musculated mandibles as adults, lacking the fused galeae (haustellum) that unite the rest of the order; a characteristically rough, fuzzy cephalic vestiture of hair-like scales; and folded, five-segmented maxillary palpi (Kristensen 1999a). These basal groups comprise three superfamilies, each assigned its own suborder and each containing a single family, the most speciose of which is the Micropterigidae. The most derived of these superfamilies (Heterobathmioidea) is united with the remaining Lepidoptera under the name Angiospermivora by Regier et al. (2015).

The glossatan superfamilies, almost 99.9% of the order, are united by the presence of a coilable haustellum. Primitive glossatans form a grade of six superfamilies with homoneurous wing venation and wing-coupling mechanisms involving jugal lobes. The most basal of these is the Eriocranioidea, the second most diverse of the homoneurous superfamilies; its only family, Eriocraniidae, is Holarctic, with about 30 species characterized by their small size and metallic-colored wings. Eriocraniids have micro-trichiated wing surfaces and, along with the Acanthopteroctetoidea and the Lophocoronoidea, have haustella that lack intrinsic musculature. The Acanthopteroctetoidea contain a single family, Acanthopteroctetidae, with five species restricted to western North America. Similarly, the Lophocoronoidea contain one family, Lophocoronidae, and all six of its species are found in Australia. These two superfamilies have been grouped with the remaining Lepidoptera under the infraordinal name Coelolepida on the basis of hollow wing scales (Fig. 13.1; Kristensen 1999b).

Neither of the remaining named primary clades within the homoneurous moths, Myoglossata or Neolepidoptera, has withstood recent tests of monophyly by Regier et al. (2015) based on the placement of Acanthopteroctetidae and the Lophocoronidae in more derived positions within the tree (Fig. 13.1; *cf.* Table 13.1). Both families had been placed by Nieukerken et al. (2011) outside "Myoglossata," purportedly on the basis of a proboscis (haustellum) with intrinsic musculature, but Regier et al. (2015) relocate the Acanthopteroctetidae within the Neopseustoidea, which previously comprised a single small family distributed in Asia, the Indian subcontinent, and western South America. Regier et al. (2015) place the Lophocoronidae as sister to the remaining homoneurous superfamilies, the Mnesarchaeoidea and Hepialoidea, which they synonymized under the latter name. These were traditionally assigned their own suborder (Exoporia), united by the uniquely configured female reproductive system. Female exoporians (hepialoids) have a separate gonopore and copulatory orifice, as do the ditrysian Lepidoptera, but lack an internal ductus seminalis. Spermatozoa deposited in the bursa copulatrix during mating travel along an external seminal groove between the ostium bursae and the ovipore for fertilization (Scoble 1992, Kristensen 1999b). The family Mnesarchaeidae contains fewer than 10 species, all endemic to New Zealand; the far more diverse and conspicuous exoporians are the Hepialoidea, four of whose component families (Palaeosetidae, Prototheoridae, Neothoridae, and Anomosetidae) were synonymized by Regier et al. (2015) under the Hepialidae, or ghost moths, which now contains more than 660 species. Hepialids are internal feeders of woody plants with drastically reduced adult mouthparts; their centers of known diversity are Australia and the Neotropics. They include some of the largest "microlepidoptera." Exoporians form the basal branch and only homoneurous clade of the Neolepidoptera, a group putatively characterized by crochet-bearing larval prolegs and adectitious, obtect pupae. However, the exporians were not admitted by the arrangement of Regier et al. (2015) on grounds of their paraphyletic inclusion of the Lophocoronoidea.

The heteroneurous "Neolepidoptera" or Heteroneura are united by numerous features, including their wing venation, retinaculo-frenate mechanism of wing coupling, and loss of the first abdominal sternum (Davis 1999).

Phylogenetically, the Heteroneura (as well as the Eulepidoptea and Euheteroneura, all subtended by a common node) straddle the monotrysian and ditrysian superfamilies; the heteroneurous monotrysians span the paraphyletic grade comprising the Nepticuloidea, the cosmopolitan Adeloidea (~584 species), the monobasic Andesianoidea endemic to Andean South America, and the ambiguously related Tischerioidea (trumpet moths, 110 species) and Palaephatoidea (57 species). These groups are referred to as the monotrysian heteroneura because they retain a single opening for copulation and oviposition (Davis 1999). Nepticuloids, the most basal heteroneurans, include the smallest lepidopterans, some with forewing lengths of 1.5 mm. The composite families of the Adeloidea have undergone some nomenclatural flux with the inversion of the nominotypical superfamily name from Incurvarioidea. They are, in decreasing order of species richness, the fairy longhorn moths (Adelidae, ~294 species), the Heliozelidae (123 species), the yucca moths (Prodoxidae, ~98 species), the Incurvariidae (~51 species), the Cecidosiidae (16 species), and the recently described monobasic Tridentaformidae. In the configuration of Regier et al. (2015), the Adeloidea and Andesianoidea represent the most basal branch of the Eulepidoptera, characterized in part by the presence of pilifers and precisely coupled galeae (haustellum). The Palaephatidae, which exhibit a Gondwanan distribution (i.e., South America, Australia, and southern Africa), and the widespread Tischeriidae represent the most likely candidates for the sister group of the Ditrysia (Davis 1999, Wiegmann et al. 2002), with which they are united under the name Euheteroneura by Regier et al. (2015). In contradiction with morphological evidence, Regier et al. (2015) obtained results suggesting polyphyly of the Palaephatoidea, with South American *Palaephatus* sister to the Ditrysia and the couplet of Australian palaephatid genera *Azaleodes* and *Ptyssoptera* sister to the Tischerioidea, but they refrained from altering the classification pending further analyses.

13.5.2 Ditrysia

The Ditrysia are characterized by a uniquely derived female reproductive system in which a separate gonopore and copulatory orifice are linked internally via the ductus seminalis (as opposed to externally, as in the exoporian configuration) (Fig. 13.2). The Ditrysia include the traditional "Macrolepidoptera" and, with the exception of the Nepticuloidea, they include all of the superfamilies that have more than 1000 described species. The number (14) of major ditrysian superfamilies with more than 1000 species nearly matches the number of minor ones.

Twenty families grouped into three diverse superfamilies – Tineoidea, Gracillarioidea, and Yponomeutoidea – represent the primitive Ditrysia. One primitive ditrysian family, the Millieriidae, is currently unplaced.

13.5.2.1 Tineoidea

The most diverse of the primitive ditrysian superfamilies includes the bagworms (Psychidae, ~1350 species), a cosmopolitan but primarily Old World group (Davis and Robinson 1999); the fungus moths and clothes moths in the cosmopolitan Tineidae (~2110 species); and the minor Old World family Eriocottidae (~80 species). Recent attention has resulted in the elevation of two tineid subfamilies to family status, the primarily Holarctic Meessiidae (248 species) and the cosmopolitan Dryadaulidae (Regier et al. 2015); and the description of a new monobasic family, the Aenigmatineidae from Australia (Kristensen et al. 2015). Other recent arrangements have reduced the New World family Acrolophidae to subfamily status (Acrolophinae) within the Tineidae (Regier et al. 2014). Adult tineoids are generally recognizable by virtue of dark bristles on the labial palpi; short, disassociated galeae; and erect scales on the frons. Most females bear a pair of ventral abdominal pseudapophyses on A10. The bagworms (Psychidae) are known for their tendency toward female neoteny, in the most extreme cases resulting in pupal mating, and several other features correlated with eruptive

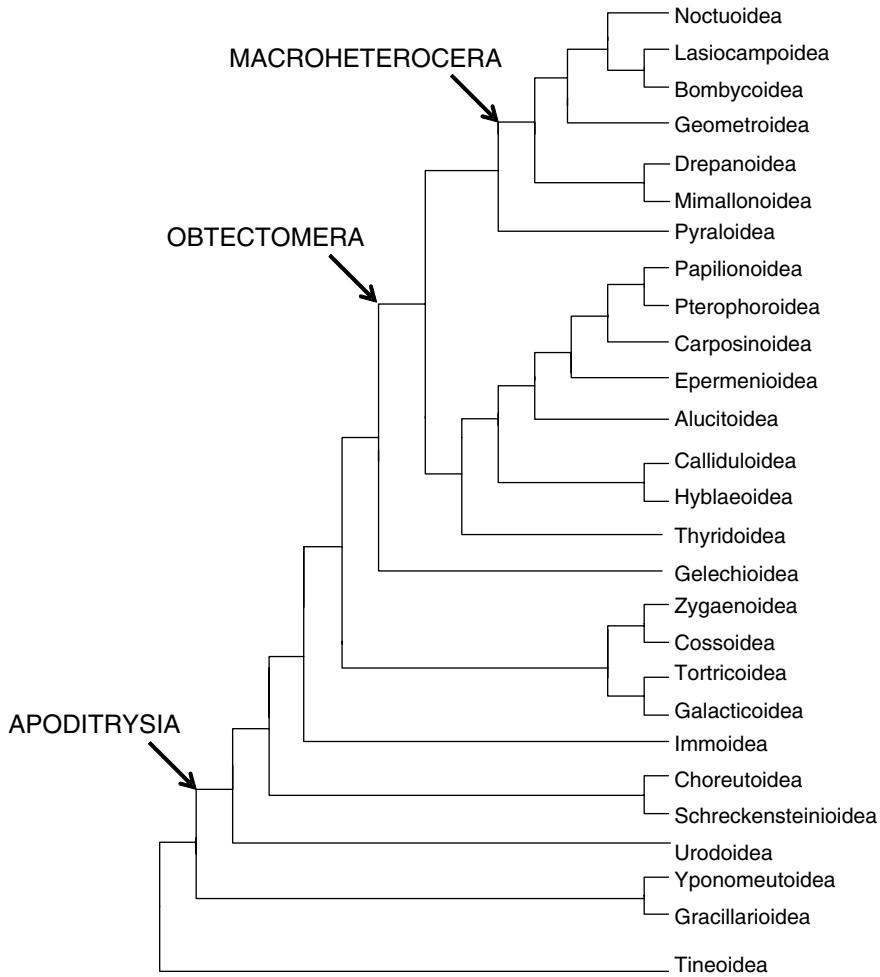

Figure 13.2 Reduction of Regier et al. (2013: figure 3), modified in part by retaining usage of Nieukerken et al. (2011) of Carposinoidea in place of Copromorphoidea. The paraphyly of Tineoidea and the polyphyly of Carposinoidea (= Copromorphoidea) and Palaephatoidea obtained in analyses of Regier et al. (2013, 2015) are not reflected; as in those studies, Whalleyanoidea and Simaethistoidea are not included.

or outbreak species, high fecundity, dispersal via larval ballooning on silken threads, and polyphagous feeding habits (Raints et al. 2009).

13.5.2.2 Gracillarioidea

The gracillarioids represent a significant radiation of more than 2000 described species of small moths whose larvae are miners of leaves and grasses and can be of significant economic importance. Many gracillariid larvae are hypermetamorphic, with early sap-feeding instars exhibiting conspicuously autapomorphic features before reverting to more eruciform or caterpillar-like forms in later stages. Gracillarioid pupae are characteristically extruded from the cocoon prior to eclosion, and adults bear spines on the abdominal terga and a smoothly scaled frons (Davis and Robinson 1999). Most of the species richness in this group is concentrated in one worldwide family, the Gracillariidae, with more than 100 genera and 1800 described species. This group is in considerable need of study.

13.5.2.3 Yponomeutoidea

In counterpoint to the gracillarioids, this cosmopolitan superfamily of more than 1756 described species represents the earliest major radiation of moths with externally feeding larvae, distributed among 11 recognized families, including the recently elevated Scythropiidae (Sohn et al. 2013, Lewis et al. 2015). The largest of these are the Glyphipterigidae or sedge moths (~535 species), Yponomeutidae or ermine moths (~363 species), and Lyonetiidae (~204 species). Among the smaller families is the commonly encountered and brightly colored Attevidae (webworms, ~50 species). The Plutellidae (~150 species) include web-building leaf skeletonizers, such as the diamondback moth *Plutella xylostella* L., which are pests of brassicaceous crops. Adult male yponomeutoids are usually diagnosed by unique pleural lobes surrounding the genitalia (Dugdale et al. 1999a).

13.5.3 Apoditrysia

The remaining 26 ditrysian superfamilies make up the Apoditrysia. The so-called higher Ditrysia are characterized by shortened apodemes with enlarged bases on sternum II (Minet 1991). A phyletic grade of pre-obtectomeran apoditrysians is made up of 14 superfamilies dominated by Gelechioidea (~18,489 species) and Torticoidea (~10,387 species), followed in order of decreasing species richness by the Zygaenoidea (~3296 species), Cossoidea (~2881 species), and Pterophoroidea (~1318 species); the remaining nine superfamilies each contain fewer than 500 described species. The composition of the Apoditrysia remains controversial, in that the large superfamily Gelechioidea is ambiguously placed (Kaila 2004).

13.5.3.1 Gelechioidea

The most diverse of the microlepidopterans, the Gelechioidea, as currently circumscribed, includes more than 18,000 described species distributed in 17 families, the rank and classification of which have been highly unstable. If the estimate of Hodges (1999) that more than 70% of the gelechioids remain undescribed is accurate, then the Gelechioidea might be the largest lepidopteran superfamily. The largest families are the Gelechiidae (~4700 species), Oecophoridae (3308), Elachistidae (~3201), Cosmopterigidae (1792), Coleophoridae (1386), and Lecithoceridae (~1200); the remaining 11 families contain under 1000 described species each. Adult gelechioids can be identified by a combination of characters, first and foremost the overlapping scales on the basal half of the haustellum. Because at least two unrelated groups (Pyraloidea and Choreutoidea) possess a similar feature, the gelechioids can be differentiated by the absence of tympanal organs (present in pyraloids) and the absence of small, naked, partially segmented maxillary palps (present in choreutids). Other gelechioid features include a smoothly scaled head and four-segmented maxillary palpi folded and parallel with the base of the haustellum, and characteristically upturned and with an elongated third segment (Hodges 1999). Gelechioid larvae can be identified in part by the location of the subdorsal pinaculum above the spiracle on A8; in the Tortricidae the pinaculum usually is anterior to the spiracle.

All of the most diverse gelechioid families and almost all the minor families are worldwide in distribution, with various centers of diversity. The Gelechiidae (twirler moths, ~4700 species) represent the largest, most economically important, and least comprehensively studied of the gelechioid families. Gelechiids are small moths with endophagous larvae identifiable in part by the colinear abdominal setae on A9.

The Oecophoridae (concealer moths, ~3308 species) have a center of species richness in Australia, and include a number of economically important pests of stored grains, textiles, and various palms (Arecaceae), as well as would-be biocontrol agents. The Elachistidae (grass miners, ~3201 species) represent an important group of graminivorous insects with several fossil genera described from Baltic Amber; adults are usually identified by their characteristically upturned feather-like forewing fringe. The Cosmopterigidae (~1792 species) are a family of

small, narrow-winged moths concentrated in the Australian region, with larvae that feed internally on various parts of their food plants. They also include aquatic species, as in the Hawaiian endemic *Hyposmocoma* (Schmitz and Rubinoff 2011). The Coleophoridae (case-bearers, ~1386 species) are concentrated in the Holarctic. Adult coleophorids are typically recognized by their visibly fringed wing margins; their larvae, as the name suggests, feed from the safety of silken cases following their early instars as internal feeders. Behaviors associated with case-building and the morphology and architecture of the cases have been the focus of phylogenetic research (Bucheli et al. 2002), paralleling analogous studies of cocoon- and case-building in caddisflies (Weaver and Morse 1986, Wiggins and Wichard 1989, Stuart and Currie 2001). The Lecithoceridae (long-horned moths, ~1200 species) are concentrated in the Australian and Oriental regions, and can be recognized from other gelechioid families by their long antennae and reduced or absent gnathos in the male genitalia (Park 2011).

13.5.3.2 Pterophoroidea

Of the remaining four most diverse pre-Obtectomeran Apoditrysia, the Pterophoroidea or plume moths are the smallest, containing a single cosmopolitan family, the Pterophoridae (~1318 species), noteworthy for their highly modified, characteristically divided wings, extremely long legs, and unique appearance at rest. Pterophorids include several important pests of ornamental plants and numerous species used in biocontrol of invasive plant species.

13.5.3.3 Tortricoidea

Notwithstanding the enigmatic genus *Heliocosma* (placed its own family, the Heliocosmidae, by Regier et al. 2013), this superfamily comprises a single highly diverse and widespread family, the Tortricidae, with more than 10,300 described species grouped in three subfamilies. The Tortricoidea include more than 700 species of economically important pests, representing the highest concentration in any microlepidopteran family and the highest taxonomic concentration of fruit and nut pests in the Lepidoptera. The most well-known of these pests include the codling moth *Cydia pomonella*, the light brown apple moth *Epiphyas postvittana*, the European grapevine moth *Lobesia botrana*, and spruce budworms (*Choristoneura* spp.). The potential economic impacts of tortricids are as far-reaching as the diversity of their food plants, threatening markets as varied as avocado, orange juice, and wine production. Adult tortricids are united by characteristic flat ovipositor lobes in the female genitalia (Horak 1999), but can be identified by a combination of characters that include an unscaled proboscis, rough-scale head, porrect or horizontal three-segmented labial palpi with a characteristically short apical segment, reduced maxillary palpi, and the presence of ocelli and chaetosemata (Horak 2006). Tortricid larvae are varied in their feeding habits, ranging from leaf rollers, flower- and litter-feeders, and gall-makers to borers of roots, fruits, and seeds. They are readily identified by the presence of a common pinaculum or saddle on A9 and the characteristic configurations of the secondary dorsal pinacula in each of the two major subfamilies, Tortricinae and Olethreutinae. These taxa overlap in their areas of concentration: the Australasian, Neotropical, and Palearctic regions for the Tortricinae versus the Nearctic, Palearctic, and Oriental regions for the Olethreutinae (Heppner 1991).

13.5.3.4 Cossoidea

The carpenter moths (Cossidae, ~971 species), clear-winged moths (Sesiidae, ~1397 species; formerly recognized as its own superfamily Sesioidea), and giant butterfly moths (Castniidae, 113 species) include the most massive of the ditrysian 'microlepidoptera'; they are stem- and wood borers with many of the features commonly associated with such habits, including grub-like coloration and motile pupae that facilitate adult eclosion. Sesiids are almost all diurnal and rarely collected, except through rearing or pheromone-trapping efforts. The Castniidae, or giant butterfly-moths, are likewise diurnal and are implicated in mimetic complexes involving a range of butterflies and other moths.

13.5.3.5 Zygaenoidea

The 12 currently recognized zygaenoid families are perhaps more diverse behaviorally and morphologically than their taxonomy suggests. They include the only two lepidopteran families (Epipyropidae and Cyclotornidae) with ectoparasitic larvae, their hosts being fulgoroid planthoppers, leafhoppers, and scale insects. Many zygaenoids are chemically defended as larvae (e.g., Dalceridae, Megalopygidae, and Limacodidae), and the most diverse zygaenoid family, the Limacodidae (slug caterpillars, ~1672 species), are as fascinating for their unique larval locomotory mechanism (Epstein 1995) and striking appearance as for their urticating spines. As in the related Cossoidea, at least one major diurnal lineage within the Zygaenidae (~1036 species) has been accompanied by chemical sequestration of pyrrolizidine alkaloids, aposematism, and mimicry. The phyletic breadth of butterflies and moths associated with the Zygaenidae via Müllerian mimicry rings in Asia alone is perhaps greater than that associated with any other lepidopteran family.

13.5.4 Obtectomera

Although supported by recent molecular work, this grouping rests on weakly corroborated morphological grounds. It includes all Apoditrysia with the first four pupal abdominal segments immobile and the pulvillus in the adult pretarsus modified with a dorsal lobe (Minet 1991). Historically, these included the "pyraloid grade" of six superfamilies and the much larger Macrolepidoptera (Kristensen and Skalski 1999), but these loose groups have largely dissolved, as will be summarized following individual superfamily treatments.

The phylogenetic position of the most conspicuous diurnal Lepidoptera, the butterflies and skippers (Papilionoidea), is among the more controversial. Several of the component papilionoid families have been recognized as superfamilies. It has been suggested that butterflies represent derived geometroid-like moths, with the enigmatic Hedylidae at the center of this discussion (Scoble 1986, Weintraub and Miller 1987). The link with hedylids was controversial when introduced, as it seemed to imply potential derivation of butterflies from Geometroidea, which would in that case have been rendered paraphyletic. The monophyly of the "Hesperioidea" was not in question; the discussion was primarily one of placement and thereby rank. Here the simplified higher classification of Nieukerken et al. (2011) is followed, in which both the skippers (Hesperiidae) and the "moth-butterflies" (Hedylidae) accompany the five true butterfly families within the Papilionoidea instead of forming their own eponymous superfamilies. This arrangement is consistent with the phylogenetic analysis of Heikkila et al. (2012), who combined morphological characters with sequence data from eight gene regions to recover [Papilionidae + [[Hedylidae + Hesperiidae] + [Pieridae + [Nymphalidae + [Riodinidae + Lycaenidae]]]]. Their results suggested an early Cretaceous origin for the butterflies *sensu lato*, with diversification accelerating post-Cretaceous–Paleogene. The exclusively Neotropical Hedylidae, with fewer than 40 described species, is the smallest of these, united in part by the reduced foreleg and characteristic adult resting posture with midlegs raised (*cf.* Thyrididae). The diverse and cosmopolitan Hesperiidae, with more than 4000 described species, is most diverse in the tropics and includes one of the largest assemblages of lepidopterous insects associated with grasses and other commelinids, the subfamily Hesperiinae, or grass skippers. Skippers are strong flyers and, with exceptions, typically drab in coloration. They form an unambiguously supported monophyletic group, united by the wide separation of antennal bases, characteristically hooked antennae, and a narrow hind wing cell formed by the union of the R and Sc veins, among other features. Skipper caterpillars are usually characterized by tapering at either end, enhancing the appearance of the enlarged head capsules common among grass-feeding Lepidoptera.

The true butterflies include, in order of decreasing size, brush-footed butterflies (Nymphalidae, > 6150 species described); the blues, coppers, and

hairstreaks (Lycaenidae, > 5200 species); the metalmarks (Riodinidae, > 1530 species); sulphurs (Pieridae, ~1164 species); and the swallowtails (Papilionidae, 570 species). Swallowtails, so named for the modified hind wings of many species, are perhaps most conspicuous of all the butterflies. Their caterpillars are almost as well known and recognized, in part, by the presence of the post-cephalic repugnatorial gland, the osmeterium. Swallowtails include the largest of the butterflies, the birdwings (Troidini) native to the Indian subcontinent, Southeast Asia, and Australasia, which are now listed by CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) and thereby heavily restricted or banned from international trade. Many papilionids feed as larvae on chemically defended hosts, for example, in the Aristolochiaceae and Apiaceae. Having evolved the ability to sequester and coopt defensive compounds such as aristolochic acid from their larval host plants, birdwings and their relatives represent a textbook example of coevolution (literally, as they feature on the cover of Futuyma's 1986 edition of *Evolutionary Biology*). Other butterflies have evolved analogous strategies for exploiting allelochemicals of their host plants: glucosinolates from Brassicales in the case of Pieridae (Edger et al. 2015); cardiac glycosides from milkweeds (Asclepiadaceae) in the case of monarchs and other Danainae (Nymphalidae) (Parsons 1965); and cyanogenic glycosides from *Passiflora* in the case of *Heliconius* (Nymphalidae) (Gilbert 1972).

Whites and sulphurs (Pieridae) are worldwide in distribution excepting New Zealand; their synapomorphies include fully developed forelegs in both sexes (*cf.* Nymphalidae) and bifid tarsal claws, distinguishing them from papilionids. Pierid pupae are suspended with the aid of a silken girdle secured abdominally rather than thoracically as in the Papilionidae.

The Riodinidae and Lycaenidae form a closely related pair of families that are worldwide in their distribution, with much of their species richness (especially that of the Riodinidae) concentrated in the Neotropics. Adult males in both families have reduced forelegs; hindwings of riodinids exhibit a uniquely configured costa. Larvae of both families tend to be dorsolaterally compressed and have evolved unique, commonly mutualistic associations with ants, which they supply with nutrient-rich secretions in return for defense against parasitoids (reviewed by Pierce et al. 2002). Some myrmecophilic riodinid larvae, the singing caterpillars of DeVries (1990, 1991), produce substrate-borne sounds to communicate with ants for protection.

The Nymphalidae include some of the most popular butterflies. Several nymphalids, most obviously the monarch *Danaus plexippus* (Danainae), but also species of the Nymphalinae, such as the red admiral *Vanessa atalanta*, are well-known seasonal migrants. Nymphalids comprise the most diverse assemblage of butterflies, both in terms of species richness and in that many of its at least 12 component subfamilies were, until relatively recently, considered to be families. Now included under the umbrella name of brush-footed butterflies are the admirals, fritillaries, longwings, monarchs, morphos, owls, and satyrs – a cosmopolitan cluster reaching its greatest richness in the Neotropics. Nymphalids are united by a variety of wing venational characters, grooves on the antennal undersides, and with exceptions reduced or atrophied forelegs in both sexes. Larvae in the Nymphalinae tend to be spined. The primary lineages are the snout butterflies (Libytheinae); the milkweed butterflies (Danainae), including the clearwing butterflies and their relatives (Ithomiini), many of which are involved in Müllerian mimicry rings by virtue of larval sequestration of pyrrolizidine alkaloids; the longwings (Heliconiinae), including *Heliconius* spp., which form the nexus of innumerable studies of mimicry and coevolution; the related, often mimetic Limenitidinae; the Nymphalinae and related subfamilies, an assemblage with broad host associations; and the Satyrinae and their relatives, including the owl butterflies, morphos, and satyrs, which collectively form the largest radiation of grass-, sedge-, and other monocot-feeding Lepidoptera. Relationships among the major nymphalid lineages have been studied intensively over the past decade.

Primary among the traditional pyraloid-grade superfamilies are the Thyridoidea, Hyblaeoidea, and Calliduloidea. Until the recent assignment of Prodidactidae to the Hyblaeoidea, each of these superfamilies included a single family of brightly colored, diurnal species. The Thyrididae are primarily pantropical with a few species in the Nearctic or Palearctic; they are readily differentiated by their characteristic wing shape and resting posture (with midlegs raised, as in the Hedylidae) (Dugdale 1999b). Like the Thyrididae, the less diverse, primarily Old World Hyblaeidae or teak moths, the primary host plants of which are within the Lamiales, can be differentiated on the basis of characters in the adult legs. Each of these families also has been included within the Pyraloidea, but as recent molecular evidence suggests, these placements are poorly supported and superfamily status is warranted. Although the Hyblaeoidea and Thyridoidea share unique modifications of the larval spinneret, Kaila et al. (2013) declined to propose a sister group relationship of the two superfamilies in recognition of apparently conflicting molecular data. The Callidulidae or butterfly-moths are found in the Old World, primarily in the Oriental region, with an endemic species in Madagascar (Minet 1999). They are united by several features of the male and female genitalia and the adult foreleg. From a phenomenological perspective, it is among the obtectomerans where we begin to see repeated origins of bright, aposematic coloration in association with adult diurnal activity, the callidulids representing a signature example. The precise placements of the Immoidea and Carposinoidea (Carposinidae and Copromorphidae; formerly Copromorphoidea) remain uncertain.

Depending on the final phylogenetic residence of the Papilionoidea, the Pyraloidea probably represent the most diverse of the obtectomeran superfamilies outside the Macroheterocera, including more than 16,000 described species, with possibly as many awaiting discovery. Pyraloids include the second largest cohort of pests (~750 species) of any lepidopteran superfamily, including rice borers, flour and meal moths (e.g., *Ephestia elutella* and *Plodia interpunctella*), wax moths (e.g., *Galleria melonella*), and the European corn borer *Ostrinia nubilalis*. Considered neither a traditional microlepidopteran nor a true macroheteroceran superfamily, pyraloid larvae are similar to macroheterocera by virtue of having two prespiracular setae instead of the microlepidopteran three. Adult pyraloids have conspicuous maxillary palpi and, as in the two large macroheteroceran moth superfamilies, bilateral ultrasound detection organs. As in the Geometroidea, these organs are abdominal but are thought to have evolved independently, and although neither is considered homologous with the thoracic tympana characteristic of the Noctuoidea, Regier et al. (2013) suggested the possibility that ultrasound detection in these groups might be attributable to a single evolutionary origin near the base of the Macroheterocera. The two component pyraloid families, the Pyralidae and Crambidae, the latter referred to as grass moths, are differentiated as adults by the configuration of the tympanic organ (Munroe and Solis 1999). In the Crambidae, these organs bear a praecinctorium, and the tympanum and conjunctiva are set at an oblique angle, whereas the Pyralidae have no praecinctorium and exhibit a co-planar arrangement. The Crambidae are the more diverse in terms of species richness (roughly 9655 versus 5921 in Pyralidae; Nieukerken et al. 2011) and number of subfamilies (13 versus five; Regier et al. 2012). The Phycitinae (~3450 species) represent the largest pyralid subfamily, and include roughly two-thirds of the described pyralids. Taxonomically, the Crambidae are dominated by the Spilomelinae (~3767 species), Crambinae (~1987 species), and Pyraustinae (~1450 species) (Regier et al. 2012). Pyraloids are noteworthy not only for their diversity of economically important pests of graminaceous crops such as rice, corn, and sugarcane, but also for their numerous grass-feeding and wetland-associated species. The Crambinae make up one of the more diverse assemblages of graminivores within the Lepidoptera and include some of the few aquatic and semi-aquatic lepidopteran larvae, as well as a number of important biocontrol

agents that are used against invasive wetland plants. Pyralids, although less diverse, affect a broader range of resources as pests of legumes, stored grains, flours, cereals, dried fruits, and managed bee hives, and as defoliators of cultivated pines. They, too, include important biocontrol agents, for example, of prickly pear (*Opuntia*; Clausen 1978).

13.5.5 Macroheterocera

The remaining superfamilies have demonstrated varying degrees of compositional as well as phylogenetic instability. Neither the pyraloid grade nor the Macroheterocera seems to be stable in its arrangement; different analyses have placed the Carposinoidea and/or the Immoidea basal within the Apoditrysia (Regier et al. 2009; Mutanen et al. 2010), and more recently the Carposinoidea firmly within the Obtectomera (Regier et al. 2013). The uncertain placement of the Papilionoidea highlights the instability of superfamilial relationships, as does the unstable composition of the Bombycoidea/Lasiocampoidea and placement of the Drepanoidea and Mimallonoidea relative to the Geometroidea (i.e., straddling the base of the Macroheterocera).

Following the treatments of Regier et al. (2009), which circumscribed Macrolepidoptera to the exclusion of butterflies (Papilionoidea), and Mutanen et al. (2010), who obtained an expanded Macrolepidoptera that included the butterflies and the Pyraloidea as well as related Thyridoidea, Hyblaeoidea, and Calliduloidea, Nieukerken et al. (2011) adopted Macroheterocera to the exclusion of the butterflies (Papilionoidea) and the sackbearers (Mimallonoidea). Subsequent empirical work has retained the Mimallonoidea within the Macroheterocera (Regier et al. 2013). Both Regier et al. (2013) and Kawahara and Breinholdt (2014) retained the circumscription of the Papilionoidea by Nieukerken et al. (2011) to include the skippers (Hesperiidae) and the moth-butterflies (Hedylidae), each of which had been recognized as superfamilies. Both Regier et al. (2009, 2013) and Kawahara and Breinholdt (2014) disassociated the butterflies from the Pyraloid grade altogether: first as sister to a Cossoidea/Sesioidea + Zygaenoidea, rendering Macrolepidoptera, Apoditrysia, and Obtectomera all polyphyletic (Regier et al. 2009); next, as embedded within an assemblage of pyraloid-grade superfamilies (Calliduloidea, Hyblaeoidea, and Thyridoidea) and pre-obtectomeran Apoditrysian superfamilies (Pterophoroidea, Alucitoidea, and Epermenioidea), collectively forming a sister group to the [Pyraloidea +Macroheterocera], all within a monophyletic Obtectomera with the Gelechioidea as the sister taxon (Regier et al. 2013); and most recently as basal within a re-composed Obtectomera that includes the Gelechioidea as follows: [[Papilionoidea + [[Gelechioidea + [Calliduloidea + Thyridoidea]] + [Pyraloidea + [Mimallonoidea + Macroheterocera]]]] (Kawahara and Breinholdt 2014). Mutanen et al. (2010) had presented similar results, with the Papilionoidea more or less embedded within traditional microlepidopteran groups.

The Bombycoidea include 10 families of large moths. The smallest families include the monotypic Carthaeidae as well as the Phiditiidae (23 species, Old World), Endromidae (59 species, Palearctic), Brahmaeidae (65 species, Old World), and Anthelidae (94 species, Australian). The remaining five range from the moderately sized Apatelodidae (145 species, New World, primarily Neotropical), Bombycidae (185 species, Old World, primarily Oriental), and Eupterotidae (339 species, Old World) to the large, diverse and cosmopolitan Sphingidae (1463 species) and Saturniidae (2349 species), the latter with its greatest diversity in the Neotropics. Except for the worldwide Saturniinae, eight of nine recognized saturniid subfamilies are continentally restricted.

Perhaps with the exception of the silk moth *Bombyx mori*, the Saturniidae and the Sphingidae include the most well-known and popular bombycoids, and are among the most intensively studied. Their respective life histories have been contrasted by Janzen (1984) and Bernays and Janzen (1988). Saturniids tend to be associated as larvae with the foliage of woody plants and do not feed as adults, bearing reduced

or vestigial mouthparts and exhibiting little tendency towards long-distance dispersal. The Hemileucinae are especially well known for their variety of defensive strategies, including urticating spines on the larvae, false eyespots on the wings, and aposematic coloration and behaviors in adults of diurnal species, possibly associated with allelochemicals synthesized *de novo*. Sphingids, by contrast, tend to specialize on various forbs and vines that bear either defensive allelochemicals or volatile compounds exploited by female moths as oviposition cues. Sphingids as a group are highly vagile and many are seasonal migrants; their presumably high energetic needs as adults may be met, in part, by means of highly efficient mouthparts. The existence and pollination activity of *Xanthopan morgani* Walker, bearing a proboscis more than 30 cm long, was predicted by Darwin and Wallace following examination of the Malagasy orchid *Angraecum sesquipedale* Thouars, which has an unusually long nectar-bearing spur unreachable by other insects.

Bombycoids are of economic importance in various ways. The mopane worm *Gonimbrasia belina* constitutes an important source of protein for indigenous southern Africans, and a significant industry surrounds its cultivation. The cultivation of the silk moth *Bombyx mori* (Bombycidae) is responsible for sericulture, established in China for more than 5000 years. Silk played a role in international commerce long before being smuggled from China to the Byzantine Empire during the 6th century AD. *Bombyx mori* is the only known truly domesticated insect, unable to reproduce in the wild. Although saturniids are rarely considered pests, outbreaks of the orange-striped oakworm *Anisota senatoria* (Ceratocampinae) in northeastern North America and the buck moth *Hemileuca maia* (Hemileucinae) in southeastern North America have resulted in the localized defoliation of wild and ornamental oaks, respectively. Several sphingid species, most notably the closely related tobacco hornworm *Manduca sexta* and tomato hornworm *Manduca quinquemaculata*, are significant farm and garden pests. Because of its size, availability, and ease in rearing, *M. sexta* has been used extensively as a model organism in insect physiology and neurobiology laboratories.

The Lasciocampoidea, the lappet moths and tent caterpillars, include a single family of nearly 2000 species worldwide in their distribution. Lasiocampids bear similarities to bombycoids in their overall appearance, reduced mouthparts, and in many cases their size. Because of their conspicuous aggregations and tent-forming behavior, tent caterpillars (*Malacosoma* spp.) are well-known pests, especially of ornamental trees, but generally do not kill the plants on which they feed. Although many lepidopterans are gregarious as larvae, *Malacosoma* caterpillars were the first presocial larvae shown to use chemical recruitment trails (Fitzgerald and Peterson 1983) and have figured more prominently in the sociobiology literature than any other lepidopterans not associated with ants (Costa 2006; Fitzgerald 1995).

Geometroidea and its five component families – Epicopeiidae (20 species), Sematuridae (40 species), Uraniidae (686 species), the recently described monobasic Pseudobistonidae, and the overwhelming Geometridae (> 23,000 species) – make up the second most diverse lepidopteran superfamily. The Geometroidea combined with the Noctuoidea make up more than 40% of described Lepidoptera species. In addition to the loss of abdominal prolegs, a reliable synapomorphy for geometroids is the shape of the larval labium, in which the spinneret is shorter than the prementum along its midline (Minet and Scoble 1999). Like the Pyraloidea, adult geometroids bear tympana on the first abdominal segment, but are readily distinguished from pyraloids by the unscaled proboscis and usually broad wing shape. Although diverse, the internal classification of the Geometridae is not excessively complicated relative to other comparably sized groups. The most recent work (Sihvonen et al. 2011) essentially supported the monophyly of the four major subfamilies (Ennominae, Larentiinae, Sterrhinnae, and Geometrinae); the remaining four (Oenochrominae, Archiearinae, Desmobathrinae,

and Orthostixinae) have not been as robustly tested, and three appear to be polyphyletic (Oenochrominae and Desmobathrinae) or, in the case of the Orthostixinae, nested within the Ennominae.

Representing the second largest lepidopteran family next to the Erebidae, the Geometridae are perhaps most familiar as inchworms, so named for the loss of larval prolegs on abdominal segments 3–5 (retaining those on A6 and A10), which produces their characteristic looping gait (enabling rapid movement) and hence the appearance of measuring or meting out distance. They can be differentiated from superficially similar loopers in the Noctuidae, which have lost or vestigial prolegs on A3–4, retaining those on both A5 and A6. Adult geometroids can appear butterfly like at rest, and include many diurnal butterfly mimics. The Geometridae include few major agricultural pests but several forest pests, including the invasive winter moth *Operophtera brumata* L. Several geometrid groups display trends toward female aptery (winglessness), dispersing primarily through larval ballooning (Edland 1971). The geometrid genus *Nemoria* provided the first known example of a tannin-induced seasonal polyphenism, in which larval mimicry of its host-plant (oak) catkins is suppressed in late-season generations when the catkins are no longer in flower to aid crypsis (Greene 1989). Each of the remaining families, other than the recently described monobasic Pseudobistonidae, is made up of primarily diurnal species variously associated with swallowtail butterflies (Papilionidae) in Müllerian mimicry rings.

With more than 40,000 described species and possibly as many undescribed, the Noctuoidea, currently arranged into six families, represent the most species-rich lepidopteran superfamily, with more than 25% of described Lepidoptera. They account for the largest family cohort of pest species (> 1000), including the bollworms (*Helicoverpa*), the most economically important insect pests worldwide. Noctuoids are characterized by larval crochets arranged in uniordinal mesoseries and by adult thoracic tympanal organs whose orientation varies by group. They include the prominent moths (Notodontidae, 3800 species), the owlets (Noctuidae, ~12,000 species), the tiger moths Arctiinae (~11,000 species, cosmopolitan with a Neotropical center of distribution), and the tussock moths Lymantriinae (~2800 species, nearly cosmopolitan but primarily Old World), the latter two formerly recognized as families but now grouped along with the underwings (*Catocala*) and other former noctuid subfamilies in the Erebidae (~25,000 species). The remaining recognized noctuoid families are the Oenosandridae (eight species, endemic to Australia), Euteliidae (520 species, cosmopolitan but primarily Afrotropical), and Nolidae (1738 species, cosmopolitan but primarily Old World tropics), the latter two of which formerly were treated as subfamilies of Noctuidae. Noctuoids are characterized by the presence of metathoracic tympanal organs and their associated structures.

In the past 15 years, the Noctuoidea has undergone perhaps the most controversial taxonomic rearrangement of any superfamily, precipitated by increasing recognition that a large cohort of the Noctuidae bore significant phylogenetic affinities to the then-recognized Arctiidae (tiger moths) and the Lymantriidae (tussock moths) (Mitchell et al. 2000, 2006; Fibiger and Lafontaine 2005; Lafontaine and Fibiger 2006). Traditionally, noctuoid families were demarcated along differences in fore- and hindwing venation and the configuration of tympanal organs, with the Oenosandridae and Notodontidae considered basal with respect to the remaining families on the basis of the trifid state of the forewing medial veins and the horizontally oriented thoracic tympana without counter-tympanal hoods (Miller 1991). The remaining noctuoids exhibit a quadrifid condition in the forewing and obliquely oriented tympana with counter-tympanal hoods. Although the noctuoids had undergone numerous rearrangements, Arctiidae and Lymantriidae remained intact as separate families while the so-called deltoid subfamilies (underwings and their relatives) were retained within the Noctuidae proper. These latter groups were differentiated

from so-called trifine noctuids in part by a quadrifine condition in the hindwing analogous to that in the forewing, and it became increasingly clear that they bore more in common with each other than with typical Noctuidae. Following an analysis of molecular data that supported earlier findings of Mitchell et al. (2006) and Weller et al. (1994), Zahiri et al. (2011) faced the alternatives of either uniting the lymantriids and arctiids within the Noctuidae to retain its monophyly, or cleaving the Noctuidae into multiple monophyletic families. Either alternative, inevitably, would render the Arctiinae and Lymantriinae as subfamilies. Rather than create a vastly expanded Noctuidae, the decision, therefore, was made to circumscribe a monophyletic Erebidae to include deltoid subfamilies as well as Arctiinae and Lymantriinae (Zahiri et al. 2011), and elevate the noctuid subfamilies Nolinae and Euteliinae to family rank. This arrangement restricts the still-enormous Noctuidae to a core of subfamilies bearing trifine venation, although exceptions ultimately might destabilize this classification. Recent analyses of relationships among the quadrifid noctuoid families have varied (*cf.* Zahiri et al. 2011, 2012, 2013a, 2013b; Yang et al. 2015). In their coverage of the Nolidae, Zahiri et al. (2013b) recovered support for the arrangement [Oenosandridae + [Notodontidae + [Euteliidae + [Erebidae + [Noctuidae + Nolidae]]]]]. Because of the widespread familiarity of noctuids *sensu lato*, these rearrangements have been accepted slowly. In terms of species richness, the result is that the Noctuidae have been reduced by more than 50%, from roughly 25,000 to 12,000 species, the remainder combined with Arctiinae and Lymantriinae to form the Erebidae of nearly 25,000 species or distributed within the elevated Euteliidae and Nolidae. Significant strides have been made in resolving relationships within Erebidae (Zahiri et al. 2012) and Nolidae (Zahiri et al. 2013b). The tribal and subfamilial classification of the trifines, the Noctuidae *sensu stricto*, is a highly unstable taxonomic morass, but one likely to congeal in the upcoming years.

13.6 Needs and Challenges for Advancing Lepidopteran Studies

Developing phylogenetic information is crucial to exploring an extensive range of questions. Still largely unexplored are the roles of climate shifts in the evolution of diapause, diet breadth, and life-history timing. Broad patterns in the evolutionary lability of host associations and what mediates diet breadth have not been explored in detail. Likewise, major questions remain regarding timing of evolutionary events involving the origins of echolocation, the coevolutionary chemical arms race, the mechanics of mimicry, and the relationships between major climatic shifts and the appearance and disappearance of major moth and butterfly groups. These endeavors require insight from a wide variety of fields, including those external to entomology. Regier et al. (2013) mention three trends: increasing body size, the transition from endophytophagy to concealed external feeding and thence to exposed external feeding, and sound detection. A fourth is a proliferation in the number of origins of diurnality and aposematism (visual and acoustic) in association with the allelochemicals synthesized *de novo* or coopted from chemically defended host plants. The ways in which Müllerian mimicry rings are amplified over macroevolutionary time have not been explored adequately, nor have higher-level phylogenetic trends of co-mimetics. But the repeated origins of similar patterns among moth and butterfly groups with widely disparate origins is noteworthy, including the convergence toward butterfly patterns within groups both ancestrally derived (e.g., Zygaenidae: Chalcosiinae) and more recently derived (e.g., Epicopeiidae) with respect to the butterflies themselves.

At a time when advances in bioinformatics, data mining, and especially genomic research coincide with unparalleled loss of habitat, a pressing need exists for deep phylogenetic research, basic alpha taxonomy, and faunal inventory alike.

Genomic data will be crucial for elucidating relationships among lepidopteran groups, but will need to be coupled with careful comparative work to better understand the origins of insect-life histories and how they reflect the history of the planet. Such efforts also will be crucial for stabilizing nomenclature across continents where closely related species have been isolated in monobasic genera (Mikkola et al. 1991). And so, although it will be critical to accelerate the pace of evolutionary research, systematics requires greater use of and more rigorous analyses of even rudimentary molecular genetic data, such as DNA barcodes, not simply for purposes of raw description but for formal diagnostic purposes.

For Lepidoptera, and insects in general, the age of discovery is far from over. Major groups of small and large moths alike might have fewer than 50% of their species described. Even with the integration of molecular data for purposes of discovery and description (Goldstein and DeSalle 2011), the documentation of life-history information required to answer evolutionary and ecological questions is both daunting and even more time sensitive than the collection of specimen material. Unfortunately, dwindling resources might not be adequate to maintain existing natural history collections that make phylogenetic and evolutionary research possible.

As the pace of scholarship enables empirical and analytical shortcuts, it will be important to ensure that the novelty of genomic data does not fuel the confusion of phylogenetic systematics with simple nomenclature (Costello et al. 2013; *cf.* de Carvalho et al. 2013). Although a growing number of tools have been developed and are being brought to bear on entomological research generally and systematic and taxonomic work in particular, systematic entomology is struggling with an increasingly rarefied professional climate and dwindling funding resources at a time when biological diversity is threatened more directly than ever before. If we are to be realistic, we must acknowledge that the current extinction crisis is not likely to abate, and that many groups of organisms will one day be known only from preserved specimens and tissues. We do not suggest that systematists will assume the roles of biological morticians. Short of proposing major infrastructural overhauls to the way resources are allocated to biological research, we might at least redouble our exploratory and expeditionary efforts in the more diverse and threatened regions, adopt techniques for collecting and indefinitely preserving genomic-grade tissues of as many taxa as possible, and mount efforts to identify diverse and under-sampled groups and generate baseline faunistic data as efficiently as possible.

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