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# 1 Evolutionary Framework for Lepidoptera Model Systems

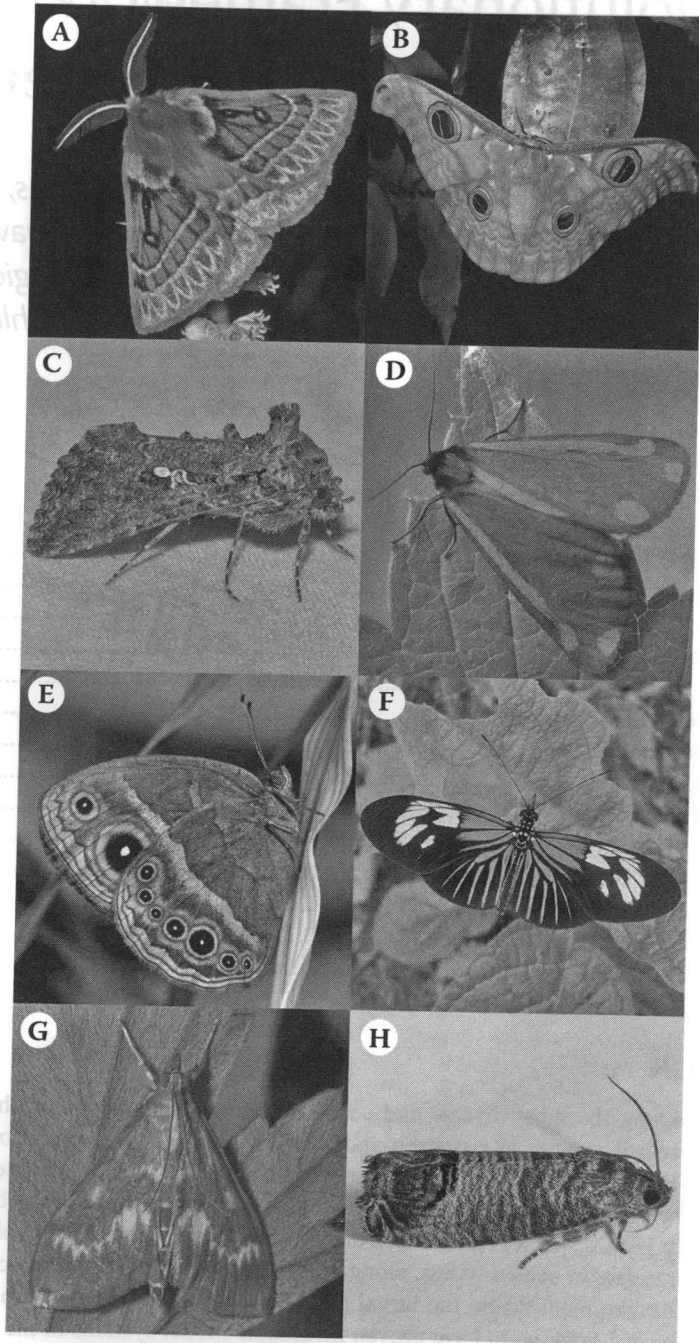
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## INTRODUCTION

Lepidoptera are among the most diverse and easily recognized organisms on the planet, with at least 150,000 described species (Kristensen and Skalski 1998). They are one of the four mega-diverse orders of holometabolous insects, together with Diptera (flies), Coleoptera (beetles), and Hymenoptera (wasps, bees, and ants). Butterflies alone are more numerous than birds, Class Aves, with approximately 18,000 species (Kristensen and Skalski 1998). Generally, Lepidoptera are characterized by the presence of scaled wings, elongate sucking mouthparts (proboscis), and complete (holometabolous) development where the larval stages are commonly referred to as “caterpillars.” Historically, species of Lepidoptera have proven invaluable model systems in the fields of development, genetics, molecular biology, physiology, evolution, and ecology (e.g., Bates 1861; Müller 1879; Ford 1964; Ehrlich and Raven 1967; Kettlewell 1973). Interest in Lepidoptera species as model systems stems from a number of biological characteristics that render this group amenable for study (Bolker 1995). Lepidopterans are charismatic, due mainly to their striking variety of wing color patterns and larval morphologies, and they are avidly collected by professionals and amateurs alike



**FIGURE 1.1** A color version of this figure follows page 176. Representatives of superfamilies containing model systems. A: Bombycoidea, *Anthela oressarcha* (A. Zwick); B: Bombycoidea, *Antheraea larissa* (A. Kawahara); C: Noctuoidea, *Trichoplusia ni* (M. Dreiling); D: Noctuoidea, *Tyria jacobaeae* (D. Dictchburn); E: Papilionoidea, *Bicyclus anynana* (A. Monteiro and W. Piel); F: Papilionoidea, *Heliconius erato* (K. Garwood); G: Pyraloidea, *Ostrinia nubilalis* (S. Nanz); H: Tortricidae, *Cydia pomonella* (N. Schneider).

(Figure 1.1; Salmon 2000). Many common species have large larvae, which facilitated early studies in development and disease, and these larvae are often relatively easy to rear in the laboratory. The economic impact of Lepidoptera on human society also has contributed to the development of lepidopteran model systems. Silk moths (*Bombyx mori*), for example, are among the few insects considered "domesticated" by humans because of the long tradition of sericulture in Asia. As a primarily phytophagous clade, many lepidopterans are economically important as major pests of agriculture and forestry. Several species discussed in this book were developed initially as model systems to understand how Lepidoptera locate mates and host plants, with the goal of using this knowledge to manage pest populations.

In addition to practical applications, lepidopteran model systems have provided insights into basic research including wing pattern formation, neural development, and the interaction of developmental genes (e.g., *Bicyclus*, *Manduca*). Further, there are a number of lepidopteran genome projects (Mita et al. 2004; Xia et al. 2004; Jiggins et al. 2005). Currently, four Genome Projects are listed on GenBank (<http://www.ncbi.nlm.nih.gov>, accessed April 16, 2008), including *B. mori* (Bombycidae), *Bicyclus anynana* (Nymphalidae), *Melitaea cinxia* (Nymphalidae), and *Spodoptera frugiperda* (Noctuidae). Comparatively, lepidopterans have relatively large genomes: *B. mori* is estimated at 475 Mbp, *Manduca sexta* at 500 Mbp, *Heliothis virescens* at 400 Mbp, and *Heliconius* at 292 Mbp (J.S. Johnston, unpublished; Goldsmith, Shimada, and Abe 2005; Jiggins et al. 2005). These genomes can be up to ~2.5 times larger than the previously described genome for *Drosophila melanogaster* (175 Mbp), and up to ~1.6 times larger than either *Apis mellifera* (236 Mbp) or *Anopheles gambiae* (280 Mbp) (Goldsmith, Shimada, and Abe 2005; Honeybee Genome Sequencing Consortium 2006). Further insights into lepidopteran genomes are provided in Chapters 2 and 6 and references therein.

In this chapter, we review how initial model system choice affects subsequent generalizations and the role of phylogenetic studies in placing model systems into a broader evolutionary context. We then review known phylogenetic relationships within superfamilies that contain multiple model systems and phylogenetic placement of these model systems. Our current knowledge of relationships among these superfamilies is being challenged by recent molecular studies, and dating the newly proposed divergences is complicated by an incomplete and poorly identified fossil record. Finally, we examine new global initiatives in lepidopteran phylogenetics that hold promise to connect a historically fragmented community. These global initiatives promise to foster a new age of lepidopteran systematics research.

## PHYLOGENETICS AND MODEL SYSTEMS

Model systems allow researchers to focus resources and effort on examining fundamental biological questions in detail. Although this focused study is essential, the true power of model systems lies in the subsequent ability to extrapolate these details across larger groups of organisms (Kellogg and Shaffer 1993; Bolker 1995). To generalize these results, comparative studies are essential and require that model systems be placed into their evolutionary context. An evolutionary framework or phylogeny can be inferred using a number of analytical approaches (Swofford et al. 1996; Holder and Lewis 2003). Phylogenetic analyses have used a range of heritable, independent characters, such as molecular (e.g., DNA, RNA, and amino acid sequences), phenotypic (e.g., morphological structures, allozymes), and developmental traits (e.g., ontogenetic stages or pathways) to infer evolutionary relationships among organisms.

Without phylogenies, knowledge gained from model systems would remain in isolation. We would be unable to generalize among silk moths (e.g., *B. mori*), European corn borer (*Ostrinia nubilalis*), and fruit fly (*Drosophila*). By understanding evolutionary relationships among organisms, hypotheses concerning the origin of key innovations (i.e., character evolution) can be generated throughout a group (Mabee 2000; Collins et al. 2005). Phylogenetics provides the means to reconstruct ancestral character states and can provide insight into character polarity and homology (Mabee 2000; Felsenstein 2004). For example, the phylogeny of Arctiidae shows that the key

innovation of pyrrolizidine alkaloid sequestration is ancestral to Arctiinae, the largest subfamily. Reconstruction of subsequent losses and gains within the subfamily then can be examined on a finer scale (e.g., Weller, Jacobson, and Conner 1999; DaCosta et al. 2006).

Phylogenetic reconstruction also allows the correlation of gene expression to morphological character expression, which may be used to hypothesize the role genes play on morphological character evolution. Long-standing morphological arguments concerning evolution of head segmentation and brains in arthropods are resolved in large part through studies on *Hox* gene expression (e.g., Cook et al. 2001). Thus, when placed in a phylogenetic context, research on model systems can provide important insights into previously intractable questions concerning morphological evolution.

In addition to providing insight into the evolution of genetic, developmental, and morphological traits, phylogenetics also can be used to identify potential bias in the use of model systems (Bolker 1995). The characteristics of model systems (e.g., ease of culture, body size, and economic importance) can inadvertently influence conclusions drawn from other studies conducted on the system. If not placed into a proper phylogenetic context, model systems may result in misleading inferences about the traits of the larger group. By placing model systems into an evolutionary framework with other models and nonmodels, potential sources of bias can be identified and erroneous generalizations avoided.

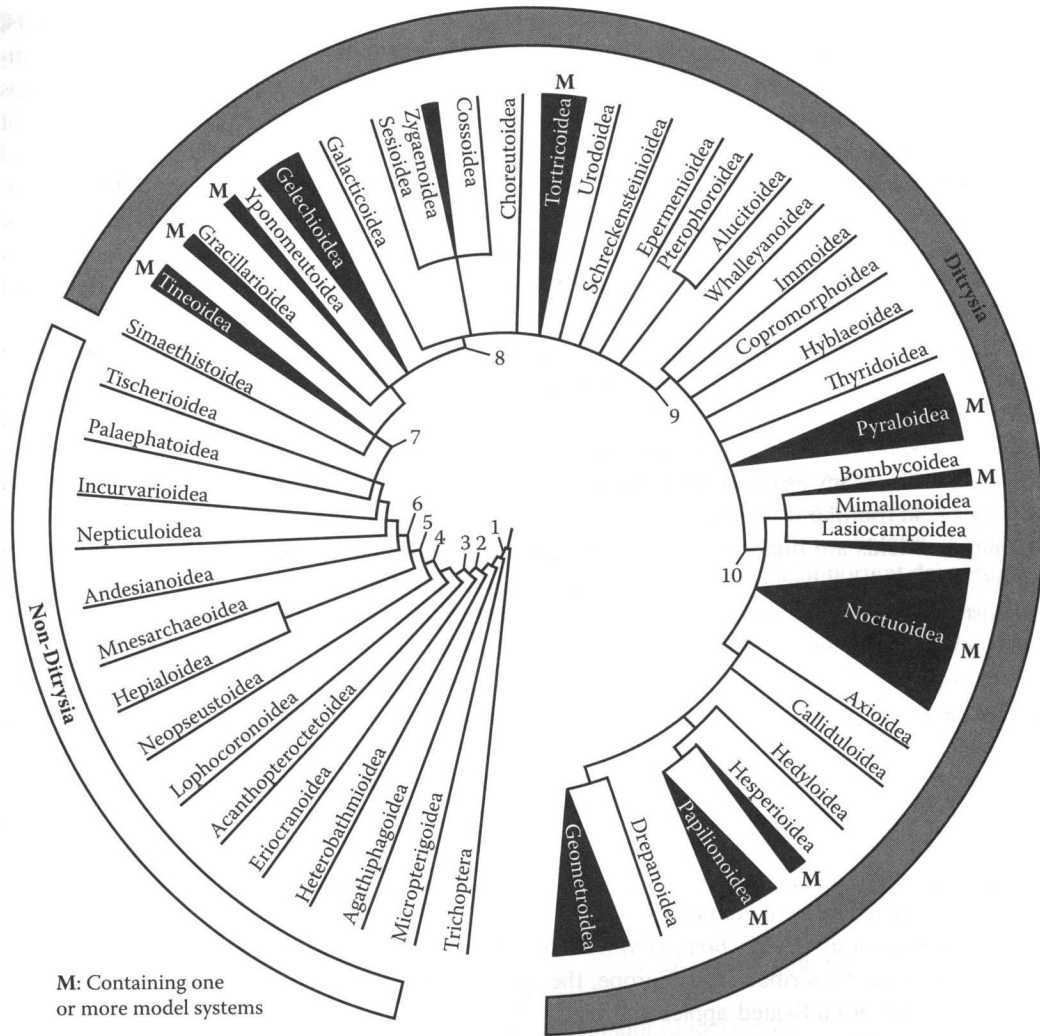
## OVERVIEW OF LEPIDOPTERAN PHYLOGENY

Currently, Lepidoptera are arranged into 126 families and 46 superfamilies (Kristensen and Skalski 1998). The current estimate of evolutionary relationships among superfamilies (summarized in Figure 1.2) is a patchwork of variably resolved phylogenies. The basal lepidopteran relationships are relatively well established based on morphology (Kristensen 1984; Davis 1986; Nielsen and Kristensen 1996; Kristensen and Skalski 1998) and confirmed with molecular data (Wiegmann et al. 2000; Wiegmann, Regier, and Mitter 2002). These early-diverging lineages or "non-ditrysians" (named groups below node 7) contain only a fraction of the total lepidopteran species diversity and contain very few model systems (Figure 1.2), and therefore are not discussed further. In contrast, the clade Ditryisia (node 7) includes approximately 99 percent of the described species, but among-superfamily relationships are poorly understood. This clade, however, contains all current model systems. Members in this lineage are grouped by a number of shared derived morphological traits (termed "synapomorphies") including specialized female genitalia (Kristensen and Skalski 1998). A review by Minet (1991) proposed several nested higher-groupings within Ditryisia based on the morphology of all life stages and hypothesized ground plans for superfamilies. We follow recent convention in provisionally adopting Minet's arrangement for presentation purposes, although this arrangement has not been tested by phylogenetic analysis until recently (see Current Research and Future Directions).

We provide a phylogenetic overview of those superfamilies that possess multiple model systems. We comment, when possible, on whether the distribution of model systems adequately captures the phylogenetic diversity of the superfamily and whether results of these studies can be extrapolated confidently to other members. We do not treat superfamilies with single model systems even if they have an extensive literature because phylogenetically, it is a sample size of one. We present our discussion in order of their phylogenetic placement in Figure 1.2, working from the tree base toward the crown.

## OVERVIEW OF SELECTED DITRYSIAN SUPERFAMILIES

Within Ditryisia, multiple model systems are found in six of the thirty-three superfamilies: Bombycoidea (e.g., silkworm moths), Noctuoidea (e.g., tiger, gypsy, cutworm moths), Papilionoidea and Hesperioidea (butterflies and skippers), Pyraloidea (snout moths), and Tortricoidea (leaf rollers) (Figure 1.1). Tortricoidea, along with several basal lineages of Lepidoptera, are sometimes referred to as "microlepidoptera" because of their small size. However, the term is confusing because



**FIGURE 1.2** Current hypothesized phylogeny of Lepidoptera superfamilies, based on morphological characters, including Trichoptera, sister group to Lepidoptera (adapted from Figure 2.2 in Kristensen and Skalski 1998). Nodes representing higher-level classifications are labeled, for example, macrolepidoptera; 1 = Lepidoptera, 2 = Glossata, 3 = Coelolepida, 4 = Myoglossata, 5 = Neolepidoptera, 6 = Heteroneura, 7 = Ditrysia (shown above), 8 = Apoditrysia, 9 = Obtectomera, 10 = Macrolepidoptera. Superfamilies containing model systems are shown. Width of branches represents approximate proportions of currently described species.

small body size occurs in “macrolepidoptera” (e.g., *Micronoctuidae*; Fibiger and Lafontaine 2005) and large moths can occur in lineages of microlepidoptera (e.g., *Limacodidae*, slug caterpillars; *Hepialidae*, ghost moths). Despite the concentration of lepidopteran model systems in Ditrysia, a number of superfamilies are not represented by model systems (Figure 1.2). Three diverse superfamilies that lack developed model systems are *Geometroidea* (e.g., inchworms), *Gelechioidea* (e.g., case bearers, concealer moths, and twirler moths), and *Zygaenoidea* (e.g., burnets and slug caterpillars), and these superfamilies should be important targets for identifying future model systems.

### Tortricioidea

*Tortricioidea*, comprised of the single family *Tortricidae*, are second only to *Gelechioidea* in terms of species richness among major microlepidopteran lineages, with about 9,100 described species

(Brown 2005). The monophyly of Tortricidae is supported by a variety of characters of the adults, larvae, and pupae. Although several groups within Tortricidae have been considered distinct families by one or more authors over the last century, it is now generally accepted that these groups represent subordinate taxa within the family (Horak 1998). The family is currently comprised of three subfamilies, Tortricinae, Chlidanotinae, and Olethreutinae, into which twenty-two tribes and 957 genera are arranged (Horak 1998; Brown 2005). Olethreutinae and Chlidanotinae are supported by convincing morphological synapomorphies, but Tortricinae is almost certainly para- or polyphyletic. Tortricid species occur on all continents except Antarctica; greatest species richness is attained in the New World tropics, where a large percent of the fauna remains to be described (Horak 1998; Brown 2005).

The common name "leaf rollers" has been applied to the family, owing to the prevalent larval habit of shelter building by folding or rolling leaves of the food plant, but tortricid larvae employ a wide range of feeding strategies, including gall inducing, stem and root boring, fruit boring, seed predating, and flower feeding. Additionally, a very few are predators or occur as inquilines. Among other characters, many tortricid adults can be recognized by a somewhat bell-shaped silhouette with the wings held rooflike when at rest.

Many tortricids are important pests of agricultural, forest, and ornamental plants—164 genera and 687 species have been recorded worldwide as economically important (Zhang 1994). Among the most thoroughly studied tortricids is spruce budworm (*Choristoneura fumiferana*, Tortricinae: Archipini), which is an important forest pest in North America, specializing on species of Pinaceae. This organism has been investigated from the perspectives of morphology (e.g., Walters, Albert, and Zacharuk 1998), pheromone chemistry (e.g., Delisle, Picimbon, and Simard 1999), host plant preferences (e.g., Albert 1991, 2003), physiology (e.g., Hock, Albert, and Sandoval 2007), behavior (e.g., Wallace, Albert, and McNeil 2004), and parasitoids and pathogens (e.g., Quayle et al. 2003). Owing to the relatively unambiguous relationship among *Choristoneura*, *Archips*, *Argyrotaenia*, *Pandemis*, *Adoxophyes*, *Clepsis*, and several other genera in Archipini, many of the morphological, biological, and ecological features of spruce budworm can be extrapolated to a single, relatively large clade with a degree of confidence.

The codling moth (*Cydia pomonella*, Olethreutinae: Grapholitini) represents another tortricid model system. Described from Europe, the species is virtually cosmopolitan today. Although primarily a pest of cultivated apples and pears (*Malus* spp. and *Pyrus* spp.; Rosaceae), this species' documented host range includes plants in six different families of dicotyledons: Fagaceae, Rutaceae, Rosaceae, Moraceae, Juglandaceae, and Proteaceae. Countless scientific studies over the past thirty years have focused on characterizing its sex pheromones, antennal receptors, pheromone production glands, and mating behaviors with the goal of disrupting reproduction (e.g., Ahmad and Al-Gharbawi 1986; Arn 1991; McDonough et al. 1993; Backman 1997; El-Sayed et al. 1999; Addison 2005; Trematerra and Sciarretta 2005). The quarantine significance of this species exerts considerable pressure on international trade agreements in regard to specific agricultural commodities (e.g., Wearing et al. 2001).

Other species of Tortricidae that have received substantial attention include Oriental fruit moth (*Grapholita molesta*, Olethreutinae: Grapholitini), which, like the codling moth, has become nearly cosmopolitan as a pest of stone and pome fruits; red-banded leafroller (*Argyrotaenia velutinana*, Tortricinae: Archipini), a highly polyphagous pest of fruit trees in North America; false codling moth (*Thaumatotibia leucotreta*, Olethreutinae: Grapholitini), an important pest of species of Solanaceae (*Capsicum* and *Solanum*) and Rutaceae (*Citrus*) in Africa; and obliquebanded leaf roller (*Choristoneura rosaceana*, Tortricinae: Archipini), another broadly polyphagous North American leaf roller. Despite the economic importance of species in Tortricidae, we lack a phylogeny for the family, and we cannot comment on the current phylogenetic distribution of these model systems, which are concentrated in only two tribes, Archipini and Grapholitini.

## Pyraloidea

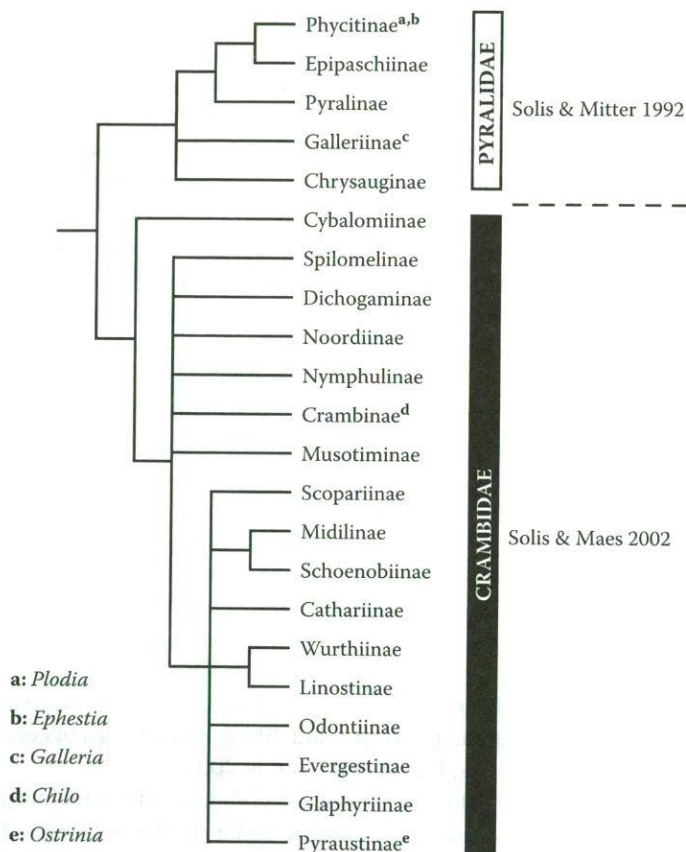
Pyraloidea, or snout moths, are a large superfamily with approximately sixteen thousand described species (Heppner 1991; Munroe and Solis 1998) and at least as many remaining to be described. A number of morphological characters support the monophyly of Pyraloidea, including the presence of paired tympanal organs (membranous hearing structures) on the second abdominal segment, a basally scaled proboscis (when present), and a characteristic wing venation pattern (Munroe and Solis 1998; Nuss 2006).

Larval habits in Pyraloidea are highly diverse. Most larvae are concealed feeders, feeding primarily on plant tissue either internally or in webbed foliage, silk, or frass (Neunzig 1987; Munroe and Solis 1998). Larvae of some species are predatory or parasitic in nests of Hymenoptera or on scale insects (e.g., Neunzig 1997), while others scavenge on nonliving plant material (e.g., stored products). Many larvae of Acentropinae (Crambidae) have developed aquatic lifestyles, feeding on submerged plants (e.g., water veneer, *Acentria ephemerella*, Crambidae: Acentropinae). Many pyraloid larvae are also important economic pests. European corn borer (*Ostrinia nubilalis*, Crambidae: Pyraustinae) and rice stem borers (*Chilo* spp. and *Scirpophaga* spp., Crambidae: Crambinae and Schoenobiinae, respectively) damage a variety of field crops, and Indian meal moth (*Plodia interpunctella*, Pyralidae: Phycitinae), Mediterranean flour moth (*Ephestia kuehniella*, Pyralidae: Phycitinae), and almond moth (*Cadra cautella*, Pyralidae: Phycitinae) are important dried-product pests (Neunzig 1987). Wax moths (*Galleria mellonella* and *Achroia grisella*, Pyralidae: Galleriinae) damage the nests and hives of bees (Neunzig 1987). Conversely, some pyralids have been used for biological control of invasive plants, although doing so carries risks. *Cactoblastis cactorum* (Pyralidae: Phycitinae), introduced for control of prickly pear cactus in Australia and elsewhere (Common 1990; Zimmermann, Moran, and Hoffmann 2000), recently has become an invasive pest of native cacti in North America (Solis, Hight, and Gordon 2004).

Currently, Pyraloidea is divided into two families, Pyralidae and Crambidae, based on a number of morphological characters (Minet 1983; Munroe and Solis 1998; Goater, Nuss, and Speidel 2005). Pyralidae contains five subfamilies, and Crambidae, sixteen to seventeen (Munroe and Solis 1998; Solis and Maes 2002; Goater, Nuss, and Speidel 2005). As is evident in the composite tree (Figure 1.3), existing morphology-based hypotheses provide little resolution of relationships among subfamilies (Solis and Mitter 1992; Solis and Maes 2002). However, ongoing molecular studies show strong promise for sorting out pyraloid relationships.

At least five pyraloid species, all pests, have become major model systems (Figure 1.3), including European corn borer (*O. nubilalis*) and rice stem borer (*Chilo suppressalis*, Crambidae: Crambinae). These two model systems have been used to study the genetics of pheromone synthesis and neural biology (Roelofs and Rooney 2003; Jurenka 2004), physiology (Hodkova and Hodek 2004; Srinivasan, Giri, and Gupta 2006), and development of insecticide resistance (Coates, Hellmich, and Lewis 2006). Greater wax moth (*Galleria mellonella*) has been used extensively to study the genetics and physiology of immune response and to model human disease pathogens (see Chapter 15). Indian meal moth (*Plodia interpunctella*) and the Mediterranean meal moth (*Ephestia kuehniella*) have been used to study, among other topics, lepidopteran gut physiology, pheromone detection, silk biosynthesis and structure, and the development of insecticide resistance (Beckemeyer and Shirk 2004; Srinivasan, Giri, and Gupta 2006; Siaussat et al. 2007). Historically, *E. kuehniella* was an early genetic model system for the study of pigment biosynthesis and wing pattern development, even prior to the development of *Drosophila melanogaster* as a standard laboratory model (Robinson 1971; Leibenguth 1986).

Although presumably not selected for this purpose, the pyraloid model systems are dispersed in an almost ideal fashion across the phylogeny, representing a diversity of subfamilies in both families. This distribution should maximize the confidence with which conclusions from the model systems collectively can be extrapolated to the rest of the superfamily, although these conclusions could be biased from being based only on pest species.



**FIGURE 1.3** A composite tree illustrating the inferred relationships among the subfamilies of Pyraloidea based on adult morphology, following Solis and Mitter (1992; Crambidae) and Solis and Maes (2002; Pyralidae). Superscripts indicate placement of model systems.

### Papilionoidea and Hesperioidea

The Papilionoidea (true butterflies) and Hesperioidea (skippers) are undoubtedly among the better known groups of insects, both among scientists and the general public (Grimaldi and Engel 2005). Their diurnal habits, aesthetically appealing appearance, and ease of study place them among the most collected and observed insects. With approximately eighteen thousand species described, the alpha taxonomy of Papilionoidea is fairly well studied compared with moths, and the total number of species may be close to its actual diversity. Also, the natural history of many species has been documented. Butterflies have been model organisms in numerous areas of biological sciences, including conservation biology, ecology, physiology, evolution, evolutionary developmental biology (evo-devo), and molecular biology. Several volumes attest to this diversity of scientific interest (Vane-Wright and Ackery 1984; Nijhout 1991; Boggs, Watt, and Ehrlich 2003; Ehrlich and Hanski 2004).

The evolutionary relationships of the major lineages have been the subject of numerous studies starting with the work of Reuter (1896). The seminal paper by Ehrlich (1958) set the stage for future work based on rigorous analyses of character sets to infer relationships of the major lineages in the group. Papilionoidea and Hesperioidea have long been considered sister taxa, mainly based on their diurnal habits, but six potential morphological characters also unite them (de Jong, Vane-Wright, and Ackery 1996). Recent molecular data support the hypothesis that the two superfamilies are sister groups (Wahlberg et al. 2005).



Hesperioidea contains just Hesperidae, the skippers, with about four thousand species. Papilionoidea contains the true butterflies, which traditionally have been placed in four or five families (e.g., Ehrlich 1958; Kristensen 1976; de Jong, Vane-Wright, and Ackery 1996; Ackery, de Jong, and Vane-Wright 1998; Wahlberg et al. 2005). Papilionidae and Pieridae are well defined, and their circumscriptions have remained stable ever since they were proposed in the early 1800s. Recent work within these families has resolved relationships of subfamilies and other subordinate groups (Caterino et al. 2001; Braby, Vila, and Pierce 2006; Nazari, Zakharov, and Sperling 2007). Riodinidae, in contrast, has been treated as either an independent family (e.g., Eliot 1973; Lamas 2004; Wahlberg et al. 2005) or a subfamily of Lycaenidae (e.g., Ehrlich 1958; Kristensen 1976; de Jong, Vane-Wright, and Ackery 1996; Ackery, de Jong, and Vane-Wright 1998). Recent molecular data suggest that riodinids form an independent lineage sister to Lycaenidae, and thus they should be considered a separate family (Wahlberg et al. 2005).

Nymphalidae has been a source of much confusion, with some authors dividing it into nine different families including Danaidae and Ithomiidae (e.g., Smart 1975). However, many of these "families" place as lineages nested within Nymphalidae (Ehrlich 1958; de Jong, Vane-Wright, and Ackery 1996; Brower 2000; Wahlberg, Weingartner, and Nylin 2003; Freitas and Brown 2004), although the only morphological synapomorphy for the family is three longitudinal ridges on the antennae (Kristensen 1976; Ackery, de Jong, and Vane-Wright 1998). A recent molecular study (Wahlberg et al. 2005) confirms that these lineages form a monophyletic group, supporting their inclusion in Nymphalidae as subfamilies or tribes.

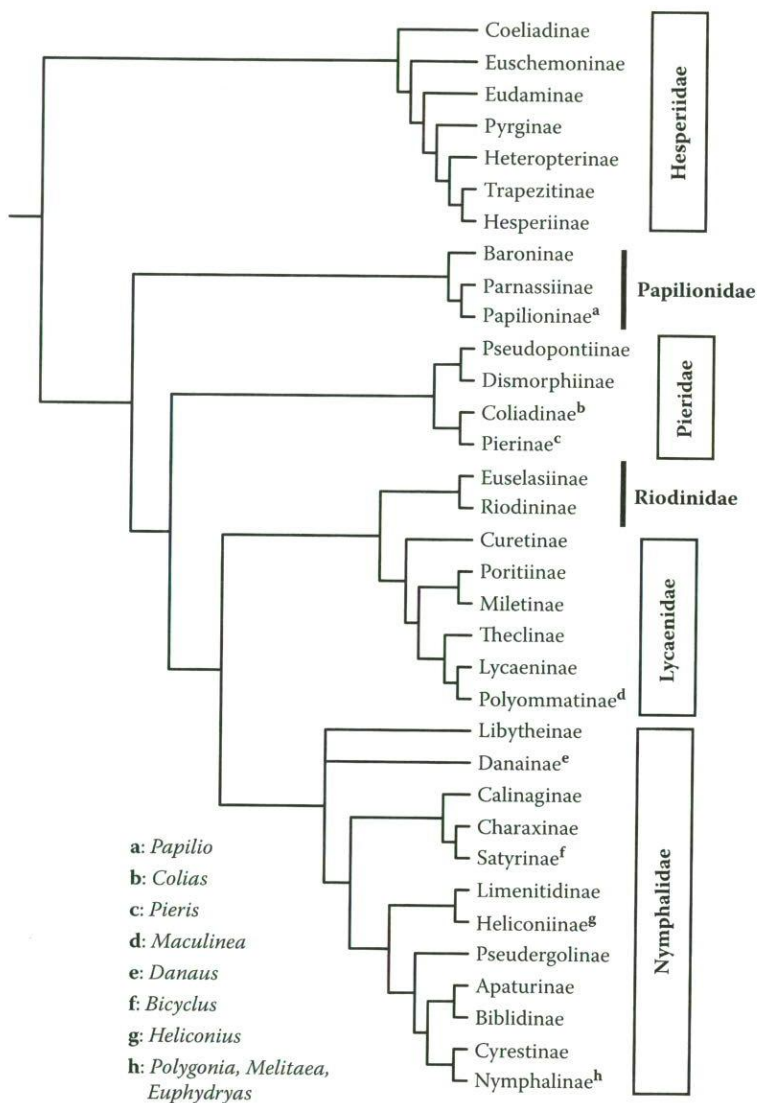
Phylogenetic relationships of the five papilionoid families (i.e., Papilionidae, Pieridae, Riodinidae, Lycaenidae, and Nymphalidae) and the family Hesperidae have been studied using morphological and molecular data (Ehrlich 1958; Kristensen 1976; de Jong, Vane-Wright, and Ackery 1996; Weller, Pashley, and Martin 1996; Wahlberg et al. 2005). Our current understanding of relationships is shown in Figure 1.4, although the position of Pieridae is unstable. In some analyses, Pieridae places as sister to Papilionidae, and more data are needed to resolve this issue.

Several butterfly species have been used as model systems in molecular biology and genetics. *Papilio* species (Papilionidae: Papilioninae) have been the focus of chemical ecology and speciation studies (e.g., Scriber, Tsubaki, and Lederhouse 1995). In Nymphalidae, checkerspot butterflies (Nymphalinae) figure prominently in studies of population biology (e.g., Ehrlich and Hanski 2004). *Heliconius* species (Heliconiinae) have been central to studies of mimicry, speciation, and the genetics of mimetic systems (e.g., Mallet, McMillan, and Jiggins 1998; see Chapter 6 for genetics of color pattern in *Heliconius*). Another important nymphalid model system is *Bicyclus anynana* (Satyriinae), a species central to studies of wing pattern formation (e.g., Beldade and Brakefield 2002; see Chapter 5 for evolution and genetics of eyespots in *Bicyclus*).

## Bombycoidea

The cosmopolitan Bombycoidea *sensu lato* ("bombycoid complex" *sensu* Minet 1994) comprises approximately five thousand described species of medium- to very large-sized moths (Figure 1.1A, B) in 650 genera and twelve families: Anthelidae, Apatelodidae, Bombycidae, Brahmaeidae (Lemoniidae), Carthaeidae, Endromidae, Eupterotidae, Lasiocampidae, Mimallonidae, Mirinidae, Saturniidae, and Sphingidae. Monophyly of Bombycoidea is supported by one thoracic (Minet 1991) and one forewing vein synapomorphy (shared derived trait) (A. Zwick, unpublished) and potentially by modification in the larval proleg cuticle (Hasenfuss 1999). The shortage of synapomorphies stems largely from a shortened adult life span, and consequently a reduction of structures commonly used for inferring phylogenetic relationships (e.g., mouthparts and wing coupling mechanisms; Minet 1991, 1994). Therefore, the relationships among bombycoid families are generally poorly understood (Figure 1.5).

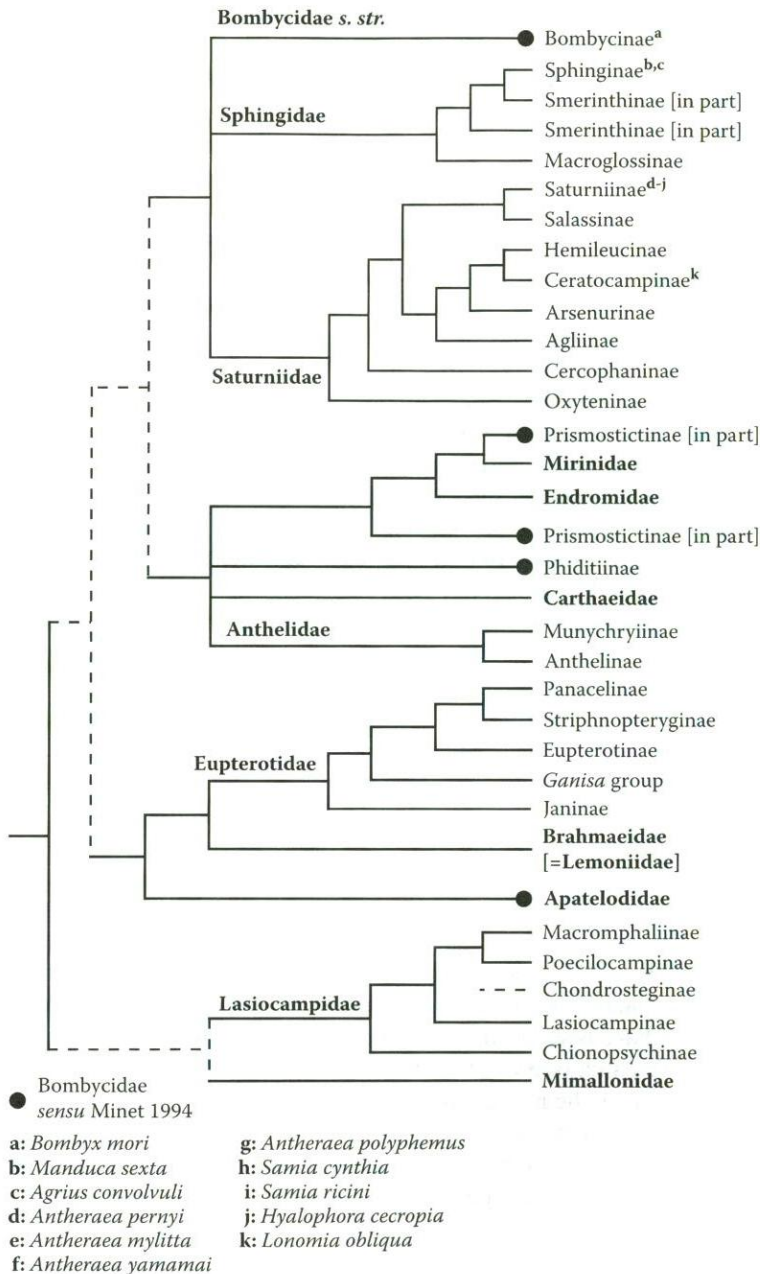
Within Bombycoidea, only three families—Bombycidae *s. str.*, Sphingidae, and Saturniidae—contain species that are widely used as model systems. These three families probably form a monophyletic group as indicated by two independent molecular studies (Regier et al. 2008;



**FIGURE 1.4** A composite tree showing the inferred relationships of butterfly families and subfamilies. Family relationships taken from Wahlberg et al. (2005), subfamily relationships within families taken from various sources: Hesperidae (Warren 2006), Papilionidae (Caterino et al. 2001), Pieridae (Braby, Vila, and Pierce 2006), Riodinidae and Lycaenidae (Wahlberg et al. 2005), and Nymphalidae (Wahlberg and Wheat 2008).

Zwick 2008), both of which partially contradict morphology-based studies of Brock (1971) and Minet (1991, 1994).

Bombycidae are best known for the domestic silkworm *B. mori* (Bombycinae), the most prominent model system in Lepidoptera. Recent molecular studies (Regier et al. 2008; Zwick 2008; Figure 1.5) demonstrate that the family (*sensu* Minet 1994) is unnatural (e.g., polyphyletic) and should be restricted to the nominate subfamily Bombycinae. Despite a wealth of knowledge for *B. mori*, virtually nothing is known about the biology of most other bombycid species. The family is in urgent need of a comprehensive taxonomic revision, and phylogenetic hypotheses are lacking for its 350 described species that are currently placed in forty genera. As a model system, the domestic



**FIGURE 1.5** Composite tree based on the molecular studies of Kawahara et al. (2009), Regier et al. (2001, 2002, 2008), and Zwick (2008). Bombycidae sensu Minet 1994 are marked with black circles.

silkworm has been the object of extensive basic, biotechnological, and sericultural research (see Goldsmith, Shimada, and Abe 2005; for a review on molecular biology and genetics, see Chapters 2 and 4). A huge quantity of molecular data is publicly available, including two genome drafts (Mita et al. 2004; Xia et al. 2004); bacterial artificial chromosome (BAC) libraries; expressed sequence tags (ESTs); and molecular linkage, genetic, and physical maps (Goldsmith, Shimada, and Abe 2005). Some genetic work has focused on *Bombyx mandarina*, the species thought to represent the wild ancestor of *B. mori* (Arunkumar, Metta, and Nagaraju 2006). However, this wealth of genetic

information on *B. mori* and *B. mandarina* contrasts starkly with the nearly complete lack of data for other bombycids.

Sphingidae, another family with model species, is comprised of three subfamilies: Sphinginae, Smerinthinae, and Macroglossinae. Recent molecular studies (Regier et al. 2001; Kawahara et al. 2009) reveal evolutionary relationships that partly contradict current subfamily and tribal classification but concur with morphological interpretations of sphingid relationships (e.g., Rothschild and Jordan 1903; Nakamura 1976; Kitching and Cadiou 2000; Kitching 2002, 2003). The taxonomy, immature stages, and biology of many sphingid species are thoroughly studied, although there are still many species that are poorly understood (Kitching and Cadiou 2000).

A well-known model organism is the tobacco hornworm, *Manduca sexta* (Sphinginae: Sphingini). This species has been used in a broad range of research on biochemistry, physiology, morphology, and nutritional ecology (Slansky 1993; Willis, Wilkins, and Goldsmith 1995). Its universality as a model system is reflected by the almost thirty-eight hundred GenBank accessions (including ESTs) and the construction of two BAC libraries (Sahara et al. 2007). An emerging model sphingid species is the cosmopolitan sweet potato hornworm *Agrius convolvuli* (Sphinginae: Acherontiini), which has been used in numerous physiological and immunological studies, some of which include molecular genetics.

Saturniidae represent the third well-known family of bombycoid moths. Current hypotheses of its higher phylogeny (Figure 1.5) are largely based on molecular studies (Regier et al. 2002, 2008; Zwick 2008), with Michener (1952) providing the only morphology-based hypothesis for relationships within the entire family. In the molecular studies, relationships among the eight subfamilies are fully resolved and statistically well supported. Phylogenetic hypotheses for other levels of divergence are limited (e.g., Friedlander et al. 1998; Rubinoff and Sperling 2002, 2004; Regier et al. 2005). As with Sphingidae, the taxonomy of Saturniidae historically has been studied extensively on a global scale, and information on immatures and life history is available for a large number of species.

Nine saturniid species are used as molecular model systems, representing only two of the eight subfamilies, Saturniinae and Ceratocampinae. Four of these models are congeners: *Antheraea pernyi*, *A. mylitta*, *A. yamamai*, and *A. polyphemus*. *Antheraea* collectively exhibits a Holarctic distribution, and the genus includes approximately seventy described species and numerous subspecies (Paukstadt, Brosch, and Paukstadt 2000). Regier et al. (2005) present a phylogenetic hypothesis for sixteen of seventy species, including four model systems. Their study examines the evolution of morphology and development of chorionic aeropyle crowns on the molecular phylogeny. *Antheraea* species have been used in sericulture and, like *B. mori* and *M. sexta*, for a wide range of fundamental research (see Goldsmith and Wilkins 1995). *Antheraea pernyi* has been an important model for studying the molecular mechanisms of the circadian clock (see Chapter 8 and references therein). However, compared to *B. mori* and *M. sexta*, the number of distinct GenBank accessions for these four *Antheraea* species is negligible, except for *A. mylitta* (i.e., approximately four thousand) and *A. yamamai* (i.e., approximately seven hundred), each of which is represented by numerous ESTs.

Three additional model systems occur in Attacini, the sister tribe to Saturniini (Figure 1.5): *Samia cynthia*, *S. ricini*, and *Hyalophora cecropia*. The taxonomy of the Asian genus *Samia* (*Phylosamia*; nineteen species) is particularly complex and confusing due to countless synonyms and inconsistent use of names. Fortunately, Peigler and Naumann (2003) recently published a comprehensive revision of the genus. In nontaxonomic literature, the species "*Samia ricini*" has been problematic and inconsistently treated as a valid species, as a subspecies of *S. cynthia* or as a form of *S. cynthia*. However, it is possible that none of these treatments is correct; *S. ricini* now is thought to be a domesticated form of *S. canningi* and unrelated to wild *S. cynthia* (Peigler and Naumann 2003). Consequently, the identity of *Samia* species in past studies has to be viewed with caution, which provides a compelling case for routine deposition of voucher specimens even in studies of model systems. Similarly, the taxonomy of the Nearctic *Hyalophora*—containing three species and numerous subspecies—continues to be controversial. All taxa readily interbreed in captivity,

and natural hybrids occur in some contact zones (Tuskes, Tuttle, and Collins 1996). The breadth of research areas for the model systems in *Samia* and *Hyalophora* is similar but not quite as large as for *Antheraea* (see Goldsmith and Wilkins 1995). The number of distinct GenBank accessions for these species is smaller than for *Antheraea*; however, an international initiative to database ESTs for these genera is under way ([www.cdfd.org.in/wildsilkbases/home.php](http://www.cdfd.org.in/wildsilkbases/home.php)), which promises to greatly increase our knowledge of their genomes.

Unlike other saturniid models, the South American *Lonomia obliqua* (Ceratocampinae), and to a lesser extent *L. achelous*, are used specifically in research on its highly poisonous larvae and the anticoagulating properties of their poison (Veiga et al. 2005). Despite this limited research scope, *L. obliqua* has the second largest number of saturniid GenBank accessions, which includes one of the few EST libraries available for Bombycoidea. *Lonomia* contains more than a dozen described species based on revisions by Lemaire (1972, 2002).

The remaining bombycoid families do not contain molecular model systems, and most are relatively poorly studied, economically insignificant, and low in species numbers. Lasiocampidae (e.g., tent caterpillars) is an important exception, with approximately fifteen hundred species in 150 genera and several significant pest species in several genera (e.g., *Malacosoma*, *Dendrolimus*, and *Trabala*). The monophyly of Lasiocampidae is strongly supported by a combination of molecular and morphological data (Zwick 2008). However, phylogenetic relationships within the family are poorly studied (Regier et al. 2001, 2008; Zwick 2008).

Based on our current, limited knowledge, the three bombycoid families containing molecular model systems seem to be more closely related to each other than to any other family (Figure 1.5) (Regier et al. 2001, 2008; Zwick 2008). To maximize the utility and value of the extraordinarily large quantity of existing data for molecular model systems in Bombycoidea, future phylogenetic studies are needed at many taxonomic levels. A model system needs to be developed in Lasiocampidae or another early diverging lineage to increase the phylogenetic breadth of current model systems in Bombycoidea. Currently, generalizations about Bombycoidea are limited by the phylogenetic placement of its model systems.

## Noctuoidea

Noctuoidea is the largest superfamily of Lepidoptera—approximately seventy thousand described species in over seventy-two hundred genera (Kitching and Rawlins 1998). The superfamily includes some of our best-known lepidopterans: Arctiidae (ermine, footman, and tiger moths), Lymantriidae (gypsy and tussock moths), Noctuidae (cutworms, deltoids, owlets, and underwings), and Notodontidae (prominents and processionary moths). Noctuoidea is defined by the possession of a thoracic tympanum (hearing organ) and associated abdominal structures in the adults, and the presence of two microdorsal setae on the larval metathorax (Hinton 1946)—except oenosandrid larvae, which have only one (Miller 1991; Kitching and Rawlins 1998).

Noctuoidea include a number of ecologically important species, including some of our most damaging forest and agricultural pests (Kitching and Rawlins 1998). Others, particularly arctiids, have been the focus of studies on chemical ecology and mating behavior (reviewed in Conner and Weller 2004). Well-known species in North America include gypsy moth (*Lymantria dispar*, Lymantriidae: Orgyiniinae), corn earworm (*Helicoverpa zea*, Noctuidae: Heliiothinae), tobacco budworm (*H. armigera*), cabbage looper (*Trichoplusia ni*, Noctuidae: Plusiinae), and fall armyworm (*Spodoptera frugiperda*, Noctuidae: Xyleninae). Caterpillars of some species possess urticating (stinging), deciduous setae that can be hazardous to humans (e.g., *L. dispar*, *Thaumetopoeia processionaria*, Notodontidae: Thaumetopoeinae; review Kitching and Rawlins 1998).

In this superfamily, basal lineages Oenosandridae, Notodontidae, and Doidae lack model systems (Miller 1991; Kitching and Rawlins 1998). Rather, model systems are concentrated in three large families, Noctuidae (about fifty thousand species; e.g., *Helicoverpa*, *Heliiothis*, *Spodoptera*), Arctiidae (about eleven thousand species; e.g., *Utetheisa ornatrix*, *Arctia caja*, *Cretonotus gangis*), and Lymantriidae (about five hundred species; e.g., *L. dispar*). These families form a clade with

a handful of problematic lineages recognized as either subfamilies or families, depending on the authority consulted (Kitching and Rawlins 1998). These families and problematic lineages have been arranged variously based on easily observed traits such as their hindwing venation, leg spination, and aspects of their larval morphology (Kitching and Rawlins 1998).

The classification of noctuoids (Figure 1.6), particularly Noctuidae, has recently undergone major shifts and rearrangements. Traditionally, Arctiidae was placed as sister to Lymantriidae; and four taxa—Aganainae (Hypsidae), Nolinae, Herminiinae, and Pantheinae—were treated as subfamilies of Arctiidae, subfamilies of Noctuidae, or separate families allied to Arctiidae (review Kitching and Rawlins 1998; Jacobson and Weller 2002; Fibiger and Lafontaine 2005). Molecular studies starting over a decade ago have suggested consistently that the remaining “noctuid” lineage divide into two main lineages or clades (Figure 1.6), superficially diagnosed by their hindwing venation. One of these, the “trifines,” contains noctuids with trifine hindwing venation (i.e.,  $M_3$ ,  $Cu1A$ ,  $Cu1B$  associated; vertical bars; Mitchell, Mitter, and Regier 2006). The other clade consists of most noctuid subfamilies with quadrifine hindwing venation and Lymantriidae and Arctiidae (Weller et al. 1994; Mitchell et al. 1997; Mitchell, Mitter, and Regier 2000). In Figure 1.6A, all taxa except Lymantriidae and Arctiidae have at one time or another been included in Noctuidae. Thus, Noctuidae in the traditional sense is not monophyletic.

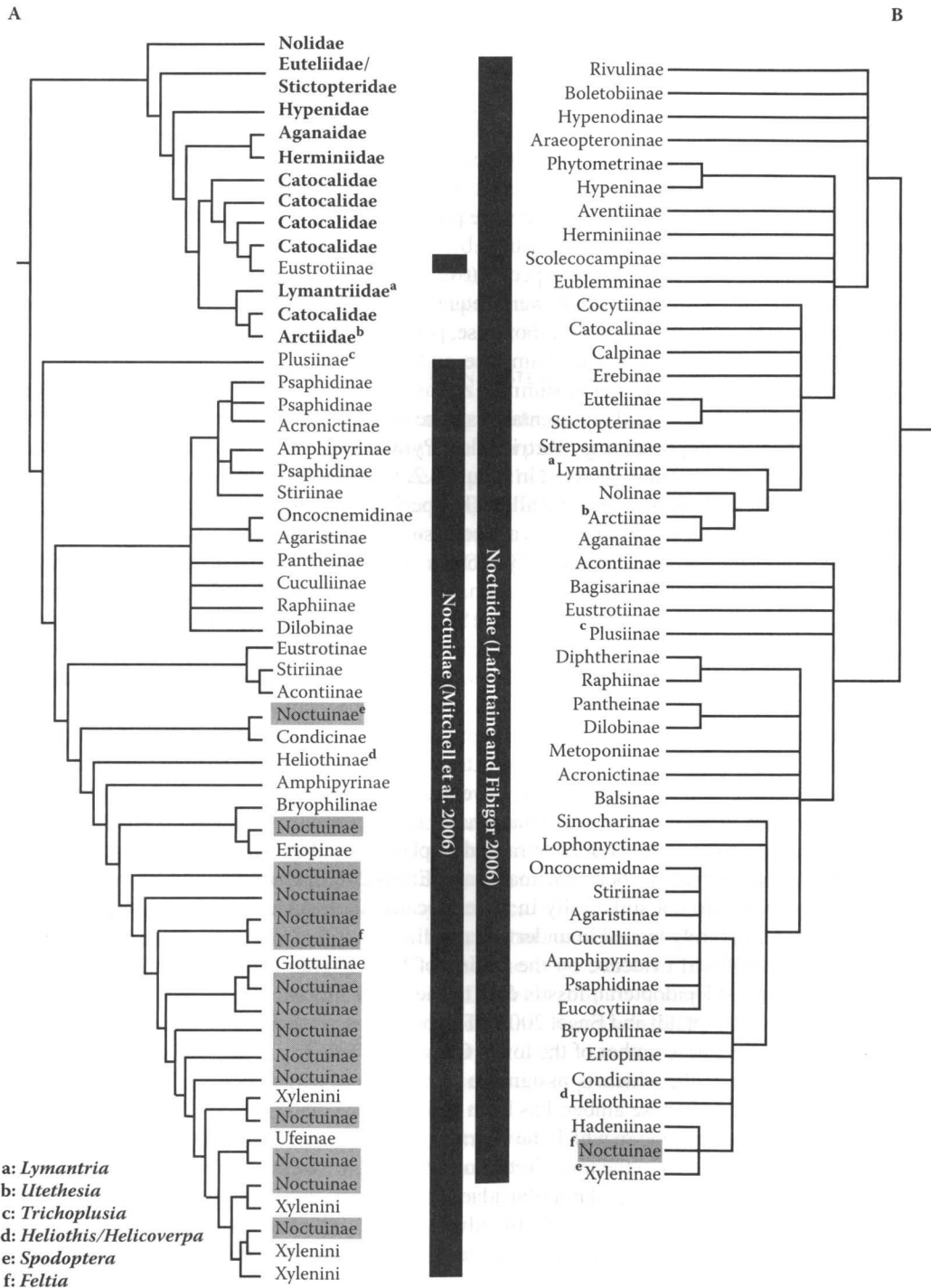
Numerous modifications to classification ensued (review Lafontaine and Fibiger 2006). Most dramatically, beginning in June 2005, three landmark publications presented detailed phylogenies and completely rewrote the classification of Noctuoidea three times (Fibiger and Lafontaine 2005; Mitchell, Mitter, and Regier 2006; Lafontaine and Fibiger 2006). These publications each have their own limitations and strengths. The molecular study (Mitchell, Mitter, and Regier 2006) has incomplete sampling of more obscure lineages but provides a rigorous data analysis of two nuclear genes encoding proteins, *elongation factor 1-alpha* (*EF-1 $\alpha$* ) and *dopa decarboxylase* (*Ddc*; Figure 1.6A), with very strong statistical support for the clades contradicted by the morphological hypotheses. The morphological conclusions (Fibiger and Lafontaine 2005; Lafontaine and Fibiger 2006) are not based on formal phylogenetic data analyses but provide an authoritative review of morphological ground plans (Figure 1.6B). Thus, discordance among results of these studies cannot be resolved without further investigation. All studies demonstrated the nonmonophyly of the traditional Noctuidae (Figure 1.6).

Model systems in Noctuoidea are concentrated in the “Noctuidae” (Figure 1.6A), which contain the majority of agricultural pests. These models span phylogenetic diversity within this clade, from *T. ni* (Plusiinae) to *Spodoptera* (Noctuinae; shaded, Figure 1.6). Recent phylogenetic studies are helping to clarify the relationship in some of these subfamilies (e.g., Heliiothinae, Fang et al. 1997; Cho et al. 2008) and genera (e.g., *Spodoptera*; Pogue 2002). The remaining model systems occur only in Arctiidae and Lymantriidae (Figure 1.6B; Arctiinae and Lymantriinae, respectively; Lafontaine and Fibiger 2006). None occur in Notodontidae, Doidae, or Oenosandridae, earlier-diverging lineages. This spotty distribution of model systems undermines the confidence with which observations can be generalized across the superfamily.

## CURRENT RESEARCH AND FUTURE DIRECTIONS

### MOLECULAR DITRYSIAN PHYLOGENIES AND THE ROLE OF FOSSILS

All the preceding discussions rest upon the phylogeny presented in Figure 1.2. While this phylogeny serves as a useful working hypothesis, the proposed superfamily relationships are highly provisional within Ditrysia. Relationships among ditrysiian superfamilies are rarely examined and have never been subject to explicit phylogenetic analysis. Only recently has research focused on understanding relationships within a few superfamilies (e.g., Bombycoidea, Papilionoidea, Pyraloidea, and Noctuoidea). Thus, a comprehensive phylogenetic framework for Lepidoptera is not yet achieved.



**FIGURE 1.6** Hypothesized relationships in the quadrafid forewing clade of Noctuoidea. no bar = quadrifine hindwing; vertical bar = trifine hindwing superfamilies; superscripts indicate placement of model systems. A. Maximum parsimony molecular tree adapted from Mitchell, Mitter, and Regier (2006) based on *EF-1α* and *Ddc* sequences (Figures 2 and 3 within). Clades reduced to represent family and subfamily relationships. B. Alternative classification and relationships proposed by Lafontaine and Fibiger (2006), with Micro-noctuidae not shown due to uncertain placement.

Fortunately, lepidopteran phylogenetic research is currently focused on understanding superfamily relationships within Ditrysia. Two ongoing, complementary initiatives began in 2006. The first, Assembling the Lepidopteran Tree of Life (LepAToL, based in the United States), is examining superfamily relationships across all lepidopteran families using nuclear gene sequences (up to twenty-six loci) from several hundred species. The second, Systematics of Ditryisian Lepidoptera (based in Finland), is examining a comparable number of species for eight nuclear and mitochondrial loci (a mostly nonoverlapping set of genes with LepAToL) and two hundred morphological characters. Progress updates for both projects are posted regularly at <http://www.leptree.net>.

An initial study of superfamily relationships by the LepAToL group were posted online as of December 2007. This study included 123 species (twenty-six superfamilies) concentrated in the clade Obtectomera (node 9, Figure 1.2). These were sequenced for about 6.7 kb from five nuclear genes encoding for proteins, including dopa decarboxylase, period, wingless, enolase, and CAD (carbamoyl-phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase).

The main results of this study can be summarized as follows: Most superfamilies were recovered as monophyletic, and when several representatives were included, relationships within superfamilies were resolved and well supported (e.g., Tortricioidea, Pyraloidea, Noctuoidea). On a broad scale, the analysis recovered several clades depicted in Figure 1.2; however, there were two significant exceptions. First, butterflies (Papilionoidea) and allies (Hesperioidea, Hedyloidea) fall outside of the macrolepidoptera clade, and these superfamilies are consistently grouped more closely with one or more microlepidopteran superfamilies. Second, Pyraloidea consistently form a sister relationship to the remaining macrolepidoptera, a novel association. Although individual nodes subtending multiple superfamilies were not strongly supported, tests (Shimodaira 2002) comparing the overall fit of the molecular data to prior phylogenetic hypotheses significantly rejected the monophyly of macrolepidoptera as previously defined (Figure 1.2). Thus, findings to date suggest that a vastly improved phylogenetic framework for Lepidoptera at many levels will be available in the near future.

Well-resolved phylogenies at multiple levels are essential for comparative studies of Lepidoptera, but a full understanding of the evolution of many traits of interest will also require knowledge of the absolute timing of reconstructed evolutionary events. The most reliable source of such knowledge is, in most cases, the fossil record. Unfortunately, the lepidopteran fossil record is sparser than that of any other major insect order (Labandeira and Sepkoski Jr. 1993), particularly in compression fossils, that is, those formed in rocks (Grimaldi and Engel 2005). Grimaldi and Engel (2005) suggest that lepidopterans do not sink easily in water because their scales interfere with wetting, and consequently they are rarely buried in underwater sediments.

On a broad scale, fossil evidence on the timing of lepidopteran evolution can be summarized as follows: The earliest lepidopteran fossils date to the lower Jurassic, about 190 million years ago (mya; Whalley 1986; Grimaldi and Engel 2005). The oldest fossils that can be assigned to any extant group are found in Lebanese amber of the lower Cretaceous (125 mya), and include *Parasabatinea aftimacrai* (Whalley 1978), which is assignable to the oldest extant family, Micropterigidae. A fossil larva, also from Lebanese amber, has been placed in the clade Glossata (Figure 1.2, node 2; Grimaldi 1996, 1999), the clade in which the characteristic adult proboscis first appears. A probable first record of Ditrysia occurs in the mid-Cretaceous (97 mya) in the form of fossil leaf mines attributed to the extant Phyllocnistinae (Gracillariidae) (Labandeira et al. 1994), although caution has been urged in interpreting such fossils (Grimaldi and Engel 2005). Although additional ditryisian fossils are lacking from the Cretaceous, the occurrence of Paleocene fossils of macrolepidoptera (56 mya) suggests that many additional ditryisian lineages arose during the Cretaceous, which ended 65.5 mya (Grimaldi and Engel 2005). Many extant ditryisian families first appear in Eocene Baltic amber (44 mya), and many others are first found in the Eocene-Oligocene Florissant shales (38 mya; reviewed in Grimaldi and Engel 2005).

To integrate fossils with current phylogenetic studies, two challenges must be addressed. First, fossils have to be placed in current molecular phylogenies. Minimally, fossil assignments to superfamily (or more precise identification to family or genus) need to be based on diagnostic



morphological features (synapomorphies). Currently, most existing identifications are based solely on subjective impressions of similarity to extant species, and most fossils have never been examined by the relevant expert (de Jong 2007). The second problem is methodological. Molecular evolution often departs from rate constancy; that is, mutations do not accumulate in a "clock-like" fashion (e.g., Kumar 2005). To allow more accurate dating of nodes based on molecular analyses, development of more sophisticated analytical approaches is under way to account for uneven mutation rates (e.g., Welch and Bromham 2005; Rutschmann 2006). In the best scenario, future analyses will include morphological matrices as well as molecular data, so that fossil placement is testable despite fragmentary remains. Thus, somewhat ironically, the full promise of molecular systematics for revealing the evolutionary history of Lepidoptera cannot be realized until morphological studies are as comprehensive in species' sampling as molecular analyses.

### VIRTUAL COMMUNITY BUILDING IN LEPIDOPTERAN SYSTEMATICS

Until the last couple decades, the work of placing lepidopteran model systems into an evolutionary context fell largely to systematists specializing in morphology. Morphologists historically worked in relative isolation with publications authored typically by one or occasionally by two researchers. The typically slow pace of research has been frustrating to others who rely on their phylogenies to place their model systems. In contrast, many researchers working on model systems publish in large collaborations (Cronin and Franks 2006). One historical barrier to community building has been the slow dissemination of taxonomic studies. Systematic works often were published as monographs by museums or regional journals, available only in the largest libraries. Only recent work is likely to be available digitally, usually beyond the financial reach of many in the global community. Historically, researchers maintained a network of personal contacts to keep abreast of advances in the field, which led to exchanges of reprints and specimens, as well as occasional visits, supplemented by conferences that facilitated scientific exchanges and growth and maintenance of social networks. Consequently, much work was conducted in isolation or small communities of researchers. In Lepidoptera, as in other insect orders, the situation led to an idiosyncratic development of morphological terminologies, often highly specialized for a particular group (e.g., genitalic terms for butterflies). Isolated by fragmented lexicons, researchers interested in studying multiple groups of Lepidoptera had to learn new terms specific to a particular family or superfamily. This situation has impeded rapid progress in lepidopteran systematics.

To remediate these barriers and foster a large, global, collaborative virtual community, several Web site initiatives have been undertaken. Some of these are taxon based, focusing on a particular superfamily; for example, the GlobIZ Pyraloidea Database (<http://www.pyraloidea.org>), geometroid Web site Forum Herbulot (<http://www.herbulot.de>), the Nymphalidae Systematics Group (<http://www.nymphalidae.utu.fi>), Tortricid.net (<http://www.tortricidae.com>), and the gelechioid work group (Gelechioidea Framework, <http://www.msstate.edu/org/mississippiantmuseum/Lepidoptera/GelechioideaFramework.htm>).

Some Web-based projects attempt to link all taxonomists or all lepidopterists in a virtual community. The European Distributed Institute of Taxonomy (EDIT; <http://www.e-taxonomy.eu>) aims to unite European taxonomic research. EDIT seeks to coordinate and digitally reorient the European contribution to the global taxonomic effort, particularly with the Global Taxonomy Initiative. Lepidoptera is a priority target group for EDIT, and along with Lepsys, a consortium for European Lepidoptera Systematists (<http://www.lepsys.eu>), coordinates lepidopteran research in Europe.

LepTree (<http://www.leptree.net>), like EDIT, supports a virtual community where both molecular and morphology-based projects are supported. To maximize openness and interactions, this Web site was created with the open source content management system Drupal (<http://www.drupal.org>) to take advantage of its discussion and collaborative authoring tools. This site is further customized to store biological and social data in an open source triple store (<http://www.openrdf.org>), and the semantically rich OWL (Web Ontology Language) and RDF (Resource Description Framework)

formats for data storage and sharing (e.g., Mabee et al. 2007). As an example of these technologies, subcommunities work together to build, cross-reference, and widely share glossaries of morphological terms that are illustrated with annotated images. Community data will be available automatically to portals such as the Encyclopedia of Life (<http://www.eol.org>) and to digital taxonomists everywhere.

These global Web site initiatives (EDIT, Lepsys, LepTree) represent an intermediate state between casual discussions and data-rich collaborations of "big science" (e.g., "collaboratories" *sensu* Arzberger and Finholt 2002). They facilitate an exchange of knowledge, terminology, and protocols, thereby fostering a larger, more global community of practice (Preece 2000). Web sites with such tools can establish virtual communities that encourage collaboration and training over large distances, in addition to disseminating results quickly and easily. Thus, the global community of lepidopteran systematists is evolving to work together efficiently to answer a broad spectrum of comparative and evolutionary questions.

### SUMMARY AND FUTURE MODEL SYSTEMS

Model systems are scattered throughout Ditrysia, and these provide insight into a wide range of biological processes. By reviewing the phylogenetic placement of these model systems, underrepresentation of several major lepidopteran groups becomes obvious, most notably the non-ditrysians as well as Geometroidea and Zygaenoidea. These gaps will need to be addressed with the choice and examination of new models in these lineages.

Evolutionary frameworks provide guidance to choosing new model systems or organisms for comparative analyses. Several authors have outlined factors to consider when developing new model systems (Mabee 2000; Santini and Stellwag 2002; Collins et al. 2005; Jenner and Willis 2007), and careful selection of comparative taxa will maximize mechanistic and comparative results. First, a model should be chosen to help further a research theme, identify plesiomorphic (ancestral or primitive) character states, or seek to resolve the origins of novel traits. For example, understanding the evolution and development of lepidopteran wing patterns (Ramos and Monteiro 2007; reviewed in Chapters 5 and 6), genome size (Gregory and Hebert 2003; Goldsmith, Shimada, and Abe 2005), or pheromone synthesis (reviewed in Chapter 10) will require judicious choice of models throughout the lepidopteran tree, as well as among members of Trichoptera. Second, model systems should be practical to obtain and culture in a laboratory setting. For example, *B. mori* proved amenable to culture, having been domesticated several thousand years ago for silk production, leading to its prominence in scientific studies. On the other hand, the larval diets and adult breeding behavior are not known for many lepidopterans, particularly the basal lineages that currently lack model systems (Figure 1.2). We need to advance our understanding of the basic biology of these lineages before we can successfully culture these taxa and develop them as viable model systems. Finally, phylogenetic sampling and relationships within and between lineages containing model systems must be examined to ensure appropriate breadth of taxon sampling relative to the trait being examined. Current European and North American initiatives will provide more robust phylogenetic frameworks for accurately assessing relationships of model and nonmodel taxa and for choosing new model systems for future exploration.

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