

21

Biodiversity of the Neuropterida (Insecta: Neuroptera, Megaloptera, and Raphidioptera)¹

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The Neuropterida are a multiordinal clade of holometabolous insects (treated here as a superorder) that encompasses the extant orders Megaloptera, Neuroptera, and Raphidioptera. Earlier classifications often treated this clade at the rank of order, under the name Neuroptera, and included within it three suborders: Planipennia (= Neuroptera *sensu stricto* (*s.s.*)), Megaloptera, and Raphidioptera. The elevation of the Megaloptera and Raphidioptera to ordinal rank is a byproduct of a broad consensus that has developed over the past several decades that the highly apomorphic nature of the Planipennia – especially based on the distinctive structure of the larval mouthparts and associated alimentary canal modifications – merits recognition at the ordinal rank. From the perspective of the historical development of the higher classification of insects, this change is only the latest step in the evolution of the concept of the order Neuroptera. When included by Linnaeus (1758) in the tenth edition of *Systema Naturae*, the order Neuroptera contained species that are now placed in about 10 insect orders, and the concept of the order has been repeatedly narrowed over the past 250 years.

With the order now, finally, restricted to a monophyletic group that is characterized by striking morphological synapomorphies, further restriction of the concept of the Neuroptera seems unlikely. Some authors also include within the superorder some extinct taxa, such as the order Glosselytrodea, which might fall outside the crown-group Neuropterida (Grimaldi and Engel 2005). The treatment here focuses primarily on the non-extinct taxa of the extant orders; extinct taxa are primarily mentioned in considerations of the relictualness of the distributions of extant groups.

No common name in English encompasses the entire superorder Neuropterida, and only the small order Raphidioptera has a common name (snakeflies) that is widely applied to all of its members. Within the orders Neuroptera and Megaloptera, most families are known by distinctive common names. These have little commonality, except for the use of the name element “lacewings,” which is a shared component of many English common names of families in the order Neuroptera. Because their common and scientific names do not align well, it is difficult to concisely discuss the Neuropterida, or its

¹ We dedicate this work to our late friend and colleague Norman Dale “Norm” Penny (1946–2016), who over the course of a long and productive career, and with an irrepressible and jovial attitude, aided and inspired many others in their pursuit of studies on neuropterid insects.

constituent orders, without using scientific names, or artificial common names derived from them.

21.1 Phylogeny

Phylogenetically, the Neuropterida have long been recognized as a monophyletic group, although morphological synapomorphies are not particularly abundant or striking. Recent phylogenetic work based on genome-scale molecular data (Misof et al. 2014) provides additional evidence for the monophyly of the Neuropterida, and supports its placement in the Holometabola as the sister group to the Coleoptera + Strepsiptera, where it has traditionally been placed on the basis of morphology alone (Kristensen 1981, 1991). Although there has long been general agreement that the orders Megaloptera, Neuroptera, and Raphidioptera are monophyletic (e.g., U. Aspöck et al. 2001, U. Aspöck and H. Aspöck 2008, Beutel et al. 2010, but see Winterton et al. 2010), the relative relationships among the orders have been the subject of many variant opinions over the years (e.g., Withycombe 1925, Willmann 1990, U. Aspöck et al. 2001, U. Aspöck and H. Aspöck 2008). Recent broad-scale phylogenetic work (e.g., Misof et al. 2014) seems to be reconfirming the monophyly of each of the three orders, and to be converging on the interordinal sister-group relationship of Raphidioptera + (Megaloptera + Neuroptera). Other recent phylogenetic works, particularly using molecular data (e.g., Haring and Aspöck 2004, Winterton et al. 2010, Liu et al. 2015), are beginning to develop an augmented framework for understanding interfamilial relationships and to lay a foundation for the future development of more detailed hypotheses of intergeneric relationships. The latter will be necessary to stabilize historically incongruent intrafamilial taxa in some families (e.g., Ascalaphidae, Chrysopidae, and Myrmeleontidae); to corroborate (or not) relationships in families whose internal phylogenetic structure is currently based on only one or a small number of previous works (e.g.,

Berothidae, Coniopterygidae, Hemerobiidae, Mantispidae, and Psychopsidae); and to establish more detailed internal phylogenetic structures for families in which subfamilial taxa are commonly recognized, but for which little or no detailed phylogenetic work currently exists (e.g., Osmylidae).

21.2 Geological Age

Recent molecular phylogenies that incorporate clade-divergence-time estimates based on molecular clock models and selected fossils (e.g., Winterton et al. 2010, Misof et al. 2014, Michel et al. 2016) place the divergence of stem neuropterids from the Strepsiptera + Coleoptera lineage sometime in the Late Carboniferous; the divergence of the Megaloptera, Neuroptera, and Raphidioptera lineages in the Permian; and the divergence of the stem lineages of most family-ranked clades of extant Neuroptera (the largest order) in the early to mid-Mesozoic, followed by continued diversification within families in the later Mesozoic and Cenozoic. It is now widely believed, based on the growing number of neuropterid (particularly neuropteran) fossils that have been described over the past several decades from Jurassic and Cretaceous deposits, that the mid-to-late Mesozoic was a major period of diversification for the Neuropterida. The current extant families that are characterized by small numbers of species and oddly and highly disjunct taxon ranges are readily (if casually) interpretable as the vestigial remnants of formerly more diverse and widespread groups that radiated during the Mesozoic – a view that continues to gain support from the rapid rate at which new fossils from the Jurassic and Cretaceous continue to be described. Although with roots that extend well into the Cretaceous, if not earlier, much of the diversification that has occurred in the two largest families of the Neuroptera, the Chrysopidae and Myrmeleontidae, undoubtedly occurred in the Cenozoic, and these two families in particular seem to be major centers of continuing radiation in the Neuropterida.

21.3 Metamorphosis and Life Stages

Although all neuropterids share the typical sequence of holometabolous life stages – egg, multiple larval instars, pupa, and adult – both the number of larval instars and intraspecific variability in instar-number show significant interordinal differences. The Megaloptera and Raphidioptera are characterized by a relatively large number of larval instars (ca. 7–11+), and the number of instars completed before pupation seems often to be indeterminate (i.e., not fixed in number). The Neuroptera have fewer larval instars, typically three (four reported in some coniopterygids, and five in some ithonids), and the number of instars passed before pupation seems to be fixed under natural conditions. Most neuropterids are characterized by standard holometabolism in which the sequential larval instars display similar body forms. Hypermetamorphosis, in which some larval instars differ substantially in form from other instars, is uncommon but occurs in at least two neuropteran families (Berothidae and Mantispidae) (Redborg 1998). The known eggs, pupae, and adults of almost all neuropterids are terrestrial (i.e., occur outside water, with the exception of the pupae of Nevrothidae, which have been reported from cocoons attached to rocks underwater); most larvae are also terrestrial, but subsurface aquatic larvae occur in four families, two in the Megaloptera and two in the Neuroptera. This observed distribution of environmental associations by life stage emphasizes that “aquatic” neuropterids are only partially so, and that the lineages with aquatic larvae are most likely secondarily adapted to freshwater environments.

21.3.1 Adults

The superficial morphology of most adult neuropterids is dominated by their wings, which are usually large relative to body size, membranous, many-veined, and variable in orientation at rest. In most neuropterids the wings are held roof-like (i.e., inclined at a more or less steep

angle along the sides of the body, with their hind margins touching or closely approximated dorsally) over the abdomen at rest. This resting posture contributes significantly to the general appearance that most people associate with neuropterid insects. However, in some taxa, the wings at rest broadly overlap across the top of the abdomen (e.g., Corydalidae and some Myrmeleontidae), are held out to the side of the body (e.g., some Ascalaphidae and some Dilaridae), or are held nearly vertically above the body (e.g., many Nemopteridae). Most neuropterids are macropterous and volant, possessing well-developed fore- and hindwings. Brachyptery, microptery, and aptery – usually most strongly affecting the hindwings, and usually associated with loss of flight capacity – are known but rare within the group (Oswald 1996). The details of the relatively complex wing venation that is found in most neuropterids are widely used for distinguishing and diagnosing taxa, particularly in the family and genus groups. Some taxa display unusual wing developments, such as the slender, elongated hindwings of nemopterids, or the coriaceous thickening of the forewing in some hemerobiids.

In addition to differences in wing outline and venation, neuropterid wings vary widely in the color and patterning of veins and membranes. Veins can be concolorous or composed of areas of contrasting color. The membrane can be transparent, translucent, or opaque; untinted, evenly tinted, or inconspicuously to conspicuously patterned; bear macrotrichia, or not; be completely covered with, partially covered with, or lack microtrichia; and produce iridescent reflections, or not. The wing margins of many neuropterans bear trichosores (minute sclerotizations of the wing margin interposed between the end-twiggings of longitudinal veins), which are unknown in megalopterans and raphidiopterans.

The diversity in wing form tends to obscure the fact that the fundamental structure of the pterothorax (and non-terminal parts of the abdomen) is similar across the Neuropterida, and little modified relative to that of many other holometabolous insect orders. Head and

prothoracic structure, however, varies significantly at the ordinal level. Adult megalopterans and raphidiopterans share a plesiomorphic prognathous head-capsule orientation, whereas neuropteran adults have a derived hypognathous head capsule. Ocelli are plesiomorphically present, but are secondarily lost in some Megaloptera and Raphidioptera and nearly all Neuroptera. Antennae are generally elongate and filiform, but pectinate or clubbed in some megalopterans and neuropterans. The prothorax is subquadrate in megalopterans and most neuropterans (with mantispids a notable exception), but narrowed, elongated, and somewhat tubular in raphidiopterans. Legs are generally slender and gressorial (adapted for walking), with no obvious specializations for running or jumping, but raptorial forelegs have evolved independently in several neuropteran lineages (e.g., Mantispidae and some Berothidae and Myrmeleontidae). The legs (especially the tarsal and pretarsal regions) of some adult neuropterans (e.g., antlions and owlflies) have become secondarily adapted for grasping and perching and are poorly suited for walking. The abdomen usually bears 10 more-or-less distinct segments, but the terminal segments are variously fused in some groups, resulting in fewer apparent segments. The male terminalia are exceedingly diverse in all three orders and usually provide definitive characters for species differentiation and an important basis for genus- and subgenus-level groupings in most families. The female terminalia also provide many characters that are useful in the same contexts. Of particular note in females is the slender, elongate ovipositor that is present in all Raphidioptera, and which has developed independently in several neuropteran families (e.g., Dilaridae and some Mantispidae).

The bodies and wings of adult neuropterids display a broad range of color schemes and patterning, most of which seem to be camouflage adaptations. Strategies involving background color matching and disruption of the body outline appear to predominate, contributing to concealment on a variety of substrates,

but particularly plant surfaces (e.g., bark, foliage, and stems), where most adults are commonly found. Bright green body coloration has developed independently in at least some species in five neuropteran families (Chrysopidae, Hemerobiidae, Ithonidae, Mantispidae, and Nymphidae).

Adult neuropterid body size is typically estimated by measurement of forewing length, which ranges from about 2 to 85 mm, resulting in forewing spans ranging from about 4 to 180 mm. Hindwing length can reach 90 mm in some neuropterans (e.g., some Nemopteridae).

Overall, the majority of neuropterid adults seem to be primarily night active, with primary diurnal activity having arisen in relatively few groups (Table 21.1). However, periods of daily adult activity have been studied in detail for only a small number of (mostly temperate European) species (e.g., Duelli 1986, Ábrahám and Mészáros 2006), and it is unclear how accurate the broad generalizations in Table 21.1 might be, particularly for taxa occurring in the warm tropics.

21.3.2 Eggs and Oviposition

All neuropterids are oviparous, and many produce eggs with distinctive chorion ornamentation. Neuropterids have evolved a wide range of fascinating morphologies and behaviors associated with oviposition. During the process of oviposition, the eggs of most species are coated with adhesive secretions that are used either to fix the eggs in place on a deposition substrate (fixed naked eggs) or to adhere fine granular materials to the egg surface (coated eggs), the latter presumably to aid concealment of the eggs (Oswald 1993a). Fixed, naked eggs typically remain firmly attached to the oviposition substrate until (and after) emergence of the first-instar larva (Montserrat 1996). Coated eggs, if deposited on surface substrates, can shift in position after deposition. Most species deposit eggs on exposed solid substrates (e.g., leaves, stems, and rocks). Others employ elongate ovipositors to deposit eggs into cracks and crevices

Table 21.1 Primary natural activity period and relative frequency of nocturnal light attraction by adults of each family of the Neuropterida.

Order	Family	Primary natural adult activity period	Light attraction
Megaloptera	Corydalidae	Some diurnal, most nocturnal	**
	Sialidae	Some diurnal, some nocturnal	*
Neuroptera	Ascalaphidae	Some diurnal, most crepuscular	**
	Berothidae	Nocturnal	***
	Chrysopidae	Some diurnal or crepuscular, most nocturnal	***
	Coniopterygidae	Crepuscular or nocturnal	***
	Dilaridae	Crepuscular or nocturnal	**
	Hemerobiidae	Crepuscular or nocturnal	***
	Ithonidae	Nocturnal	*
	Mantispidae	Most diurnal, some crepuscular or nocturnal	***
	Myrmeleontidae	Some diurnal, most nocturnal	**
	Nemopteridae	Most diurnal, some crepuscular or nocturnal	**
	Nevrorthidae	Diurnal	*
	Nymphidae	Nocturnal	***
	Osmylidae	Crepuscular(?) or nocturnal	***
	Psychopsidae	Nocturnal	***
Sisyridae	Crepuscular or nocturnal	**	
Raphidioptera	Inocelliidae	Diurnal	*
	Raphidiidae	Diurnal	*

Key: ***, adults of most species are apparently attracted to lights at night; **, adults of many species are attracted to lights at night, but adults of other species are not attracted to lights; *, adults of most species are apparently not attracted to lights at night.

in uneven surfaces (e.g., bark and decaying plant material); use digging structures on the end of the abdomen to deposit eggs below the surface in granular substrates (e.g., sand, soil, and dust accumulations); or simply deposit coated eggs on the surface of the ground (Aspöck 2002). Nearly all species oviposit with the female standing on the substrate, but a small number of species seem to oviposit while in flight (Psychopsidae).

Fixed, naked eggs can be sessile or stalked. Sessile eggs are fixed to the substrate on their sides or by their non-micropylar ends. Stalked eggs are not known in the Megaloptera or Raphidioptera, but have evolved independently

in at least four different families of the Neuroptera (Berothidae, Chrysopidae, Mantispidae, and Nymphidae). Stalked eggs consist of an egg attached by its non-micropylar pole to the free end of a silk fiber. Although one egg per stalk is typical, multiple eggs attached to the same stalk are sometimes seen. Stalks can be single and discrete or deposited closely together, sometimes with the stalks partially joined. Egg-stalk silks are composed of proteinaceous compounds produced in the female colleterial glands (Canard et al. 1984). Depending on the rigidity of the stalk, it may or may not support the weight of the egg. Erect, rigidly stalked, eggs can be deposited in any orientation relative to the force of gravity.

Eggs with flaccid stalks are typically pendant in form and laid so that they hang more or less freely. Eggs, both sessile and stalked, are deposited singly, in small groups, or in larger groups containing up to hundreds of eggs (Redborg 1998). Large groups of sessile eggs are generally laid in contiguous masses, which may consist of one or more layers of eggs. Some species cover their egg masses with a protective coating, which can be composed of silk fibers (e.g., some Sisyridae) or of non-fibrous materials of varying texture and composition (e.g., Corydalidae). Large groups of stalked eggs generally consist of fields of closely adjacent, but individually deposited, eggs.

Some ascalaphids produce two morphologically distinct forms of eggs (fertile eggs and infertile repagula), which are produced in differentiated ovarioles in the female ovaries (Henry 1978). During oviposition on plant stems, the repagula are placed in an interrupted band around the plant stem proximal to the deposition site of the fertile eggs. In at least some species the repagula are coated with a secretion that is repellant to ants, which reverse direction after antennating the repagula, thus shielding the fertile eggs from discovery. Other neuropterid species produce multi-egg groupings that are particularly intriguing, and quite striking. *Nymphes myrmeleonoides* (Neuroptera: Nymphidae), for example, produces egg clutches that consist of a series of approximately 25 long-stalked eggs that are arranged in a horseshoe-shaped arch; the stalked eggs are bent inward toward the middle of the arch and each pair of adjacent stalked eggs is joined by a longitudinally oriented unstalked egg (New 1981). Exactly how the female accomplishes this interesting ovipositional architecture (Fig. 21.3a) has yet to be documented, and whether it is characteristic of the family is unknown.

The neuropteran species that produce stalked eggs or silk-covered masses of sessile eggs seem to be the only known taxa in the Insecta that use silk fibers produced from two different glandular sources.

21.3.3 Larvae

Neuropterid larvae are characterized by a well-sclerotized, prognathous head capsule; three gressorially legged thoracic segments; and a 10-segmented abdomen that may bear prominent dorsal, lateral, or ventral processes. The plesiomorphic neuropterid larval body form appears to be campodeiform, a form that is found in all Megaloptera and Raphidioptera and many Neuroptera. This body form is generally associated with actively mobile larvae. Other neuropterans display a variety of body-form specializations, including flattening and broadening of the thorax and abdomen, the development of elongate cuticular processes (scoli) on some thoracic and abdominal segments, or the shortening and dorsoventral thickening of the abdomen. These modifications tend to be associated with less-active larvae and the development of specialized larval life-history strategies.

The larvae of the Neuroptera differ strikingly from those of the Megaloptera and Raphidioptera in several fundamental respects. Larvae of the Megaloptera and Raphidioptera have typical chewing mouthparts and a continuous alimentary canal adapted for passing the particulate material that is produced by masticating solid food; the Malpighian tubules are not adapted for the production of silk proteins. Larvae of the Neuroptera have distinctively derived mouthparts that are highly modified for fluid feeding and an alimentary canal that is functionally discontinuous at the midgut–hindgut junction (i.e., the gut is constricted at that point to a degree that prevents the passage of any materials, fluids, or fine particulates that enter the midgut); the Malpighian tubules are adapted for the production of silk proteins. After leaving the Malpighian tubules, the liquid silk passes through the hindgut and exits the body through the anus; the proteins are converted to solid silk fibers by stretching the liquid after it emerges from the body. Silk fibers are used by the larvae of all neuropteran families for the production of cocoons in which pupation

occurs. Neuropteran larvae with slender abdomens typically have sufficient flexibility to permit the application of silk over a relatively broad areal range for cocoon construction. In neuropterans in which much of the abdomen is broadened or thickened, the distal abdominal segments typically remain more slender, probably as an adaptation to retain flexibility for the distribution of silk. In the most highly modified silking systems (e.g., Myrmeleontidae and Ascalaphidae), the tenth abdominal somite is narrowed, elongated, and sclerotized to form a tubular spinneret; this spinneret is normally retracted into the ninth abdominal segment and is probably exerted primarily during active silking for cocoon construction.

Larval neuropterans imbibe fluids through two hollow “jaws.” Each jaw is composed of a coadapted mouthpart complex that consists of the styletiform ipsilateral mandible (dorsal) and maxilla (ventral), which are joined on one side by a sliding tongue-and-groove joint and which enclose between them a single food canal that runs from the base of the jaw to a point close below its apex. The food canal is formed from a pair of shallow longitudinal scrobes that are developed on the opposed faces of the stylets. The food canal functions as the channel through which digestive enzymes pass before they are injected into the body of a prey item, and also as the channel through which extra-orally digested liquid food is drawn back into the body of the feeding larva.

The jaws articulate on the anterior margin of the head capsule and are either straight (i.e., non-opposable) or medially curved (and opposable). At the level of the base of the Neuroptera, the opposability of jaws can be interpreted as either plesiomorphic (if the curved-jawed Nevrothidae is taken as the basal-most lineage of the Neuroptera), or derived (if the straight-jawed Coniopterygidae is taken as basal). In either case, current interfamilial phylogenies suggest that the opposable jaws in the larvae of the Hemerobiidae + Chrysopidae and the Myrmeleontoidea have been derived from

ancestors with non-opposable jaws. Functionally, opposable jaws are presumed to be a beneficial adaptation for capturing and holding prey. The medial margin of the mandible is unarmed or bears one or more elongate, fixed teeth (each derived from a highly modified, pedicellate seta) that seem to aid in holding prey in opposable-jawed taxa. In straight-jawed taxa, the bases of the jaws typically lie adjacent to each other; in opposable-jawed taxa the jaw bases are generally more widely separated. In both cases, an articulated labrum appears to be absent and the anteromedian region of the head capsule – which in most insects is typically the location of the entrance into the mouth, as in Megaloptera and Raphidioptera – is tightly closed between the jaws to direct sucking force laterally to the bases of the jaw canals.

In most neuropterans, the maxillary stylet also incorporates a separate, fully enclosed “venom” canal, which runs from the base of the stylet (where it links to the venom gland) to an inconspicuous opening near the stylet apex. Other glands (e.g., “salivary glands” and “labial glands”) are also associated with the bases of the jaws. The specific functions of the products of each of these glands are poorly studied and not well understood, although secretions from them certainly function in the immobilization and extra-oral digestion of prey. In species with non-opposable jaws, immobilizing venom (from one or more possible source glands) is injected, followed by jaw withdrawal while the venom takes effect, in turn followed by reinsertion of the jaws to begin feeding. In species with opposable jaws, the jaws may or may not be removed from the prey item between envenomation and the beginning of feeding.

21.3.4 Pupae

All known neuropterid pupae are exarate and denticous, but the detailed morphology of neuropterid pupae remains a little-studied and poorly documented area. Some structures of interest are known – such as the dorsal

abdominal hooks on some neuropteran pupae, differences in pupal mandible form, and differences in antennal location and orientation – but the paucity of both descriptive and comparative studies provides little basis for making generalizations about pupal structure. A comprehensive comparative study of the pupal stage would be of considerable interest and could have substantial phylogenetic value.

21.4 Biology

Documented lifespans of individual neuropterans range from a few weeks to about six years. Two- to three-year lifespans are not uncommon in the Megaloptera and Raphidioptera, four- to five-year lifespans are known for some larger megalopterans that live in cool temperate streams (New and Theischinger 1993), and lifespans of up to six years have been observed for some Raphidioptera species under captive conditions (H. Aspöck et al. 1991). Proportionately, most of the lifespan is spent in the larval stages in most species. The adults of most neuropterids live for only a few weeks or a few months, although species that overwinter as adults in temperate regions can live for considerably longer. Larval instar count is not intimately tied to the lifespan of individuals or to the generation time of species. Typical neuropteran species with three larval instars can be multivoltine (particularly in smaller species and in warmer tropical regions), univoltine (characteristic of temperate populations of many species), or semivoltine (particularly in larger species and in cold or arid regions). Some species are facultatively univoltine/multivoltine or univoltine/semivoltine, with the voltinism characteristic of a particular area based on factors such as dormancy, temperature, and the quantity and quality of available food. In some groups, individuals are often somewhat plastic in their ability (within limits) to extend their lifespans under unfavorable conditions.

All neuropterid adults are terrestrial. Most are associated to some extent with the aerial

parts of plants, where they roost or hunt for prey. A smaller number of species are geophilous as adults, either as perchers on ground-associated substrates (rocks, sand, or soil; e.g., some Myrmeleontidae) or as active members of the litter fauna (rarely; e.g., some Coniopterygidae and Hemerobiidae).

The microhabitats characteristically occupied by neuropterid larvae are much more diverse. Fully aquatic larvae occur in four families, two in the Megaloptera (Corydalidae and Sialidae) and two in the Neuroptera (Nevrorthidae and Sisyridae). A few neuropteran species (some Osmylidae) have larvae that have been characterized as “subaquatic” (i.e., geophilous in water-edge microhabitats). Aquatic larvae can be primarily inhabitants of the (near) surfaces of benthic sediments (Corydalidae and Nevrorthidae), burrowers in such sediments (Sialidae), or associated with specific elements of the benthos (e.g., frequenting encrusting sponges; Sisyridae). The number of times that aquatic larvae have independently evolved in the Neuropterida is a question with a long history and considerable current interest. With the Megaloptera (which have aquatic larvae) increasingly viewed as the most likely extant sister group to the Neuroptera, the answer to this question is closely linked to the question of whether the basal lineage (or lineages) of extant Neuroptera possesses aquatic or terrestrial larvae. In recent years, different phylogenies have been proposed that consider either an “aquatic family” (Nevrorthidae) or a “terrestrial family” (Coniopterygidae) as basal in the Neuroptera. As the phylogenetic question has yet to be resolved conclusively, opinions continue to differ on how to interpret the evolution of the life-history trait of aquatic larvae.

Most neuropterid larvae, however, are terrestrial, either geophilous or phytophilous, and have no close association with standing or running water. Most geophilous larvae (e.g., many Myrmeleontidae, Ascalaphidae, and Nemopteridae) are cryptozoic and usually occupy near-surface microhabitats (e.g., ground litter, surface sand and dust, and rock surfaces and crevices),

but some are (or appear to be) more fully subterranean (e.g., some Myrmeleontidae, Nemopteridae, Dilaridae, and Ithonidae), burrowing more deeply into soils or sediments. Some subterranean larvae (e.g., some Dilaridae and Nemopteridae, and perhaps some Ithonidae) seem to be deep wanderers that are adapted for feeding on subterranean prey, whereas other larvae may use ground-deposited sediments primarily to temporarily escape predation or adverse surface environmental conditions. Larvae in the latter class are capable of regular vertical movements in soils or sediments on a daily (e.g., some Myrmeleontidae in sandy substrates) or seasonal (e.g., some Corydalidae in stream beds) basis.

Most phytophilous larvae are associated with the exposed surfaces of living plants (e.g., most Hemerobiidae and Chrysopidae, some Ascalaphidae and Nymphidae); others are more typically associated with concealed spaces in dead or decomposing plant materials (e.g., in or under bark and in decaying trees and logs; some Psychopsidae, Berothidae, Dilaridae, Osmylidae, and Raphidioptera). Some larvae are specialized predators of other arthropods and live most of their lives within constructions produced by the species on which they prey (e.g., some Mantispidae in egg sacs of spiders, some Chrysopidae and Nemopteridae in nests of ants, and some Mantispidae in nests of bees and wasps).

Although commonly assumed to all be predators, adult neuropterids actually display a wide variety of feeding strategies. Predation is certainly the most common feeding mode, but some adults are known to be non-feeding (or essentially so), pollenivorous (feeding on pollen), or glyciphagous (feeding on honeydew; typically scraped from material dried on plant surfaces). Some adults also feed (at least occasionally) on tree sap, flower nectar, or other plant materials. However, in gut-content studies of adult neuropterids, it is generally unclear whether, when they are present in small amounts, the discovered plant materials were consumed preferentially or consumed casually

as part of grooming activities or while feeding on other materials (e.g., honeydew). Similarly, the generality of casual behavioral observations that sometimes associate neuropterid adults with plant and flower feeding is often uncertain. That said, regular pollenivory seems to be well established in a number of taxa whose guts are regularly packed with pollen or whose mouthparts seem to possess specific modifications for extracting pollen from flowers (e.g., some Berothidae and Nemopteridae). Glyciphagy is well documented in a number of neuropterans, and in the most highly developed systems, yeasts may be maintained in a well-tracheated foregut diverticulum to aid digestion. In nearly all groups, feeding occurs with the adult standing on or near the food material. In some neuropterans, however, aerial predation has been demonstrated or is suspected (e.g., Ascalaphidae and some Myrmeleontidae).

With the possible exception of some ithonids – some of which may be saprophagous or phytophagous, but whose larval biologies remain poorly known (Faulkner 1990) – all known neuropterid larvae feed naturally on small animals of appropriate size, mostly insects and other arthropods. Although the feeding strategies of the vast majority of neuropterid larvae can be characterized as predaceous, some blur the distinction between predation, parasitism, and parasitoidism. The latter is particularly true for mantispids, which, at various times or in different species, are predators (a single mantispid larva feeding on multiple eggs in a spider egg sac; multiple mantispid larvae feeding on a single bee or wasp larva), parasites (maintenance feeding by a larval mantispid on spider hemolymph during a period of phoresy), or parasitoids (a single mantispid larva feeding externally on and killing a single bee or wasp larva) (Redborg 1998).

Predaceous larvae display a number of different prey-acquisition strategies. Most employ active search strategies to locate and capture dispersed prey; others employ energy-conserving sit-and-wait strategies, which can involve the construction of a physical pitfall trap (some

Myrmeleontidae). The larvae of the majority of neuropterids are usually considered to be more or less general predators, whose host range is limited primarily by factors such as prey size, availability, and mobility. However, only a few species' host ranges have been studied in detail under natural conditions, so our knowledge of host breadth and the factors that influence it are fragmentary. In neuropterid taxa that seem to have specialized feeding associations (e.g., on sponges, termites, or spiders, or the larvae of ants, bees, or wasps), little is confidently known about the true ranges of prey species that might be fed upon in nature, owing to sparse association records. Conversely, evidence such as the disproportionate association of some species with particular kinds of plants (e.g., tree species) suggests that some neuropteran species that are otherwise assumed to be general predators might have more specific feeding requirements than initially suspected (i.e., on specialist phytophagous arthropods associated with particular plant taxa). In some species, the initial location of suitable prey by larvae may be facilitated by female oviposition in favorable locations or microhabitats (e.g., some Chrysopidae and Berothidae). The location of suitable prey can also involve highly specialized behaviors, such as phoresy. In addition to capturing living prey, some neuropterid larvae, particularly in the Megaloptera and Raphidioptera, scavenge on the remains of dead or dying animals.

Last-instar neuropteran larvae spin a silken cocoon in which they pupate. Megalopteran and raphidiopteran larvae do not produce cocoons; they generally excavate a small hollow cell in a concealed location (e.g., in soil, gravel, rotten wood, or under-bark debris) within which pupation occurs. At the end of the pupal period, the well-developed pupal mandibles are typically instrumental in aiding the pharate adult's escape from the cocoon or pupal chamber, after which the pharate adult may wander for some distance before eclosing from the pupal cuticle. The mobility of the pharate adult is a critical aspect of some specialized life-history strategies. For example, in *Plega hagenella* (Neuroptera:

Mantispidae), mobile pharate adults were able to escape unharmed from nests of the host bee *Melipona subnitida* (Hymenoptera: Apidae), whereas manipulation experiments showed that new adults whose pupal cuticles were artificially removed were quickly recognized by nest bees and rapidly destroyed (Maia-Silva et al. 2013).

Larval neuropterids that occupy visually exposed microhabitats (mostly neuropteran larvae that live externally on plant or rock surfaces), particularly if diurnally active, display a range of color schemes and patterns that seem to be camouflage adaptations. As in adults, background color matching and disruptive outline coloration appear to be major strategies. Physical disruption of the body outline (e.g., through the development of thoracic and abdominal scoli) and self-decoration (e.g., "trash carrying") are additional strategies that are well developed in some Neuroptera (Tauber et al. 2014). Self-decoration may also play a protective role beyond camouflage by providing a physical barrier between the larva and would-be predators (e.g., ants).

In natural ecosystems, neuropterid insects are members of the large class of small predators that provide the critical ecological service of controlling population levels of other small arthropods, particularly herbivorous insects. In freshwater ecosystems, corydalid larvae are often among the largest invertebrate predators, and may play particularly important ecological roles in such systems.

21.5 Distribution

Neuropterids are found on all continents except Antarctica, as well as on numerous remote oceanic islands (many of which have endemic species). Most families of significant size (and whose distributions are not relictual) are most diverse in the tropical and subtropical regions. In 2010 (J. D. Oswald, unpublished data), the approximate species diversity by biogeographic region was as follows: Palearctic, 1440 species; Afrotropical, 1390; Oriental, 1260; Neotropical

1170; Australian, 710; Nearctic, 480; and Oceania, 130. The five countries with the highest documented species diversity were: China, 850 species; Australia, 598; United States, 468; Brazil, 413; and South Africa, 379. Although the relative diversity rank of biogeographic regions is unlikely to change dramatically over time, the list of top diversity countries will probably change as the neuropterid faunas of many countries in tropical latitudes, most of which are currently under-studied and under-sampled, become better known.

21.6 Overview of Orders and Families

Relative to other order-ranked insect taxa, the orders that constitute the Neuropterida are not particularly rich in species. The Raphidioptera (248 spp.) and Megaloptera (373 spp.) are the two smallest orders in the Holometabola, and the third and fourth smallest orders in the Insecta (only Zoraptera and Notoptera, each with fewer than 100 species, are smaller). The order Neuroptera (5813 spp.) is somewhat larger, ranking sixth in size among the 11 orders of the Holometabola, and eleventh among the 28 orders of insects. The species-level diversity of the Neuroptera is similar to that of the insect orders Odonata, Psocoptera, Phthiraptera, and Thysanoptera. A list of the current orders and families of the Neuropterida is given in Table 21.2, together with an indication of their genus- and species-level diversity. A more complete classification of the Neuropterida is given in Table 21.3, also with genus- and species-level diversity counts. In the classification used here, the former families Polystoechotidae and Rapismatidae are included within the Ithonidae, and the sometimes-recognized family Rhachiberthidae is treated here as a subfamily of the Berothidae.

The classification and all taxon diversity counts used in this work are from the work of Oswald (2015), which incorporates new taxa and taxonomic changes known to the author

through September 2013. It has not been possible to include additional taxa that have been described since that time, or to include classification changes suggested in several important phylogenetic works that have appeared over the past two years, although notes on the latter are included in several of the family treatments below. In these family treatments, characterizations of the species diversity of family-group taxa are based on the following scale: very small (< 50 species), small (50–99), moderate (100–499), large (500–999), and very large (> 999). Using these size classes, the 19 families of the Neuropterida have the following frequencies: five very small, three small, seven moderate, two large, and two very large. Characterizations of the physical size of adults are based on the following scale of forewing lengths: very small (2–5 mm), small (6–15 mm), medium (16–25 mm), large (26–50 mm), and very large (> 50 mm). Because no Neuropterida are known from Antarctica, this continent is excluded from discussions of continental distributions (i.e., “found on all continents” = “found on all continents except Antarctica”).

The best extended single-source reviews published to date for each of the three orders of the Neuropterida are the following: Neuroptera, New (1989); Megaloptera, New and Theischinger (1993); and Raphidioptera, H. Aspöck et al. (1991). The treatments of the Neuroptera (New 1991a), Megaloptera (Theischinger 1991), and Raphidioptera (H. Aspöck and U. Aspöck 1991) in *The Insects of Australia* remain useful shorter summaries. Oswald and Penny (1991) cataloged the genus-group names of the Neuropterida. Comprehensive and regularly updated online catalogs (Oswald 2015) and bibliographies (Oswald 2016) are also available for taxa and literature pertinent to each of the three orders. Two additional useful works that broadly review the biodiversity of the Neuropterida, and that contain useful compendia of representative color illustrations of numerous species, are those of U. Aspöck and H. Aspöck (1999, 2007).

Table 21.2 An alphabetical list of the orders and families of the extant Neuropterida of the world (after Oswald 2015), with counts of genera and species.

Order	Family	Genera	Species
Megaloptera	Corydalidae	27	295
	Sialidae	8	78
Neuroptera	Ascalaphidae	100	431
	Berothidae	28	126
	Chrysopidae	81	1,415
	Coniopterygidae	23	571
	Dilaridae	4	77
	Hemerobiidae	28	591
	Ithonidae	10	39
	Mantispidae	44	395
	Myrmeleontidae	198	1,659
	Nemopteridae	36	146
	Nevrorthidae	4	19
	Nymphidae	8	35
	Osmylidae	30	212
	Psychopsidae	5	26
	Sisyridae	4	71
Raphidioptera	Inocelliidae	7	42
	Raphidiidae	26	206
Megaloptera (total)		35	373
Neuroptera (total)		603	5,813
Raphidioptera (total)		33	248
Neuropterida (total)		671	6,434

Table 21.3 A higher classification (order to tribe) of the extant Neuropterida of the world (after Oswald 2015).

Order	Family	Subfamily	Tribe	Genera	Species
Megaloptera	Corydalidae	Chauliodinae		18	135
		Corydalinae		9	160
	Sialidae		8	78	
Neuroptera	Ascalaphidae	Albardiinae		1	1
		Ascalaphinae		71	328
		Acmonotini		2	2
		Ascalaphini		18	55
		Encyoposini		9	38

Table 21.3 (Continued)

Order	Family	Subfamily	Tribe	Genera	Species
			Hybrisini	3	12
			Proctarrelabrini	4	16
			Suhalacsini	6	79
			Ululodini	3	57
			Ululomyiini	1	1
			<i>Incertae sedis</i>	25	68
		Haplogleniinae		26	95
			Allocormodini	1	7
			Campylophlebiini	1	1
			Melambrotini	11	24
			Proctolyrini	1	6
			Tmesibasini	1	10
			<i>Incertae sedis</i>	11	47
		<i>Incertae sedis</i>		1	7
	Berothidae	Berothimerobiinae		1	1
		Berothinae		12	89
		Cyrenoberothinae		3	3
		Nosybinae		4	13
		Nyrminae		1	1
		Protobiellinae		2	2
		Rhachiberothinae		3	13
		Trichomatinae		2	3
		<i>Incertae sedis</i>		1	1
	Chrysopidae	Apochrysininae		6	25
		Chrysopinae		64	1,364
			Ankylopterygini	5	101
			Belonopterygini	15	155
			Chrysopini	36	912
			Leucochrysinini	7	195
			<i>Incertae Sedis</i>	1	1
		Nothochrysininae		9	24
		<i>Incertae sedis</i>		2	2
	Coniopterygidae	Aleuropteryginae		12	201
			Aleuropterygini	2	101
			Coniocampsini	1	24
			Fontenelleini	9	72

(Continued)

Table 21.3 (Continued)

Order	Family	Subfamily	Tribe	Genera	Species
		Brucheiserinae		2	4
		Coniopteryginae		9	370
			Coniopterygini	6	277
			Conwentziini	3	93
	Dilaridae	Dilarinae		3	55
		Nallachiinae		1	22
	Hemerobiidae	Adelphohemerobiinae		1	2
		Carobiinae		1	9
		Drepanacrinae		3	9
		Drepanepteryginae		3	38
		Hemerobiinae		5	228
		Megalominae		1	40
		Microminae		5	111
		Notiobiellinae		4	84
		Psychobiellinae		1	2
		Sympheroibiinae		3	65
		<i>Incertae sedis</i>		1	3
	Ithonidae			10	39
	Mantispidae	Calomantispinae		2	6
		Drepanicinae		4	37
		Mantispinae		35	319
		Symphrasinae		3	33
	Myrmeleontidae	Myrmeleontinae		174	1,509
			Acanthaclisini	16	103
			Brachynemurini	16	91
			Dendroleontini	36	187
			Gnopholeontini	4	10
			Lemolemini	7	14
			Maulini	2	2
			Myrmecaelurini	16	149
			Myrmeleontini	13	242
			Nemoleontini	61	631
			Nesoleontini	3	80

Table 21.3 (Continued)

Order	Family	Subfamily	Tribe	Genera	Species
		Palparinae		22	140
			Dimarini	3	8
			Palparidiini	1	3
			Palparini	16	124
			Pseudimarini	1	2
			<i>Incertae sedis</i>	1	3
		Stilbopteryginae		2	10
	Nemopteridae	Crocinae		17	48
			Crocini	7	18
			Necrophylini	9	29
			Pastranaiini	1	1
		Nemopterinae		19	98
	Nevrorthidae			4	19
	Nymphidae			8	35
	Osmyidae	Eidoporisminae		1	1
		Gumillinae		1	2
		Kempyninae		4	20
		Osmylinae		7	38
		Porisminae		1	1
		Protosmylinae		3	11
		Spilosmylinae		5	118
		Stenosmylinae		7	20
		<i>Incertae sedis</i>		1	1
	Psychopsidae	Psychopsinae		2	18
		Zygophlebiinae		3	8
	Sisyridae			4	71
Raphidioptera	Inocelliidae	Inocelliinae		7	42
			Inocelliini	5	37
			Neghini	2	5
	Raphidiidae	Raphidiinae		26	206
			Agullini	1	17
			Alenini	1	10
			Raphidiini	24	179
Totals				671	6,434

Suborders, superfamilies, and subtribes have been excluded. Orders are listed alphabetically and all subtaxa are listed alphabetically within each higher taxon. Counts of genera and species are for the lowest-ranked taxon in each row.

21.6.1 Order Megaloptera

21.6.1.1 Family Corydalidae (Fig. 21.1a)

The Corydalidae, fishflies (Chaulioidinae) and dobsonflies (Corydalinae), are a moderate-sized family (295 species in 27 genera) with aggressively predaceous aquatic larvae and large to very large (forewing length up to ca. 85 mm), mostly non-feeding adults. The family is most species-rich in montane regions with pristine, high-gradient, gravel-bottomed, cold-water streams and rivers, which are the preferred habitat for the larvae of most species. The family is represented on most continents, although absent from Europe and poorly represented in Africa. The group is particularly diverse in the Oriental Region in the mountains of southern China and northern Indochina west to the Himalayas. A smaller number of species are adapted to lower-gradient, warmer-water streams and springs, which correlates with the family's lower species diversity in the low-latitude tropics outside mountainous regions. The family is particularly well known for the extremely long male mandibles of some species of the genera *Corydalus* (North and South America) and *Acanthacorydalis* (eastern Asia). Where found, this trait is the result of strong allometric growth and is distinctly sexually dimorphic. Perhaps best known in *Corydalus*, recent phylogenetic work (Contreras-Ramos 1998) has shown that full development of this trait is mostly restricted to a few species in a relatively derived northern clade within the genus.

Most corydalid adults are rather inconspicuously colored, but some species are strikingly marked with bold black and pale color patterns (e.g., *Nigronia*), or are largely bright yellow in life

(*Chloronia*). Because of their large size and riparian habits, corydalid adults became known to entomologists early on, and the first species was described by Linnaeus (1758), even though no species are native to Europe or the adjacent areas surrounding the Mediterranean and Black Seas. The large average size of corydalids and the preference of the larvae of many species for cold montane streams are factors that contribute to the particularly long lifespans of many species (3–5 years is not uncommon), although other species are univoltine, especially in warmer waters. Overall, however, corydalid species probably have the longest average lifespan of any family in the Neuropterida. Two subfamilies – Chaulioidinae and Corydalinae – are generally recognized on the basis of adult head and terminalic traits, and both seem to be monophyletic. Several intergeneric phylogenetic works have contributed to the development of a relatively advanced and solid basis for interpreting higher-level relationships in the family (Glorioso 1981, Penny 1993, Liu et al. 2012b). The extensive corydalid fauna of China and adjacent southeastern Asia has been treated in recent years in a large series of papers by Liu and colleagues, much of which is summarized or cited by Yang and Liu (2010) and Liu et al. (2012b, 2016). Good faunal works exist for Australia (Theischinger 1983) and southern Africa (Liu et al. 2013), and the revisions of *Corydalus* by Contreras-Ramos (1998) and *Chloronia* by Penny and Flint (1982) effectively cover much of the fauna of Central and South America.

21.6.1.2 Family Sialidae (Fig. 21.1b,c)

The Sialidae, alderflies, are a small family (78 species in eight genera) with predaceous aquatic

Figure 21.1 Representative adults and larvae of the orders Megaloptera and Raphidioptera. (a) *Corydalus* sp., adult, Brazil (Megaloptera: Corydalidae). (b) *Sialis lutaria*, adult, Poland (Megaloptera: Sialidae). (c) *Sialis lutaria*, larva, Czech Republic (Megaloptera: Sialidae). (d) Ascalaphidae sp., larva, Nicaragua (Neuroptera: Ascalaphidae). (e) *Suphalomitus* sp., adult, Australia (Neuroptera: Ascalaphidae). (f) *Spermophorella* sp., adult, Australia (Neuroptera: Berothidae). (g) Chrysopidae sp., larvae, Colombia (Neuroptera: Chrysopidae). (h) *Hypochrysa elegans*, adult, Belgium (Neuroptera: Chrysopidae). Photo credits: Arthur Anker (a), Łukasz Prajznc (b), Jan Hamrsky (c), Marshal Hedin (d), Craig Nieminski (e), Shaun Winterton (f), Robert Oelman (g), Gilles San Martin (h). (See color plate section for the color representation of this figure.)



larvae and small, largely non-feeding adults (forewing length ca. 10–15 mm). However, unlike the Corydalidae, whose larvae tend to prefer gravelly substrates in streams with at least moderate currents, sialid larva are primarily burrowers in fine-grained, muddy sediments. Thus, although their microhabitats include pools in lotic environments, they are also characteristic of lentic waters. The family is represented on all continents (including Europe), although quite restricted in distribution on most of the southern continents. The majority of species are found in the cool to cold temperate regions of the globe (mostly in the north, fewer in the south), and are quite uncommon in lowland tropical areas. At least in temperate North America, adults in southern populations tend to emerge early in the year, during the colder months. Alderflies are similar in overall body form and appearance worldwide and most are uniformly black (or nearly so), although some species have partially pale or reddish coloration, particularly on the head and prothorax. Adults are weak fliers and rarely stray far from their aquatic larval habitats. Sialid larvae seem to be mostly general predators of a variety of small aquatic organisms, mostly insects and other arthropods.

The monophyly of alderflies has never been seriously questioned and has been supported by a wide-ranging morphological phylogenetic analysis (Liu et al. 2015), which also provides a much-needed, well-documented hypothesis for the pattern of phylogenetic relationships among the major lineages in the family. No subfamilies or tribes are currently recognized among the extant members of the family, which is ripe for a comprehensive revisionary treatment.

21.6.2 Order Neuroptera

21.6.2.1 Family Ascalaphidae (Fig. 21.1d,e)

The Ascalaphidae, owlflies, are a moderate-sized family (431 species in 100 genera) with predaceous terrestrial larvae and small to very large predaceous adults (forewing length ca. 15–60 mm). The family is known from all

continents, but only the largest subfamily, Ascalaphinae, is similarly cosmopolitan. The other two subfamilies are more restricted in distribution: Albardiinae is known from a single species, *Albardia furcata*, from Brazil, and Haplogleniinae is found in the Afrotropical, Neotropical (with one or two species extending into the southern Nearctic) and Oriental Regions. The adult body form is similar to that of antlions, with abdomen and wings elongated, but ascalaphid bodies are generally more robust, and the long antennae (found in almost all species) are distinctive. In many respects, owlflies are among the most highly derived of all neuropterids. This is particularly true of their flight capabilities, which are probably the most “advanced” in the superorder. Adult owlflies are active aerial predators, and have been likened to dragonflies in their hunting abilities and agility in the air. Most species appear to be active (only?) during the hours of twilight (particularly at dusk) and to spend the rest of the day perched, but some Old World species are distinctly diurnal. Some species perch with the abdomen flexed dorsally at a wide angle to the resting substrate. A few South America species form communal roosting aggregations (an uncommon behavior for predators), to which some of the same individuals return on multiple days (Hogue and Penny 1988, Gomes-Filho 2000).

The biologies and ecologies of ascalaphids are poorly known. For adults, this is at least in part due to the crepuscular activity period of most species, and also to their high mobility. The diurnal species of Eurasia are the best known. Owlfly larvae are solitary, sedentary predators; known species are primarily inhabitants of the litter and soil (Badano and Pantaleoni 2014b), live on the stems and leaves of plants, or climb on other elevated objects (e.g., rocks and fence posts). Larvae are usually distinctly flattened and bear prominent lateral scoli; many lie in wait for prey with their jaws opened at extremely large angles (180–270 °). Adult females of some South American species lay abortive eggs, called repagula, which, although apparently primarily

defensive in function, may serve as a first food source for newly eclosed first-instar larvae.

The phylogeny of the family has been poorly explored. In the past, it has widely been assumed to be monophyletic, but the interrelationships of putatively basal ascalaphids and antlions (particularly the Albardiinae and Stilbopteryginae) might not be as clear cut as once thought (Winterton et al. 2010, Michel et al. 2016), and the monophyly of both groups is currently the subject of active investigation. It is widely believed that the current intrafamilial classification of the family is highly artificial. Many of the currently recognized suprageneric taxa are poorly defined and likely not monophyletic (Badano and Pantaleoni 2014b). Species-level monographs are available for some regions – that is, Australia (New 1984b), Europe (Badano and Pantaleoni 2014b), South America (Penny 1981a, b), and southern Africa (Tjeder 1992, Tjeder and Hansson 1992) – but accurate species identification is difficult to impossible in many parts of the world.

21.6.2.2 Family Berothidae (Fig. 21.1f)

The Berothidae, beaded lacewings, are a moderate-sized family (126 species in 28 genera) with predaceous terrestrial larvae and small adults (forewing length ca. 6–15 mm). The family is widespread, with representation on all continents, but is relatively poorly represented in the New World. The faunas of Africa and southern Asia are relatively diverse, and Australia has a distinctive endemic fauna (Aspöck and Randolph 2014). Of the eight subfamilies treated here, only the largest subfamily, Berothinae, is subcosmopolitan. All of the other subfamilies are small and restricted in distribution: Berothimerobiinae from Chile, Cyrenoberothinae from Chile and Southern Africa, Nosybinae and Rhachiberothinae from the Afrotropical Region, Nyrminae from Anatolia, Protobiellinae from Australia and New Zealand, and Trichomatinae from Australia (Aspöck and Randolph 2014, Makarkin and Ohl 2015). Adult berothids superficially resemble small hemerobiids, are primarily nocturnal, and exhibit a variety of dietary

preferences, including pollen, small arthropods, and fungi (Monserrat 2006). At least some species lay stalked eggs. The biologies of berothid species are mostly unknown, and the larvae of only six genera have been described to date (Aspöck and Randolph 2014). Larvae of some Berothinae are known to be hypermetamorphic, with active, feeding first- and third-instar larvae and a quiescent, non-feeding second instar. These species live and feed inside termite nests, but it is still unknown whether this behavior and habitat is characteristic for the entire family (Wedmann et al. 2013).

The limits and monophyly of the Berothidae are currently unsettled questions. Although most of the family seems to represent a good clade, discussion is ongoing about its relationship with the Mantispidae, and the proper position of the raptorial-forelegged rhachiberothines, which have been treated in the Berothidae (Makarkin and Ohl 2015), in the Mantispidae (Willmann 1990), or as a separate family (Aspöck and Mansell 1994, Aspöck and Randolph 2014, Liu et al. 2015). If the rhachiberothines prove to be sister to either the main body of the Berothidae or the Mantispidae, a conservative treatment that placed the rhachiberothines as a subtaxon in whichever family is appropriate would have the benefit of not artificially increasing the number of family-ranked taxa in the Neuroptera. The composition of berothid subfamilies at the genus level is also currently under active discussion (Aspöck and Randolph 2014, Makarkin and Ohl 2015), but progress toward a more stable phylogeny and classification of the family is being made. In any event, the classification presented here will require future modification. A useful key to all of the genera (except the Rhachiberothinae) has recently been published (Aspöck and Randolph 2014), but few species-level keys are available (Faulkner 1992, Winterton 2010, Machado and Krolow 2016).

21.6.2.3 Family Chrysopidae (Fig. 21.1g,h)

The Chrysopidae, green lacewings, are a very large family (1415 species in 81 genera) with

predaceous terrestrial larvae and small to large, mostly predaceous adults (forewing length ca. 3–35 mm). The family is cosmopolitan in distribution, with significant faunas on all continents. Three subfamilies are commonly recognized: the Chrysopinae are cosmopolitan (and contain ca. 97% of the world species); the Apochrysiniae are restricted to tropical areas in Africa, Asia, Australia, and the Americas; and the Nothochrysiniae are widespread across Europe, Australia, southern Africa, South America, and western North America (Brooks and Barnard 1990). Chrysopids are ubiquitous and prominent elements of the insect faunas of most habitats, where many come readily to lights. Among entomologists, green lacewings are probably the most widely recognized of all neuropterid insect groups. Although many members of the general public also recognize them, their small size, nocturnal habits, and well-camouflaged bodies detract from their popular prominence.

The adults of most species are rather uniform in appearance, with a compact body and large, transparent wings held nearly vertically along the sides of the body. As their English common name suggests, most species are bright green, but other species show a wide range of other color schemes that incorporate black, brown, yellow, red, and orange. Although many species are predaceous as adults, many other species are not. Non-predaceous adults feed on a variety of other substances, but perhaps most prominently on pollen, nectar, and honeydew (usually dried on the surfaces of plants). The adults of some species possess particularly interesting morphologies and behaviors that have attracted special attention. Among these are the tympanal organ at the base of the radial vein in most species (this is among the smallest “ears” known in insects and is tuned to detect the frequencies of echolocating bats) (Miller 1984), and duetting courtship behaviors (mostly in *Chrysoperla* species, males and females duet using volleys of abdominal oscillations with vibratory signals transmitted through the substrate on which the pair stands) (Henry et al. 2013). With minor exceptions (i.e., the genus

Anomalochrysa), female chrysopids lay their eggs atop silken stalks, generally on plants.

The majority of chrysopid larvae seem to be associated with the leaves and stems of plants, where their phytophagous arthropod prey commonly feed. However, the larvae of other species occupy a broader range of microhabitats and exhibit a more diverse set of feeding strategies and preferences. Some species, for example, are found in ground litter and prey on a wide variety of small organisms, even snails (Jones 1941). Others are specialized predators feeding in the nests of certain ant species (Principi 1946). Principi and Canard (1984) present a wide-ranging discussion of chrysopid feeding. The larvae of many plant-inhabiting species are active and voracious predators of soft-bodied arthropods, particularly aphids, which have made them valuable to, and widely used in, biological control programs. A prominent characteristic of the larval biology of many species is their penchant for self-decoration. Commonly described as “trash carrying” or “debris-carrying,” the larvae of many (but distinctly not all) species actively place various kinds of debris on their dorsal surfaces – probably functioning as camouflage, a physical barrier to predation, or both – which often bear specialized morphological structures to support and retain the debris (e.g., elongate scoli and hooked setae; Tauber et al. 2014). Much of the biological literature on the Chrysopidae is concisely summarized by Canard et al. (1984).

The monophyly of the Chrysopidae as currently constituted seems well established (Winterton and Brooks 2002, Winterton and de Freitas 2006, Winterton et al. 2010). The monophyly of its subfamilies and tribes, however, is currently under active investigation, and it is likely that the composition and classification of a number of these will require changes based on new phylogenetic work. Brooks and Barnard (1990) provided a checklist to the world species, summary treatments for each genus, and a key to the world genera. Other significant works on the Chrysopidae include those of Tjeder (1966), H. Aspöck et al. (1980), New (1980), Dorokhova

(1987), Ghosh (1990), Tsukaguchi (1995), X.-k. Yang (1997), X.-k. Yang et al. (2005), Brooks (1997), de Freitas and Penny (2001), and Winterton and Brooks (2002). Species-level identification of chrysopids is relatively difficult, often requiring examination of male terminalic characters. Similarly, some genera cannot be keyed without recourse to male terminalia. In many parts of the world, species-level identification of chrysopids is difficult to impossible with existing literature.

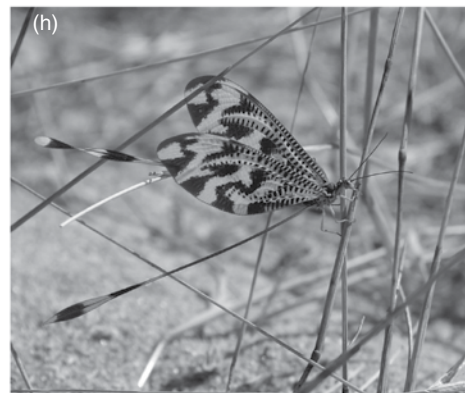
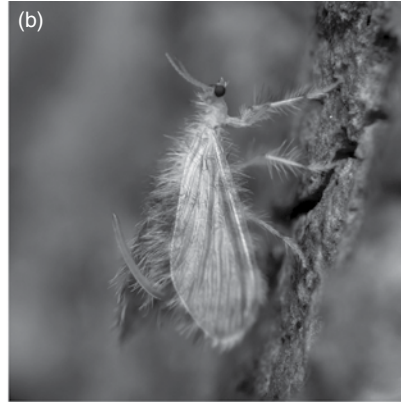
21.6.2.4 Family Coniopterygidae (Fig. 21.2a)

The Coniopterygidae, dustywings, are a large family (571 species in 23 genera) with predaceous terrestrial larvae and very small to medium-sized adults (forewing length 2–6 mm in most species; > 9 mm in some Brucheiserinae). The family is cosmopolitan in distribution, with significant faunas on all continents, but is particularly diverse in the Neotropical and Palearctic Regions. The two largest subfamilies – Coniopteryginae and Aleuropteryginae – are also cosmopolitan, but the small relictual subfamily Brucheiserinae is known only from Chile and Argentina (Sziráki 2011). Dustywings are the smallest members of the order Neuroptera. Their small size, short broad wings, highly reduced venation, and habit of coating the body with a whitish waxy powder produced from special body glands render them isolated among neuropterans. Larvae and adults are predators and are generally found in trees and bushes (Meinander 1972). The larvae are active predators, often feeding heavily on scale insects, mites, and whiteflies, and for this reason are sometimes used in biological control programs. The phylogenetic position of the family in the Neuroptera is still under discussion. It is considered an important group phylogenetically, having been placed at the base (i.e., sister to the remaining Neuroptera) or near the base of the order by almost all workers over the past century. The ultimate resolution of its position has implications for interpreting the ancestrally aquatic or terrestrial nature of stem-lineage neuropterans. Although treated by

Meinander (1972), on which the classification used here is based, the internal relationships and higher classification of the family are in need of a broad, modern, phylogenetic study. Meinander (1972) comprehensively revised the family, which resulted in a flurry of additional taxonomic work and precipitated the subsequent species catalogs of Meinander (1990) and Sziráki (2011). The latter work contains comprehensive keys to the world species and is the preferred starting point for entry into the literature of the group.

21.6.2.5 Family Dilaridae (Fig. 21.2b)

The Dilaridae, pleasing lacewings, are a small family (77 species in four genera) with predaceous larvae and very small to small adults (forewing length ca. 4–12 mm). The family is widespread; species are known from all continents except Australia, but the family is poorly represented in Africa. Most species (> 95%) are assigned to the genera *Dilar* and *Nallachus*. Adults are distinctive in having relatively broad wings that are densely setose, males possessing pectinate antennae, and females bearing an elongate ovipositor. New World *Nallachus* species tend to rest with their wings spread out to the sides of the body and resemble small moths. The biologies of dilarid species are poorly known. The larvae of only a few species (< 10%) have been described (mostly from first instars only, and from only two genera, *Dilar* and *Nallachus*). The best-known species is *Nallachus americanus*, from the eastern United States, the larvae of which have been reported from under the bark of dead trees, feeding on soft-bodied arthropods (Gurney 1947, MacLeod and Spiegler 1961). Larvae of *Dilar* have been collected from soil samples in Eurasia (Ghilarov 1962), and the larvae of that genus are probably subterranean. Two subfamilies are generally recognized: Dilarinae, with three genera (*Berothella*, *Dilar*, and *Neonallachus*) in the Oriental and Southern Palearctic Regions; and Nallachiinae, with one genus (*Nallachus*) in the New World, but with two outlier species, one in southern Africa and one in Vietnam (Oswald



1998a). The monophyly of the family seems well established and its classification has been stable. Oswald (1998a) cataloged the world species, but a considerable number of new species have been published since then, particularly from China and southeastern Asia (Zhang et al. 2014a; 2014b; 2014c; 2015, 2016). Keys are available for the species of the Neotropical Region (Adams 1970, Machado and Rafael 2010a) and Europe (Monserrat 1988b, Aspöck et al. 2015).

21.6.2.6 Family Hemerobiidae (Fig. 21.2c)

The Hemerobiidae, brown lacewings, are a large family (591 species in 28 genera) with predaceous terrestrial larvae and very small to medium-sized predaceous adults (forewing length ca. 3–18 mm). The family is cosmopolitan in distribution, with significant faunas on all continents. Many remote oceanic islands have endemic species, and the family contains the largest number of flightless species (11, Oswald 1996) of any family in the Neuropterida. The group is well represented in temperate and montane regions and apparently less abundant in lowland tropical areas. The adults of most species are rather uniform in appearance – a compact body dominated by dull brown to yellowish wings – but a few species are pale to bright green. Except for the anomalous and putatively basal species *Adelphohemerobius enigmaramus*, all species are characterized by multiple oblique branches arising from the posterior margin of the radius (Oswald 1994). Similar to the Chrysopidae, the larvae and adults are primarily found on plants, mostly trees and shrubs, less commonly on herbaceous vegetation. The flightless species seem to occupy geophilous-type habitats. The larvae are generally similar in form to chrysopterid larvae,

but (contrary to some early reports) are always naked, never bearing thoracic or abdominal scoli or self-decoration. The eggs are never stalked and are typically laid on plants. Although most species have traditionally been considered general predators as adults and larvae, the host range of many species might prove to be more selective when examined in more detail (Monserrat and Marín 2001). The active predatory nature of the adults and larvae of some species has led to their use in biological control programs.

The monophyly of the family, as currently constituted, seems well established. Ten subfamilies are currently recognized, based on the phylogenetic work of Oswald (1993b, 1994) and Garzón-Orduña et al. (2016). Intriguingly, although the recent morphology + molecular phylogeny of Garzón-Orduña et al. (2016) supports the monophyly of most of the groups identified by Oswald (1993b, 1994) as subfamilies on the basis of morphology alone, it recovered a radically different pattern of basal relationships among them, which will likely require a reconsideration of the internal classification of the family. Monserrat (1990) includes a checklist of world species; Oswald (1993b) presents a key to the world genera and a summary of each genus. Several good regional treatments are also available: southern Africa (Tjeder 1961), Australia and New Guinea (New 1988a, b), Costa Rica (Monserrat 2002), Europe (H. Aspöck et al. 1980), and Russia (Dorokhova 1987).

21.6.2.7 Family Ithonidae (Fig. 21.2d)

The Ithonidae, moth lacewings and giant lacewings, are a very small family (39 species in 10 genera) with small to large adults (forewing

Figure 21.2 Representative adults and larvae of the order Neuroptera. (a) Coniopterygidae sp., adult, Spain (Neuroptera: Coniopterygidae). (b) *Nallachus americanus*, adult female, United States (Neuroptera: Dilaridae). (c) *Drepanopteryx phalaenoides*, adult, Belgium (Neuroptera: Hemerobiidae). (d) *Ithone fulva*, adult, Australia (Neuroptera: Ithonidae). (e) *Zeugomantispa minuta*, adult, United States (Neuroptera: Mantispidae). (f) *Synclisis baetica*, larva, Italy (Neuroptera: Myrmeleontidae). (g) *Austrogymnocnemia edwardsi*, adult, Australia (Neuroptera: Myrmeleontidae). (h) *Nemoptera sinuata*, adult, Portugal (Neuroptera: Nemopteridae). Photo credits: Katja Schulz (a,b), Gilles San Martin (c), Shaun Winterton (d,g), Patrick Coin (e), Franco Pampero (f), Joaquim Muchaxo (h).

length ca. 15–40 mm). The family consists of a morphologically heterogeneous, but apparently monophyletic, assemblage of highly disjunct and narrowly endemic genera that are dispersed across the continents of Asia, Australia, North America, and South America. The genera and their distributions are as follows. New World: *Adamsia* (Central America), *Fontecilla* (Chile), *Narodona* (Mexico), *Oliarces* (southwestern USA and northwestern Mexico), *Platystoechotes* (California, eastern USA; J. D. Oswald, unpublished data), and *Polystoechotes* (southern Canada south to Panama, Chile). Old World and Australia: *Ithone*, *Megalithone*, and *Varnia* (all from Australia), and *Rapisma* (southeastern Asia).

Adults are generally robust, with setose bodies and large wings with complex venation. Little is known about the biologies of the species, and most of the available information is based on *Oliarces* and a few Australian species. These species are characterized by adult mass emergences of short duration (a few days), during which mating takes place and after which the species appear to “disappear” (Riek 1974, Faulkner 1990). Larvae have been demonstrated to be subterranean in *Oliarces* and *Ithone*, and are strongly suspected of being so in at least several of the other genera (probably all are subterranean). The few known larvae are fossorial and scarabaeiform. They had at one time been assumed to be predaceous, but the evidence from the few biological studies available has found little direct evidence to support this. The alternative view that the larvae are saprophagous or phytophagous (Gallard 1932) – feeding on or around plant roots (which would be unique in the Neuropterida) – has been gaining currency in recent decades, but as yet there is no definitive observational evidence to support this view, even if available circumstantial evidence suggests its possibility.

The taxa now included in the Ithonidae *sensu lato* (*s.l.*) were for many years placed in three separate families: Ithonidae *s.s.*, Polystoechotidae, and Rapismatidae. The artificiality of this arrangement had been suspected for many

years, but formal modification of the taxonomy of the group was only recently catalyzed by the detailed phylogenetic work of Winterton and Makarkin (2010), who presented evidence for the monophyly of the collective assemblage. As a recently formed aggregate, the Ithonidae *s.l.* have never been comprehensively revised in their current form, and the literature of the group exists under all three family names. *Rapisma* (formerly in the family Rapismatidae) was revised by Barnard (1981), information on *Polystoechotes* and *Platystoechotes* (formerly in the family Polystoechotidae) can be found in the works of Carpenter (1940) and Oswald (1998c), and the Australian genera (formerly in Ithonidae *s.s.*) were last revised by Riek (1974). The other genera have never been revised in a broad comparative context; their literature is scattered, but much of it is cited by Winterton and Makarkin (2010), which also includes a key to all 10 of the genera now included in the family.

21.6.2.8 Family Mantispidae (Fig. 21.2e)

The Mantispidae, mantisflies, are a moderate-sized family (395 species in 44 genera) with predaceous (*s.l.*) terrestrial larvae and distinctive very small to large adults (forewing length ca. 5–35 mm). The family is broadly distributed across all continents, but only the largest subfamily, Mantispinae, is similarly cosmopolitan. The other three generally recognized subfamilies are more restricted in distribution: Calomantispinae from Australia and southern North America; Drepanicinae historically from Australia and South America, but recently also from China (Liu et al. 2015); and Symphrasinae from South America to southern North America (Ohl 2004). The family is widely known for the characteristic body form of its adults, whose elongated prothoraces and prominently raptorial forelegs resemble small praying mantids (Mantodea). The adults are voracious predators, whose diets are composed of a large variety of small arthropod species that they can capture with their forelegs. Adults are usually solitary, but records of large aggregations exist for some species (e.g., *Trichoscelia* sp. and *Climaciella*

brunnea). Most adults have transparent wings and bodies somberly colored in browns, yellows, and dull reds. Other species, however, are bright green or colored to mimic the bold patterns of stinging wasps and bees (Redborg and MacLeod 1983).

The life histories of mantispids are distinctive within the Neuropterida. The larval stages are hypermetamorphic, with an active first instar and increasingly sedentary second and third instars. The best-known and most distinctive life histories are found in the Mantispininae, which as mature larvae seem to feed exclusively on spider eggs. Two primary strategies are used to find these eggs. In the first, the campodeiform first-instar larva locates a spider egg sac by active search, then burrows through the silk of the sac to gain access to the eggs; in the second strategy, the first-instar larva boards a passing spider, spends a period of time riding on it phoretically (sometimes feeding ectoparasitically on spider haemolymph), then leaves the spider as the spider spins an egg sac and oviposits into the sac. Some mantispid species use both strategies; others use one or the other exclusively (Redborg 1998). After molting in the egg sac, the second- and third-instar larvae become increasingly grub-like and less mobile, feeding on spider eggs until pupating in a separate silken cocoon spun inside the silk of the spider egg sac. The immature stages of the three non-mantispinine subfamilies are poorly known. Most also appear to be hypermetamorphic, but feed on non-spider prey. Larvae of the Symphrasinae seem to prey mainly on the larvae of Hymenoptera, some displaying complex behaviors (Dejean and Canard 1990, Maia-Silva et al. 2013). The larval activities of the Calomantispinae and Drepanicinae are largely unknown, with the few available records suggesting that they might feed on the immature stages of Coleoptera, Diptera, Hymenoptera, and Lepidoptera (MacLeod and Redborg 1982).

The monophyly of the family seems well established (Liu et al. 2014), but discussion is ongoing about the position of the Rhachiberothinae, which has been treated as a subfamily of

the Berothidae (as included here) or Mantispidae (Willmann 1990), or placed in a separate family (Aspöck and Mansell 1994). Each of the extant members of the four commonly recognized subfamilies seems to constitute a distinct clade (Liu et al. 2015). Ohl (2004) cataloged the world species, and several regional monographs are available: Africa (Snyman et al. 2012), North and South America (Penny 1982, Hoffman 2002, Machado and Rafael 2010b, Ardila-Camacho and Garcia 2015), and Australia (Lambkin 1986a, b).

21.6.2.9 Family Myrmeleontidae (Fig. 21.2f,g)

The Myrmeleontidae, antlions or “doodlebugs,” are a very large family (1659 species in 198 genera) with predaceous terrestrial larvae and small to very large adults (forewing length ca. 10–75 mm). The family is known from all continents, but only the subfamily Myrmeleontinae is cosmopolitan. The other two subfamilies are restricted in distribution: Stilbopteryginae from Australia, and Palparinae from the Old World (particularly the Afrotropical Region) and South America (two small genera) (Stange 2004). Antlion adults are easily distinguished from other neuropterans based on their relatively short, clubbed antennae and elongate abdomen and wings (many superficially resemble damselflies). Adults of Stilbopteryginae and Palparinae are generally more robust, with wings usually large and colorful in the Palparinae, which contains the largest species in the family. The adults of the Myrmeleontinae are generally smaller, with duller colors and body shapes varying from robust and prominently pilose to gracile and inconspicuously setose. Adults are usually nocturnally active and predaceous on small insects, but some species have been documented as feeding on vegetable material (Guillette et al. 2009).

Despite being fairly common, adult antlions are generally inconspicuous and infrequently encountered. The unobtrusive nature of most antlion adults is enhanced by their tendency to remain largely immobile, generally perched on small plant stems during the day, a behavior that

is closely linked to the modified tarsal and (especially) pretarsal structure of their legs, which are adapted for grasping, not walking. More conspicuous and much more widely known are the predaceous larvae of some species, on which their English common name is based. Antlion larvae have a characteristic body form, which consists of an ovoid body (thorax and abdomen), a flat head, and long, curved, toothed jaws. The jaws are opposable and used to capture prey, which are mainly ants and other small ground-dwelling insects and arthropods (Badano and Pantaleoni 2014a). The larvae of most species live in sandy soils, and the most conspicuous of these are those that build small conical pitfall traps, which they use to capture prey and within which they spend most of their lives (Devetak et al. 2005). Less commonly known is that the majority of antlion species (ca. 70%) are characterized by larvae that do not build pits. The larvae of most of these species live shallowly buried in sand, silt, soil, or other near-ground substrates and localize prey by detecting the substrate-borne vibrations that they produce as they walk or crawl. Others work deeper in the sand, or are associated with tree holes, caves, rock faces, under bark, under stones, or other similar microhabitats (Miller and Stange 2012).

The monophyly of the family has yet to be firmly established, and will remain unclear until more comprehensive analyses of the relationships existing among putatively basal or plesiomorphic myrmeleontids (particularly the Stilbopteryginae) and ascalaphids (particularly the Albardiinae and Haplogleniinae) have been completed. Currently, the most extensive phylogenetic treatment of the Myrmeleontidae is the recent molecular work of Michel et al. (2016). They recovered both the Ascalaphidae and Myrmeleontidae as monophyletic, with *Stilbopteryx* sister to other included Myrmeleontidae in some, but not all, analyses. Although this is suggestive, the analysis lacks *Albardia* and has poor sampling density for several other critical taxa (e.g., only one stilbopterygine myrmeleontid and one haplogleniine ascalaphid are

included); greater sampling will be necessary to make a stronger case for the monophyly of both families. The analysis of Michel et al. (2016) includes the densest taxon sampling to date for a phylogenetic analysis of the Myrmeleontidae (90+ species), and provides support for the monophyly of many commonly-recognized tribes. Two notable features of the analysis, however, are the relatively low support values for many of the nodes lying along the backbone of the tree, and the strong Old World emphasis of its in-group taxon sampling. It will be interesting to see whether support for backbone nodes can be increased by future increases in overall taxon sampling density and by the inclusion of a broader range of antlion tribes from other areas of the globe. The study of Michel et al. (2016) is a major step forward in our understanding of antlion phylogeny, and represents a new starting point for reconsideration of the currently confused and conflicting suprageneric classifications in use by different authors for the most diverse family in the order Neuroptera.

Stange (2004) cataloged and reviewed the world antlion fauna, and his classification is currently the most commonly used (as here). However, the monophyly of most of the taxa in this classification (and the classifications of others, e.g., Krivokhatsky 2011) have yet to be critically tested. A number of useful regional taxonomic monographs exist, many with keys that can aid in identification, but accurate species-level identification of antlions is still difficult to impossible in many parts of the world with existing published resources. Some of the more recent and helpful monographs include the following: Africa (Mansell 1985, 1987), Australia (New 1985a, 1985b, 1985c), Europe (Badano and Pantaleoni 2014a), North America (Stange 1994), and Russia (Krivokhatsky 2011).

21.6.2.10 Family Nemopteridae (Fig. 21.2h)

The Nemopteridae, spoon-winged (Nemopterinae) and thread-winged (Crocinae) lacewings, are a moderate-sized family (146 species in 36 genera) with predaceous terrestrial larvae

and medium-sized to very large adults (forewing length ca. 7–35 mm, hindwing length ca. 19–90 mm). The two subfamilies that are commonly recognized have similar distributions in the arid parts of Africa, Australia, western South America, and the Mediterranean to Oriental area (Portugal to India). About two-thirds of the species occur in southern Africa (Tjeder 1967), and the family is known from North America only from fossils. Adult nemopterids are among the most visually striking of all neuropterans. The forewings are oval and “normal” in form, but the hindwings are reduced to slender shafts and greatly elongated. In the Nemopterinae, the hindwings typically bear some form of apical or subapical dilation; in the Crocinae, which are usually smaller in overall size, the hindwings taper to a slender thread without a dilation. In many species the head capsule is projected ventrally into an elongate rostrum, and the mouthparts are specially modified for extracting pollen from flowers, on which the majority of adults feed. The primary activity period of adults is either nocturnal or diurnal (Tjeder 1967). Nemopterid larvae are geophilous. Those of the Crocinae typically have the anterior portion of the prothorax elongated into a distinct neck, and are found in shallow dust and debris in crevices, caves, and similar situations (Mansell 1980). Larvae of the Nemopterinae lack elongated necks and, to the extent known, seem to be more subterranean, living below the surface in sand and soil and feeding on burrowing insect larvae, perhaps particularly ant larvae (Tjeder 1967, Monserrat 1996).

The monophyly of the family and both subfamilies seems well supported (Winterton et al. 2010, Sole et al. 2013). Crocine species are more highly derived morphologically in many respects and have been proposed as a separate family (Monserrat 1996), but that suggestion has not been widely adopted. Hölzel (1975) revised the world Crocinae, and several good regional treatments of varying taxonomic scope are available: southern Africa (Tjeder 1967; Mansell 1980, 1981a, 1981b), Australia (Mansell

1983a), South America (Mansell 1983b), and Europe (Monserrat 1988a).

21.6.2.11 Family Nevrothidae

The Nevrothidae, nevrothid lacewings, are a very small family (19 species in four genera) with predaceous aquatic larvae and small terrestrial adults (forewing length ca. 6–10 mm). The distribution of extant species is relictual, with species restricted to one of three areas of endemism: southern Europe and northern Africa (*Nevrothus*, five species), eastern Australia (*Austronevrothus*, two species), or eastern Asia (*Nipponevrothus*, 11 species (China and Japan), and *Sinonevrothus*, one species (China)). Nothing seems to be known about adult feeding; larvae are presumed to feed on small arthropods (as in other Neuroptera) that are found in freshwater streams, but available details are few. The larvae have hook-tipped jaws, so are presumed to be able to grasp and hold prey. Larvae of all species seem to be restricted to clear, unpolluted, but not necessarily cold streams. Adults are typically found on adjacent vegetation (Malicky 1984). No subfamilies or tribes are recognized. The family is of considerable phylogenetic interest, as it has been interpreted as the most basal lineage within the Neuroptera (U. Aspöck and H. Aspöck 2008, Beutel et al. 2010), although other families have also been proposed to occupy that position. Wichard et al. (2010) provide a review of the family, including keys, an intergeneric phylogenetic hypothesis, and a biogeographic discussion, which encompass extant and extinct genera. Until 1967, the group was included as a subfamily in the Sisyridae. The family has yet to be comprehensively revised in its present form, and most of the available literature is taxonomic in character.

21.6.2.12 Family Nymphidae (Fig. 21.3a,b)

The Nymphidae, split-footed lacewings, are a very small family (35 species in eight genera) with predaceous terrestrial larvae and medium to large (forewing length ca. 18–40 mm) predaceous adults. The distribution of extant species

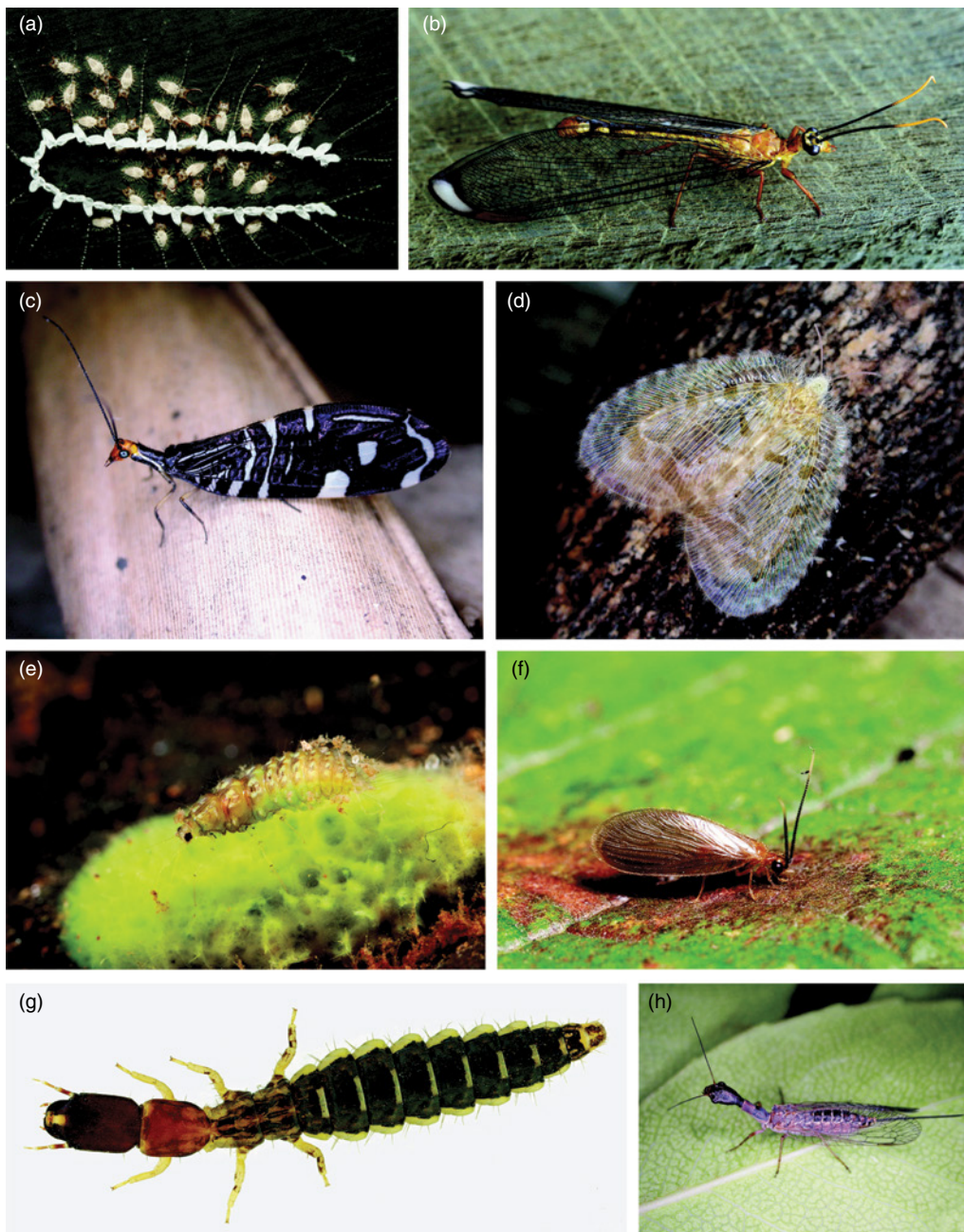


Figure 21.3 Representative adults and larvae of the orders Neuroptera and Raphidioptera. (a) *Nymphes myrmeleonoides*, eggs and first instar larvae, Australia (Neuroptera: Nymphidae). (b) *Nymphes myrmeleonoides*, adult, Australia (Neuroptera: Nymphidae). (c) *Porismus strigatus*, adult, Australia (Neuroptera: Osmylidae). (d) *Psychopsis insolens*, adult, Australia (Neuroptera: Psychopsidae). (e) *Sisyra fuscata*, larva, Czech Republic (Neuroptera: Sisyridae). (f) *Sisyra terminalis*, adult, Belgium (Neuroptera: Sisyridae). (g) *Parainocellia bicolor*, larva, Italy (Raphidioptera: Inocelliidae). (h) *Agulla* sp., adult, United States (Raphidioptera: Raphidiidae). Photo credits: Jim McLean (a), Michael Jefferies (b), Shaun Winterton (c,d,h), Jan Hamrsky (e), Gilles San Martin (f), Marcello Romano (g). (See color plate section for the color representation of this figure.)

encompasses Australia (mostly eastern), the island of New Guinea, and one unconfirmed record from the Philippines, but this distribution is highly relictual, as extinct species of the family are known from Asia, Europe, and North and South America. Little biological information is available for the family; larval instars (mostly only first instars) are known for only about 10% of the species. These have robust heads with elongate, strongly curved jaws that bear a single mandibular tooth. Thoraces and abdomens are moderately broad to nearly circular and most segments bear elongate scoli. The larvae of the few known species seem to be either inhabitants of leaf surfaces or ground litter.

No subfamilies are listed here, but the recent work of Shi et al. (2015) supports and reasonably suggests the division of the extant species into two subfamilies – Nymphinae and Myiodactylinae – a modern resurrection of the early 20th century division of the group into the separate families Nymphidae *s.s.* and Myiodactylidae. The Myiodactylinae include relatively short-bodied forms with oval wings (often green and superficially similar to green lacewings); the Nymphinae include relatively long-bodied forms with more elongate, slender wings (superficially similar to antlions). The two largest genera are *Osmylops* and *Myiodactylus*, which together contain more than 60% of the species. The family is notable for the large and often conspicuous terminalic structures of its males, which are used to couple with females. New (1981, 1987) monographed the Australian and New Guinean species, respectively, and (1984a) reviewed intergeneric relationships in the family; Oswald (1997, 1998b) revised the genus *Osmylops*.

21.6.2.13 Family Osmylidae (Fig. 21.3c)

The Osmylidae are a moderate-sized family (212 species in 30 genera) with predaceous larvae and small to large adults (forewing length ca. 15–30 mm). Extant species are known from all continents except North America, where the family is known only from fossils. The fam-

ily is most diverse in the Australian and Oriental Regions. The Australian fauna is believed to hold the deepest extant phylogenetic diversity in the group. Eight subfamilies are currently recognized, each with a restricted distribution: Eidoporisminae and Porisminae from Australia; Stenosmylinae and Kempyninae from Australia and South America; Gumillinae from South America; Protosmylinae from the Oriental Region; Osmylinae from the Palearctic and Oriental Regions; and Spilosmylinae, the most diverse subfamily (with ca. 55% of the family's species), widespread in the Old World and Australia except Europe (New 1989). The adults are sometimes confused with chrysopids, but can be separated from them on the basis of venational characters and by the presence (in osmylids, except *Gumilla*) of distinct ocelli (an uncommon trait in adult neuropterans). Adults are generally found near water bodies, but some species can be found in drier areas as well, particularly some Australian species (New 1991b, Monserrat 2014). Where known, adults seem to be primarily predaceous, but some specimens have been recorded as taking vegetable material, too (Monserrat 2014). The biologies of few species of osmylids are known, and perceptions about osmylid biology are heavily influenced by the biology of its best-known species, the European *Osmylus fulvicephalus*. The larvae of this species are subaquatic, living as active predators on small arthropods in moist-ground areas along the edges of small streams. Although apparently shared with some other osmylid groups, this aquatic association is not true for all members of the family, as the larvae of some Australian species have been collected under bark in areas not closely associated with water (New 1986, Winterton et al. 2010, Monserrat 2014).

The phylogeny of the family is poorly known, but is generally believed to be monophyletic (Winterton et al. 2010). The monophyly and phylogenetic interrelationships of the eight subfamilies have yet to be critically investigated. Keys are available for the species in some

regions: Australia (New 1983, 1989), Oriental Region (New 1991b, Sekimoto and Yoshizawa 2011), Europe (Monserrat 2014), and South America (Ardila-Camacho and Noriega 2014, Martins et al. 2016).

21.6.2.14 Family Psychopsidae (Fig. 21.3d)

The Psychopsidae, silky lacewings, are a very small family (26 species in five genera) with predaceous terrestrial larvae and small to large (forewing length ca. 10–35 mm) predaceous adults. The distribution of extant species is distinctly relictual, with individual species restricted to one of three areas of endemism: southern Africa (eight species), Australia (13 species), or southeastern Asia (five species). Extinct members of the family are known from other continents. Most species are uncommon in the field (and probably locally distributed), and their biologies are poorly known. Some Australian species have been found under the bark of *Eucalyptus* trees, where they may aggregate around sap flows and feed on other insects attracted to the same. Adults hold their wings roof-like over the abdomen, but at a low angle, so that specimens at rest are wide and relatively flat. Most adults are inconspicuously colored, but the wings of some Australian species bear distinctive bands and colored markings. The oviposition system of silky lacewings is absolutely unique within the Neuropterida. Females possess a large, membrane-lined chamber that is invaginated from the venter into the bulbous apex of the abdomen. The female uses a pair of articulated scraping appendages to produce finely granular mineral or vegetable matter, which is packed into the chamber. The granular material is then used to coat the eggs as they emerge from the ovipore, a complex behavior that is apparently accomplished while the female is flying and immediately before in-flight oviposition (Oswald 1993a).

Two subfamilies – Zygophlebiinae and Psychopsinae – have been recognized. The family was last broadly monographed by Oswald (1993a), which contains genus-level treatments and keys, and a catalog of the species. Tjeder

(1960) and New (1988c) monographed the South African and Australian species, respectively, and Oswald (1995) reviewed the sole Southeast Asian genus, *Balmes*.

21.6.2.15 Family Sisyridae (Fig. 21.3e,f)

The Sisyridae, spongillaflies, are a small family (71 species in four genera) with predaceous or parasitic aquatic larvae and very small to small (forewing length ca. 4–10 mm) terrestrial adults, which have been shown to be predators and scavengers on small arthropods and to also consume pollen, honeydew, and fungal material (Pupedis 1987). Adult spongillaflies superficially resemble brown lacewings, for which they are often mistaken. Larval sisyrids feed primarily on freshwater sponges (most of which are encrusting in form), and secondarily on a few other groups of aquatic invertebrates, such as bryozoans (Weißmair 2005, Notteghem 2016). Larvae feed by inserting their extremely slender straight jaws into individual sponge cells and extracting their contents. After locating an appropriate food source or host, the sisyrid larva usually does not leave the host unless it dies. The sponge feeding of sisyrid larvae has been characterized as either predaceous or parasitic, and arguments can be made for either view. The family is subcosmopolitan in distribution – principally because its largest genus, *Sisyra*, is subcosmopolitan – and most diverse in warm tropical areas where freshwater sponges are more abundant. Most sisyrid species (> 90%) are contained in the two genera *Sisyra* and *Climacia*, the latter of which is restricted to the New World. Of the remaining two genera, *Sisyborina* is Afrotropical and *Sisyrina* is Oriental and Australian. The last comprehensive, worldwide revision of the Sisyridae was that of Navás (1935), which is now out of date. Monserrat (1977) listed the world species, and several useful regional revisions and reviews are available: Bowles (2006, North America north of Mexico), Flint (2006, Neotropical Region), Monserrat (1981, Oriental Region), Parfin and Gurney (1956, New World), Penny

(1981, Amazon basin), Tjeder (1957, southern Africa), and Weißmair (1999, Europe).

21.6.3 Order Raphidioptera

21.6.3.1 Family Inocelliidae (Fig. 21.3g)

The Inocelliidae, inocelliid snakeflies, are a very small family (42 species in seven genera) with predaceous larvae and small to medium-sized (forewing length ca. 6–21 mm) adults; it contains approximately 15% of the world raphidiopteran species. Adults of this family are distinguished, by the absence of ocelli, from the raphidiid snakeflies, which possess ocelli. The distribution of the family is essentially the same as that of the Raphidiidae. What little is known about the biology of the family is mostly similar to that of the Raphidiidae, but with several distinctive features: all known inocelliid larvae are corticolous (none geophilous); the general feeding habit of adults, although poorly known, does not seem to be predaceous (as in raphidiids); and inocelliid mating behavior appears to involve the physical attachment of the male's head to the ventral surface of the female's abdomen, using a pair of unique holdfast organs that evert from the male's antennal toruli (no such organs or head attachment is known in the raphidiids) (U. Aspöck et al. 1994).

Although the monophyly of the family seems well established (Haring et al. 2011, H. Aspöck et al. 2012), additional work is needed to establish phylogenetic relationships within the family. The family was monographed by H. Aspöck et al. (1991) as part of their comprehensive revision of the world Raphidioptera. That work contains keys for taxa recognized up to that time. Additional helpful recent works include those by H. Aspöck et al. (2012) and Liu et al. (2009, 2010b, 2012).

21.6.3.2 Family Raphidiidae (Fig. 21.3h)

The Raphidiidae, raphidiid snakeflies, are a moderate-sized family (206 species in 26 genera) with predaceous larvae and aggressively predaceous small to medium-sized (forewing length

ca. 6–18 mm) adults; it contains approximately 85% of the world raphidiopteran species. Adults of this family are distinguished by the presence of ocelli from the inocelliid snakeflies, which lack them. The family is entirely restricted to the Northern Hemisphere, principally in three major distributional centers (which are generally shared by the Inocelliidae): the Mediterranean (Europe, Middle East, and northern Africa), central Asia, and western North America (southwestern Canada to southern Mexico). The distribution of the family is distinctly confined to areas with temperate climates, and southern records are restricted to progressively higher altitudes (H. Aspöck et al. 1998). The intriguing distribution of this family has been attributed, in part, to the requirement of larvae for exposure to a period of low temperature to induce pupation (H. Aspöck 2002). Under artificial conditions, larvae not subjected to low temperatures continue to molt as larviform individuals but at some point begin to display developmental anomalies that partially incorporate pupal traits (prothetely). It has been hypothesized (H. Aspöck 1998) that the limitation of extant Raphidioptera to cool-adapted species in the Northern Hemisphere may be an historical artefact of the Cretaceous–Tertiary impact event, eliminating a formerly more extensive, warm-adapted snakefly fauna that existed in the Mesozoic.

Adults are arboreal predators that feed broadly on a wide range of small arthropods, particularly aphids (H. Aspöck 2002). Females lay eggs under the bark of living trees, or in the leaf litter or soil, with the help of their long ovipositor. Larvae are predators of soft-bodied arthropods, particularly insect eggs and larvae; many are associated with the bark of trees (corticolous), whereas others are found in ground litter (geophilous) (H. Aspöck 2002). The monophyly of the family is well established, but work is ongoing to develop a better understanding of its internal intergeneric relationships (Haring et al. 2011, U. Aspöck et al. 2012). The family was comprehensively monographed by H. Aspöck et al. (1991), which contains keys

for taxa recognized up to that time. The works of H. Aspöck et al. (1998, 1999) and Liu et al. (2010a) provide points of entry into the more recent work on the family.

21.7 Societal Importance

Most of the general public do not know neuropterid insects by name, but many will recall having played with larval antlions in their pits as children; having seen delicate green lacewing adults gathered around porchlights on warm summer nights; or (in North America) remember the large and fearsome-looking (but actually harmless) mandibles of a male dobsonfly, perhaps having seen one on a wall near a light or on a trip to a local river or lake. Others, more observant and with a more highly honed curiosity of the natural world, might have noted with some wonder that the small “trash packet” they discovered wandering around on a leaf or stem turned out to be a decorated green lacewing larva, or have mistaken a mantisfly, with its large grasping forelegs, for a tiny praying mantid. As a group, neuropterids are widespread and fairly ubiquitous insects, but most are rather inconspicuous and go unnoticed by most people, particularly as the adults of most species are active primarily or only at night.

Those with more entomological knowledge will know more about the interesting behaviors and biologies of the common species, as well as know that neuropterids are generally predaceous insects, and therefore broadly classed as “beneficials.” It is this predatory behavior, exploited in the service of human agriculture, which accords neuropterid insects their primary societal importance. The voracious feeding capacity and actively mobile prey-searching behavior displayed by the larvae of species in several families (particularly the Chrysopidae, Hemerobiidae, and Coniopterygidae) make them effective biological control agents of some of the most important pests of agriculture and horticulture (Senior and McEwen 2001). Many species naturally invade

agricultural ecosystems, and these populations can be artificially augmented to provide primary or contributory control of a wide range of phytophagous arthropod pests, including aphids, scale insects, and mites (Canard 2001). A number of species have been used as key components in the integrated pest management (IPM) strategies deployed in a variety of crops (e.g., apple, cherries, citrus, nuts, and ornamental plants; Szentkirályi 2001a, 2001b). An important factor contributing to the efficacy of neuropterans in IPM programs is that techniques have been developed for the large-scale rearing of several species, particularly green lacewings in the genus *Chrysoperla*. This has enabled the development of a commercial market for these species and facilitated their use in augmentative biological control on a range of different crops and in a variety of different cropping systems (Nordlund et al. 2001). An extensive body of literature related to the beneficial use of neuropterans in agricultural and horticultural systems is summarized by McEwen et al. (2001). Paradoxically, in some specialized agricultural contexts the predatory nature of neuropterans is detrimental, rather than beneficial, such as mantispid larvae preying on managed stingless bee colonies (Maia-Silva et al. 2013). Even more paradoxically, in a few cases predation may be viewed as either beneficial or detrimental in essentially identical agricultural systems, depending on the desired “crop”; for example, larval hemerobiids (*Symphorobius* sp.) preying on cochineal scale insects (*Dactylopius* sp.: Hemiptera: Dactylopiidae) is viewed as beneficial if the crop is the *Opuntia* cactus, upon which the scale is considered a pest (Pacheco-Rueda 2011), but is viewed as detrimental if the “crop” is the scale insect itself, commercially reared on *Opuntia* as a source of red dye.

Neuropterid insects also intersect with human activities in a variety of other more peripheral contexts. Corydalid larvae have been sold and consumed as human food (“magotaro-mushi”) in parts of eastern Asia (Sasaki 1915), and the harvesting of “hellgrammites” (also

larval corydalids) supports a small commercial bait fishery in the eastern United States (Nielsen and Orth 1988). Antlion larvae are used in several traditional contexts – as oracles, as a treatment against fever, and to initiate breast growth in young girls – by several native cultures in Africa (Kutalek and Prinz 2004).

Neuropterans are also well represented in expressions of human artistry, both ancient and modern (Kevan 1992, Monserrat 2010). Although much of this usage is in visual imagery, a quick perusal of the Web will also reveal usage in the physical arts and crafts (e.g., jewelry, needlework, and pottery), literature (e.g., juvenile fiction: “Ace Lacewing: bug detective”), music (e.g., “Lacewing,” a band), and video. The word lacewing in particular, a compact and euphonious compound of two connotation-rich English words, has proven to be evocative and metaphorically flexible and is widely used in a variety of contexts. Caricatures of neuropterid biology and morphology have even entered the popular imagination through the mass media – plucked from a terrarium filled with sand, the long-jawed parasite aurally administered to Commander Chekov to render him susceptible to mind control in the space fantasy movie *Star Trek II: The Wrath of Khan* certainly seems to have been inspired by antlion biology and morphology, even if considerable artistic license was taken with the facts in the end.

21.8 Scientific Importance

The phylogenetic position of the Neuropterida as one of the near-basal lineages in the Holometabola, and particularly its position as the presumptive sister group to the megaclade Coleoptera + Strepsiptera (the most species-rich clade in all of Animalia), has long grounded a deep general interest in matters pertaining to the Neuropterida among systematic entomologists. The fact that the superorder contains, within a relatively small number of species, such a large and varying array of strikingly different

biologies and life histories contributes significantly to the fascination with the group by entomologists outside the realm of systematics. The diverse and often highly specialized morphological, physiological, and behavioral systems developed in the Neuropterida have led to their use to investigate a wide variety of scientific concepts and phenomena.

Over the course of nearly 50 years, Charles Henry and colleagues have investigated the obligatory duetting behavior displayed during courtship by (some) green lacewings in the genus *Chrysoperla*. Recently reviewed by Henry et al. (2013), this model system involves the reciprocal exchange of substrate-borne vibrational signals produced by abdominal oscillations in duetting, conspecific, heterosexual pairs. This short-range communication system has led to sympatric speciation within the genus at local and regional scales, and to the production of a swarm of sibling species across the globe. This work has been influential in the theoretical development of sympatric speciation models, and has particular relevance to the use of chrysopids in biological control, much of which is based on *Chrysoperla* species.

Substrate-borne vibrations have also been investigated in the Neuropterida from the perspective of the morphological and physiological systems through which vibrations are sensed (e.g., Devetak 1998) and the use of sand-borne vibrations by antlion larvae to detect and localize prey (e.g., Devetak 2014).

The advanced visual systems of adult ascalaphids, many of which have eye lobes bearing differentiated ommatidia, have been the subject of studies focusing on the physiological adaptations of eyes to detect different wavelengths of light (e.g., Gribakin et al. 1995). The capabilities of advanced sensory systems have also been a central theme in studies involving hearing in green lacewings (Miller and MacLeod 1966, Miller and Olesen 1979, Miller 1984), which have one of the smallest “ears” known in insects.

Finally, pit-building antlions have proven to be a remarkably interesting and flexible system for conducting manipulation experiments on a

wide range of practical and theoretical topics, including (to name just a few) dispersion and group selection theory (Wilson 1974, Simberloff et al. 1978, Boake et al. 1984, Day and Zalucki 2000), the biomechanics of trap construction (Lucas 1982, Griffiths 1986), and the optimality and suboptimality of foraging (Bond 1980, Griffiths 1981, Lucas 1983, Scharf et al. 2011).

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