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PREDATORY AND PARASITIC LEPIDOPTERA: CARNIVORES LIVING ON PLANTS

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ABSTRACT. Moths and butterflies whose larvae do not feed on plants represent a decided minority slice of lepidopteran diversity, yet offer insights into the ecology and evolution of feeding habits. This paper summarizes the life histories of the known predatory and parasitic lepidopteran taxa, focusing in detail on current research in the butterfly family Lycaenidae, a group disproportionately rich in aphytophagous feeders and myrmecophilous habits.

More than 99 percent of the 160,000 species of Lepidoptera eat plants (Strong et al. 1984, Common 1990). Plant feeding is generally associated with high rates of evolutionary diversification—while only 9 of the 30 extant orders of insects (Kristensen 1991) feed on plants, these orders contain more than half of the total number of insect species (Ehrlich & Raven 1964, Southwood 1973, Mitter et al. 1988, cf. Labandiera & Sepkoski 1993). Phytophagous species are characterized by specialized diets, with fewer than 10 percent having host ranges of more than three plant families (Bernays 1988, 1989), and butterflies being particularly hostplant-specific (e.g., Remington & Pease 1955, Remington 1963, Ehrlich & Raven 1964).

This kind of life history specialization and its effects on population structure may have contributed to the diversification of phytophages by promoting population subdivision and isolation (Futuyma & Moreno 1988, Thompson 1994). Many studies have identified selective forces giving rise to differences in niche breadth (Berenbaum 1981, Scriber 1983, Rausher 1983, Denno & McClure 1983, Strong et al. 1984, Futuyma & Moreno 1988, Thompson 1994). In particular, research on the Lepidoptera has emphasized how host choice may be governed on the one hand by the distribution of toxic secondary compounds and/or "enemy free space," and on the other by the need to acquire adequate nutrients (e.g., Lawton & McNeill 1979, Atsatt 1981a, Strong et al. 1984, Bernays & Graham 1988, Stamp & Casey 1993).

Since most species of moths and butterflies consume plants, comparatively little research has focused on the ecology and evolution of predatory taxa. Cottrell (1984) conducted a comprehensive analysis of aphytophagy in butterflies, but did not include moths. Reviews and experimental treatments of cannibalism in the Lepidoptera and other insects (e.g., Fox 1975, Polis 1981, Schweitzer 1979a, 1979b, Elgar & Crespi 1992) contain useful discussions of the biology of carnivorous species. However, it has been more than fifty years since a full survey of the life histories of predatory Lepidoptera has been published (Balduf 1931, 1938, 1939, Brues 1936, Clausen 1940). The great emphasis on phytophagous species overlooks the considerable dietary diversity exhibited by Lepidoptera as a whole, and yet a consideration of both the scope of this diversity and its limitations can provide valuable insight into the ecology and evolution of the group.

The rarity of carnivorous Lepidoptera is particularly striking considering the enormous dietary range exhibited by other holometabolous orders containing phytophages, such as Coleoptera, Hymenoptera and Diptera. Only about 200 species representing eight superfamilies are known to be obligate predators or parasites. Moreover, as predators, lepidopterans are remarkably unadventuresome, feeding mostly on slow, soft-bodied scale insects, eggs of other insects or ant brood. The few parasitic species are primarily parasites of other insects.

In this review, I summarize what is currently known about the life histories of moths and butterflies with carnivorous larvae, and discuss outstanding features of their ecology and evolution. The review begins with a description of traits that appear to be associated with obligately carnivorous life styles, and then focuses on recent research into predatory species in the butterfly family Lycaenidae. It concludes with discussion intended to stimulate further inquiry into the evolution of carnivory in the group.

Balduf (1938) recognized four main types of entomophagous caterpillars: (1) cannibals, which largely represent diversions from otherwise phytophagous lifestyles; (2) occasional predators, which include species that sometimes attack non-conspecific caterpillars and scavengers that sometimes take prey living in the same habitat; (3) habitual predators, such as species that regularly feed on homopterans or insects such as ants; and (4) parasites/parasitoids, including the few species that undergo either part of, or their entire development feeding on a single host. This review primarily concerns species in categories 3 and 4, which together comprise the group of obligate carnivores, while the members of 1 and 2 are facultatively entomophagous. As a rule of thumb, I consider parasites/parasitoids to be those that consume their hosts in units of less than one, whereas true predators kill and consume more than one prey. I have not distinguished here between parasites and parasitoids (that ultimately kill their hosts), in part because relatively little is known about whether or not parasitic Lepidoptera eventually do kill their hosts. The term parasite is used hereafter in this collective sense.

The life histories of entomophagous Lepidoptera are summarized in three tables. Table 1 covers the life histories of carnivorous moths. Table 2 summarizes carnivorous groups within the butterfly family Lycaenidae other than Miletinae. Table 3 focuses on feeding specializations within the wholly carnivorous lycaenid subfamily Miletinae. I have attempted to include every record of obligate predatory or parasitic behavior I could find. Because of the lack of complete life history information for many groups, this summary is inevitably tentative, and will evolve as new information becomes available. I have not attempted to summarize the numerous records of scavenging, lichen feeding or cannibalism in the group, although I discuss their possible significance. Because a caterpillar is usually observed consuming only one prey item at the time of collection, inference and/or interpretation is sometimes necessary in designating species as predators or parasites. I have indicated in the Tables those instances where parasitism or predation have been strongly inferred for a particular species or group, rather than confirmed by direct observation.

The arrangement of taxa within the Tables follows the classification for the Lepidoptera put forward by Nielsen & Common (1991) and Scoble (1992). The broad outlines of this classification were provided by Kristensen & Nielsen (1983), Kristensen (1984a, 1984b), and Nielsen (1989), and more detailed information on the Australian taxa have been supplied by Common (1992). I refer here to "Homoptera" for clarity with respect to older literature, although "Hemiptera" is the appropriate designation for this group (their arrangement in Table 1 follows Carver et al. 1991). In the case of the Lycaenidae, controversy remains concerning the relationships among the main lineages, as well as relationships within each of the groups. I follow the classification proposed by Eliot (1973), which was modified by Fiedler (1991), and which Eliot revised in 1992 (Eliot in Corbet et al. 1992), as well as Eliot's revision of the Miletini (1988). In his 1992 revision, Eliot included the riodinines as a subfamily of the Lycaenidae (Ehrlich 1958, Kristensen 1976, cf. Harvey 1987, Robbins 1988, Scott & Wright 1990), and I will refer to them here as a subfamily, recognizing that their appropriate taxonomic rank remains uncertain.

I. OVERVIEW OF PREDATORY LEPIDOPTERA

Convergently derived origins. Fossil remains suggest that the larvae of the earliest Lepidoptera fed on mosses, while the adults possessed mandibulate mouthparts and fed on pollen (Kukalova-Peck 1991). The most "primitive" extant Lepidoptera are in the suborder Zeugloptera, containing the homoneurous family, the Micropterigidae, which are considered to be the sister group to all other Lepidoptera (Common 1990, Nielsen & Common 1991). Zeuglopteran larvae have been described (Kristenson 1991:140) as "'soil animals' occurring in moist situations (bryophyte growths, etc.) which would seem to be only a small step away from genuine aquatic habitats" which characterize the larval habitats of their close relatives, the Trichoptera (see also Powell 1980, Tuskes & Smith 1984). In New Zealand, members of the genus *Sabatinca* feed on liverworts. In Australia, larvae have been collected from rotten logs in Queensland. Other species are known to feed on herbaceous plants, including grasses (Nielsen & Common 1991). From these accounts, we can conclude that the Micropterigidae are primarily plant or detritus feeders. Carnivory is therefore likely to represent a derived condition in the Lepidoptera, although without appropriate phylogenies in each case, the polarity of shifts in feeding specialization must remain speculative. Nevertheless, the occurrence of predatory habits in eight separate lepidopteran superfamilies (Table 1) suggests that the trait has arisen convergently several times.

A closer examination of the phylogenetic distribution of carnivory reveals further evidence of convergent origins. Within the butterflies, the family Lycaenidae (sensu Ehrlich 1958, Eliot in Corbet et al. 1992) contains about 5,455 described species, or close to 32% of all butterflies (Shields 1989). At least 80 species are known to be carnivorous or to feed on substances other than plants (Tables 2 & 3), and an additional circa 70 species are suspected to be aphytophagous. Cottrell (1984) argued that aphytophagy evolved independently at least eight times in the Lycaenidae (not including the riodinines), and DeVries et al. (1992) have recently added two instances of aphytophagy in the Riodininae that may well represent an independent origin.

Phylogenetic distribution of predatory and parasitic species. Obligately predatory and parasitic Lepidoptera occur in the Tineoidea, Gelechioidea, Tortricoidea, Zygaenoidea, Pyraloidea, Geometroidea, Noctuoidea and Papilionoidea (Tables 1, 2 & 3). The only entirely carnivorous families are the Epipyropidae and the Cyclotornidae in the Zygaenoidea. The Epipyropidae is a small family of perhaps as many as 40 species in 11 genera (Davis 1987 and pers. comm., Krampl & Dlabola 1983). The larvae are parasitic on Homoptera, primarily leafhoppers and also cicadas, and even on other Lepidoptera (Common 1990). The Cyclotornidae is a family containing five described species and at least seven undescribed species in the genus *Cyclotorna* that is endemic to Australia (Common 1990). The larvae of these species feed parasitically on Homoptera, and then switch to preying on ant brood (described below, Dodd 1912). With an estimated 120 species in four tribes (Eliot 1988, 1992), all of whose larvae are thought to be carnivorous, the subfamily Miletinae of the Lycaenidae is the most well-developed clade of predatory Lepidoptera (Table 2). The Lycaenidae also possesses the most diverse range of aphytophagous taxa, including representatives from 31 genera in 3 subfamilies (Tables 2 & 3).

Close relatives of entomophagous Lepidoptera commonly exhibit one or more of three ecological traits that may have been important in the evolution of carnivory: some are scavengers on insect remains or spider eggs; others are mycophages or feed on lichen; and still others associate intimately with ants. For example, most of the species in *Stathmopoda* in the Oecophoridae, *Batrachedra* in the Batrachedridae, *Blastobasis* in the Blastobasidae, *Pyroderces* in the Cosmopterigidae, and *Vitula* in the Phycitinae are specialized to feed on coccids, but each genus also contains one or two species that scavenge on droppings in bird nests, spider eggs and/or insect remains in spider webs, detritus in deserted paper wasp or bumblebee nests, insects trapped in pitcher plants, or galls (Common 1990). Scavengers on animal products or remains that occasionally prey on other insects are especially common in the Tineoidea, which also contains several obligately predatory species (Table 1). Since members of the basal group of Lepidoptera, the Micropterigidae, are plant and detritus feeders, it is unclear in these instances whether scavenging on detritus and dead insects is a precursor to the evolution of predatory behavior on groups such as Homoptera, or vice versa. Both feeding strategies may have arisen independently from phytophagy, although on intuitive grounds at least, this seems less parsimonious.

Lichen feeding is typical among the Liptenini in the Lycaenidae, and Balduf (1938) argued that lichen feeding may have been an important precursor to the homopterophagy found in the closely related Miletinae. This proposal awaits phylogenetic investigation. Lichen feeding and/or mycophagy have been recorded among the Hepialidae, Tineidae, Psychidae, Oecophoridae, Cosmopterigidae, Scythrididae, Pyralidae, Noctuidae, and Arctiidae (Common 1990, Powell et al. 1995), and, with one or two exceptions, these groups also contain entomophagous species. However, these families are also numerically large, and thus, again, further phylogenetic work will be necessary before we understand the relationship between lichenivory/fungivory and carnivory.

Finally, a clear relationship exists between larval associations with ants and all forms of aphytophagy in the Lycaenidae (Cottrell 1984), as is discussed at greater length below.

Phylogenetic distribution of prey. The great majority of carnivorous Lepidoptera feed on other arthropods as caterpillars. A striking exception can be found in the adults of the noctuid "vampire moth," *Calyptra eustrigata* Hampson, which have piercing mouthparts and suck the blood of ungulates. A number of other species are phoretic upon, or feed on the feces of vertebrate species, including *Cryptoces choloepi* Dyar, the "sloth moth," which rides on the backs of sloths, hopping off to oviposit on their feces (Waage & Montgomery 1976, Davis et al. 1986). However, in contrast to orders such as Diptera and Hymenoptera, no species of Lepidoptera have been described that can inject venom or otherwise paralyze their prey.

Entomophagous Lepidoptera are largely specialized to feed on Homoptera (Table 1). Within the Homoptera, a wide variety of taxa are sampled, but the largely sessile, colonial and soft-bodied families of the Sternorrhyncha (which includes the psyllids, aphids, scale insects and mealybugs) are preferred to the hopping insects of the Auchenorrhyncha. Of the 112 homopterophagous species in Table 1, 83 (74%) feed on Sternorrhyncha. A notable exception to this general pattern is found among the Epipyropidae and Cyclotornidae. Most of the larvae of these taxa are parasitic, and tend to be associated with Auchenorrhyncha, especially the Fulgoridea.

Of the some 130 obligately predatory or parasitic moths listed in Table 1, only 9 are clearly documented to consume ants during at least some portion of their life cycle (although another 8 are suspected to be myrmecophagous, and many more species in the genera *Cyclotorna*, *Niphopyralis* and *Hypophrictis* may also feed on ants). Five species have been noted to feed on insect and spider eggs, and 15 ambush small insects. In the butterfly family Lycaenidae, myrmecophagy is considerably more common, with at least 55 species (68%) of the 81 listed in Tables 2 and 3 feeding on ant regurgitations or ant brood during at least some portion of their life cycle. As many as 34 species (42%) have been recorded feeding on Homoptera, and again, the majority of these are on members of the Sternorrhyncha (the percentages add to 110% because some species are both homopterophagous and myrmecophagous).

Degree of specialization. In many cases, we still know relatively little about the diet breadth of predatory species because prey are not always identified, with many of the homopteran species noted simply as "scales." However, sufficient examples exist to indicate that predatory Lepidoptera, like their herbivorous counterparts, vary considerably in the breadth of their trophic niche: some are specialists with respect to the taxa they attack, whereas others are generalists. Within the Noctuidae, apart from a species that feeds on insects trapped by pitcher plants (*Eublemma radda* Swinhoe), the entire genus *Eublemma* is carnivorous on scale insects. *Eublemma amabilis* Moore in India feeds only on *Kerria (Laccifer)*, whereas *Eublemma scitula* Rambur feeds on *Kerria (Laccifer)*, *Anomalococcus*, *Lecanium*, *Ceroplastes*, and *Pulvinaria* (Glover & Negi 1935, Hinton 1981). Within the Lycaenidae, females of the aphidophagous species, *Taraka hamada* Druce, lay eggs in response to bamboo grass infested by their customary woolly aphid prey, *Ceratovacuna* *japonica* Takahashi but ignore bamboo grass infested by an alternative aphid, *Melanaphis bambusae* Fullaway (Pierce, unpubl. data).

In general, myrmecophages are highly specialized with respect to their hosts. For example, although species of European *Maculinea* in the Lycaenoidea can be adopted into the nests of a number of ant species, their survival is host specific (Thomas et al. 1989). In a complex interaction involving a miletine butterfly, *Miletus biggsii* Distant, that feeds on aphids and coccids, the females are thought to use ants (a species in the genus *Dolichoderus*) as cues in oviposition, so that in effect, the ants indirectly select the species of homopteran prey (Maschwitz et al. 1988).

Myrmecophagy in Lepidoptera other than Lycaenidae. In addition to the lycaenids (discussed below), species from several genera of moths consume ants, and again we see an intrageneric association of predation with other forms of aphytophagy. The tineid genus *Hypophrictis* contains about 25 species in the Old World tropics, many of which may be myrmecophagous (Robinson et al. 1994). The life histories of only two species have been documented: *Hypophrictis dolichoderella* Roepke feeds on the brood of the ant *Dolichoderus bituberculatus* Mayr (Robinson et al. 1994), while the larvae of *H. saprophaga* Diakinoff are scavengers in *Bombus* nests in Sumatra (Diakonoff 1948). The larvae of these species live in flattened cases, which may serve to protect them against prey. In the Pyralidae (Wurthiinae), Robinson et al. (1994) speculate that all 28 species of the Indo-Australian genus *Niphopyralis* are myrmecophagous. The larvae of *Niphopyralis aurivillii* Kemner appear to mimic ant recognition signals, which gains them favorable acceptance in nests of *Polyrachis bicolor* Fr. Smith, where they feed on the brood (Kemner 1923). The larvae of *Niphopyralis myrmecophila* Roepke consume the brood of weaver ants, *Oecophylla smaragdina* Fabr. (Roepke 1916), in Java.

The most specialized myrmecophages are found among the Australian endemic family Cyclotornidae, exemplified by *Cyclotorna monocentra* Meyr. The larvae of these moths begin life as parasites of leaf-hoppers in the Cicadellidae, and then move to the nests of meat ants, *Iridomyrmex purpureus* Smith, where they complete their development by feeding on the brood. Dodd (1912) observed that females of this species lay large numbers of eggs near the trails of ants attending the leaf-hoppers. The first instar larva spins a pad of silk on the abdomen of the host beneath the wings, with a small sac at the anterior end to protect the larval head. Once the larva leaves the leaf-hopper, it builds an oval, flat cocoon where it molts into a broad, dorsoventrally flattened larva with a small head that can retract into the prothorax. It adopts a particular posture when encountered by a meat ant, raising the anterior half of the body and curling its posterior over its back to expose the anus. Following inspection, a meat ant will carry the larva into the nest, where it becomes a predator on the ant brood. In the nest, the larva continues to produce an anal secretion that is attractive to the ants. Its behavior is remarkably convergent with that of certain species of staphylinid beetles, whose larvae have specialized exocrine glands to ensure appeasement and adoption by the ants that they parasitize (Holldobler 1971). Once the larva has completed development, which may take weeks or possibly months, it emerges from the ant nest, and spins its cocoon in a protected spot nearby (Common 1990). In addition to *Cyclotorna monocentra*, the larvae of *C. egena* Meyr. have been reared in South Australia from larvae associated with *Eriococcus* scale insects on *Eucalyptus*, and it seems likely that additional species will share aspects of this unusual life history.

In the Miletinae, one species, *Allotinus apries* Fruhstorfer, appears to have a similarly complex life history. The first instar larva of this species feeds on coccids tended by ants in the genus *Myrmicaria*. The second instar has unusual lateral thoracic phlanges that are thought to be involved in eliciting the ants to pick up the larva and carry it into the brood chamber, where it feeds on ant brood and/or regurgitations until pupation (Maschwitz et al. 1988).

Ambush predators. The only ambush predators known among the Lepidoptera are Hawaiian members of the geometrid genus *Eupithecia* (Montgomery 1982). The genus *Eupithecia* is found in every faunal region, and the larvae of most *Eupithecia* species are flower or seed feeders. However, 15 species of *Eupithecia* found in Hawaii consume only live-caught insects and spiders. The "inchworm" caterpillars of these species, such as *Eupithecia orichloris* Meyr., perch on the edges of leaves and plant stems, waiting for prey. When a small insect touches the posterior abdomen of the caterpillar, within an instant (estimated at 1/12th of a second), it loops backwards and seizes the prey with its thoracic legs. It rights itself again to consume its prey. Montgomery (1982) suggests that this unique feeding specialization arose in the Hawaiian fauna in part because of the historical lack of entomophagous insect groups there such as ants, mantids, mantispids and ambush bugs (Zimmerman 1948). Moreover, like many members of the Lycaenidae (described below), the fact that most of the phytophagous members of *Eupithecia* prefer the nitrogen-rich parts of their host plants, such as flowers, pollen and seed pods, may have predisposed them physiologically to a concentrated protein diet.

Adaptations for consuming food other than plants. Aphytophagy in all its forms requires considerable specialization. Feeding on honeydew sources requires an ability to appease ants that are in competition for those same resources (Malicky 1970, DeVries & Baker 1989). Consumption of homopterans requires not only the ability to appease ants that may be tending the homopterans, but adaptations for finding homopteran prey, some of which are both patchy and ephemeral in their distributions. Feeding on ants requires extreme chemical and morphological specialization to find and penetrate ant nests (Thomas et al. 1989, 1993, Elmes et al. 1991a, 1991b, 1994, Thomas & Wardlaw 1992, DeVries et al. 1993). Lepidoptera consuming either Homoptera or ants must have the appropriate digestive physiology to develop upon only one or two prey types (e.g., Stanley-Samuelson et al. 1990, Dadd 1983). Those caterpillars that feed on ant regurgitations must not only be able to penetrate the ant nest by means of chemical camouflage (as in the genus *Maculinea*) or brute force (as in the genus *Liphyra*), but they must also be able to mimic the appropriate behavioral cues to solicit regurgitations from their host ants (e.g., Holldobler 1971).

Larvae of many of the species listed in Tables 1, 2 & 3 protect themselves in similar ways, suggesting that trophic convergence can result in concomitant defensive convergence. The most common behavior is to spin a silken web that functions as a shelter while the larva feeds on homopteran prey. For example, the larvae of both *Taraka hamada* (Lycaenidae) and *Oedematopoda semirubra* Meyr. (Heliodinidae) feed on the woolly aphid, *Ceratovacuna japonica* in Japan, and the larvae of both species weave silken shelters which protect them against the soldier caste produced by these aphids. Some species act as wolves in sheeps' clothing by accumulating wax and/or other homopteran camouflage which they carry on their backs. Whether homopterophagous lepidopterans can respond to the alarm pheromones and/or other chemical signals of their homopteran prey remains to be demonstrated.

The adults of many species of homopterophagous Lycaenidae have unusually long and sclerotized legs and abdomens, which may protect them against attacks by ants when ovipositing near their homopteran prey (e.g., Cottrell 1984, Kitching 1987, Maschwitz et al. 1988). It is widely thought that these adults may also secrete volatile compounds that protect them against ant attacks, although none have as yet been identified. Finally, the adults of species that eclose within their host ants' nests are often cloaked in deciduous scales that aid them in safely exiting from the nest (e.g., Dodd 1912, Johnson & Valentine 1986).

The larvae of myrmecophilous lycaenids are well known for possessing unusually thick cuticles (Malicky 1969, 1970), although this can vary among species (Thomas et al. 1991). Most are chemically camouflaged to gain favorable recognition by their host ants (Henning 1983), although species such as *Liphyra brassolis* Westw. are defended by their tank-like morphology (Johnson & Valentine 1986). Chemically camouflaged species have specialized exocrine glands that secrete substances that mimic ant recognition signals (Malicky 1969, Cottrell 1984). They also can mimic ants behaviorally, possibly even imitating host ant acoustical communication signals (DeVries et al. 1993). Females of some species use ants and/or homopterans as cues in oviposition (Atsatt 1981, Pierce & Elgar 1985, Maschwitz et al. 1985).

Predatory Lepidoptera often are unusually variable in their development. Some species vary greatly in time taken to reach maturity (Henning 1984, Common 1990). Others vary with respect to the final adult size (Banno 1990). Some lay thousands of eggs that hatch over several months, thereby providing a wide time window for larvae to find suitable hosts (Kirkpatrick 1947). Others can withstand long periods of starvation or low moisture conditions (Hinton 1981, Banno 1990, Thomas & Wardlaw 1992). Presumably these are developmental responses to specializing on host distribution and phenology (e.g., Elmes et al. 1991b). Carnivorous species may also be physiologically better able to withstand periods of starvation and/or low moisture than their phytophagous relatives (Banno 1990).

Among the Lycaenidae, many species have been recorded to feed on the secretions of extra-floral nectaries (e.g., DeVries & Baker 1989). This behavior may enable larvae to withstand periods of time when food (either foliage or prey) is in short supply. The adults of homopterophagous butterflies often spend long hours feeding on the honeydew of their prey (Fukuda et al. 1984, Maschwitz et al. 1988, Banno 1990), and again, this behavior may enable adults to live for considerably longer periods, perhaps allowing them to wait until the density of their intended prey is appropriate for oviposition.

Possible insights from cannibalism. Many species of Lepidoptera are cannibalistic both in the laboratory and the field (Fox 1975, Polis 1981, Schweitzer 1979a, 1979b). In particular, pyralids and noctuids demonstrate numerous instances of cannibalism and incidental predatory behavior (Table 1, see Balduf 1938). Dethier (1937, 1939) found that different species vary with respect to conditions eliciting cannibalism, but that hunger, crowding and thirst are prime factors in influencing this behavior. Members of the Lycaenidae are particularly well-known for cannibalistic tendencies (Mattson 1980), and the question naturally arises as to whether factors giving rise to cannibalistic behavior also give rise to predatory behavior.

Diet breadth of phytophagous species may be associated with the likelihood of occasional cannibalism. In his discussion of cannibalism in the noctuid tribe Lithophanini, Schweitzer (1979b) found that of the 8 non-cannibalistic genera, 9 (50%) of the 18 species were polyphagous.

However, of the 6 cannibalistic genera, 11 (73%) of the 15 species were polyphagous, three were intermediate, and only one was restricted in its diet. He suggested from these data that a polyphagous diet may predispose a species to cannibalism (or that a restricted diet may somehow inhibit a species from expressing this behavior), although firm conclusions are again not possible without a phylogeny for the group.

Experimental studies of cannibalism by other noctuid species have found cannibalism rates to increase with a decline in food quality. Al-Zubaidi & Capinera (1983) found a negative correlation between percent cannibalism and foliar nitrogen content of host plants (sugarbeet) that had been treated with different amounts of fertilizer. Similarly, Raffa (1987) showed that larvae of the fall armyworm, *Spodoptera frugiperda* J. E. Smith, were more likely to be cannibalistic when reared on a less preferred host, red kidney bean seedlings, than on their preferred diet of corn seedlings, and that this higher degree of cannibalism helped them to compensate digestively for feeding on the less suitable host. Joyner & Gould (1985) demonstrated nutritional benefits to cannibalism by *Heliothis zea* Boddie under low moisture conditions.

Although much is known about factors governing insect feeding (e.g., Gelperin 1971, Bernays & Chapman 1974, Bernays 1988, 1989, Bernays & Graham 1989, Simpson & Bernays 1983, Simpson et al. 1988), little of this work has focused on cannibalistic feeding behaviors. Dethier (1939) found that larvae of *Estigmene acrea* Drury and *Isia isabella* J. E. Smith (Arctiidae) were stimulated to cannibalize conspecifics whose tissues were exposed by having been crushed or cut open. Heinig (1989) showed that the emptiness of the gut, as well as deficiencies in water, ions, and amino acids, played a role in eliciting cannibalism in the noctuid species *Agrotis segetum* Denis & Schiff. and *Mamestra brassicae* (L.). In particular, he found that levels of trehalose in the haemolymph were particularly important in predicting cannibalistic behavior in *M. brassicae*. Other factors, such as larval density (Breden & Chippendale 1989), time of fasting (Abdel-Salam & El-Lakwah 1973), age and larval size (Semlitsch & West 1988, Dial & Adler 1990), genetic predispositions (Richter 1990) and even parasitism (Dindo & Cesari 1985) can influence rates of cannibalism.

Several studies of cannibalism have investigated the potential difficulties of being restricted to carnivorous diets. Dethier (1939) concluded that both *Estigmene acrea* and *Isea isabella* could meet all their dietary requirements by cannibalism. Tripathi & Singh (1990) found that development of *Heliothis armigera* (Hubner) was possible only when larvae were given conspecific prey, and not when they were given larvae of different species as prey. Bernays and Cornelius (1989) found that generalist caterpillar prey were more palatable than specialists to the generalist predator, *Iridomyrmex humilis* Mayr. In related research, Stanley-Samuelson et al. (1990) investigated the nutritional challenges posed by diets that consist entirely of ant larvae and pupae, with particular interest in the acquisition of polyunsaturated fatty acids that are usually only available from eating plants. They found that the fatty acid composition of fly parasites that feed entirely on ants closely matched those of their ant prey.

Most physiological studies of cannibalism have focused on the possible nutritional benefits to be gained from this behavior in terms of growth and development. Bogner and Eisner (1991, 1992) added an interesting twist to this approach when they demonstrated that larvae of the arctiid moth, *Utetheisa ornatrix* L., are more likely to cannibalize eggs and pupae that are rich in pyrrolizidine alkaloids (PA) than those that are free of PAs. The PAs themselves are powerful phagostimulants for the larvae of this species. The moths sequester PAs for protection against predation, and they usually acquire these substances from their host plants. It is reasonable to postulate that procurement of additional defensive secondary compounds such as PAs may represent a more general, hitherto unappreciated selective mechanism favoring cannibalism in chemically protected species. This would depend, however, on the nature of defense in these species. It might be unlikely to play a strong role, for example, among species that advertise their unpalatability through aposematic displays, since the relative number of distasteful models is crucial in maintaining effective defense in these species.

II. CARNIVORY IN THE LYCAENIDAE

A possible preadaptation for the evolution of carnivory in the Lycaenidae is the close association that the caterpillars of many species have with ants (Cottrell 1984, Pierce 1987, Fiedler 1991, DeVries 1991a). These associations can be mutualistic or parasitic, and range from loose interactions in which caterpillars are not tended but not attacked by ants, to those in which the caterpillars are occasionally tended by ants (often by many species), to yet others in which caterpillars are obligately dependent upon a single species of host ant for food or defense. Typically, the caterpillars of mutualistic species produce nutritious secretions of sugars and amino acids for ants in exchange for protection against insect predators (e.g., Pierce & Easteal 1986, Pierce et al. 1987, DeVries 1988, 1991, Fiedler & Maschwitz 1988, 1989a). In order to produce these secretions, caterpillars must feed on high quality food sources. For example, in the case of the ant-associated lycaenid, *Jalmenus evagoras* Don., larvae feeding on nitrogen-enriched plants were more attractive to attendant ants and had greater survivorship in the field than larvae on nitrogen-poor controls, and females preferred to lay eggs on the higher quality plants (Baylis & Pierce 1991). Phytophagous lycaenid larvae of many species have a predilection for nitrogen-rich parts of plants such as flowers and terminal foliage, and also frequently exhibit cannibalistic behavior (Mattson 1980).

A variety of larval glands are involved in maintaining lycaenid/ant associations, and these have been reviewed in some detail (Cottrell 1984, Malicky 1969, Downey & Allyn 1973, 1979, Kitching & Luke 1985, Tautz & Fiedler 1994). Three of these glands appear to be of central importance, and have been systematically examined in many species. These are: (1) the pore cupola organs (PCOs), single-celled epidermal glands found in the epidermis, and thought to secrete substances that appease and attract ants; (2) the dorsal nectary organ (DNO), a large secretory organ located on the seventh abdominal segment, which, upon solicitation, secretes a sweet and nutritious reward for ants; and (3) the tentacular organs (TOs), eversible, finger-like projections that flank the DNO on the eighth abdominal segment and appear to secrete volatile substances. The exact function of the TOs is still not entirely clear, although they tend to be everted under conditions of danger or alarm when a larva would be most likely to signal to its attendant ants (Axen & Leimar 1993, Axen pers. comm.). All lycaenid larvae that have been examined possess PCOs; many species have a DNO; others have TOs; and others have both a DNO and TOs.

Of the approximately 1,000 species of lycaenids for which full life histories have been described (review in Fiedler 1991), about 80 have been directly observed to feed on homopterans, honeydew, ants or ant regurgitations, or inferred to feed on ants or ant regurgitations because they spend the entire larval period inside ant nests without other apparent food sources (Tables 2 & 3). Because of incomplete information, this number represents only a fraction of the total number that are predatory (including, for example, all of the Miletinae) but whose life histories are as yet unknown. In some genera, such as *Maculinea,* all members of the genus feed on plants in the early instars, and then on ant and/or ant regurgitations in later instars, and all the ones that have been studied are species-specific with respect to ants hosts (Thomas et al. 1989). In others, such as *Arhopala* or *Spindasis,* only one or two species in an otherwise herbivorous genus feed on ants, ant regurgitations and/or honeydew (K. Dunn pers. comm., Fukuda et al. 1984).

Lycaenids other than Miletinae. Predation in lycaenid taxa other than Miletinae consists largely of myrmecophagous species whose larvae eat ants or ant regurgitations (Table 2). Only a few records exist of non-miletines that feed on Homoptera. However, these records are from species in tribes in two different subfamilies, and each is likely to represent an independent evolution of homopterophagy. Within the subfamily Lycaeninae, larvae of *Shirozua jonasi* Janson (Theclini) feed on aphids in addition to regurgitations from attendant ants, *Camponotus japonicus* Mayr (Fukuda et al. 1984, but see Yamaguchi 1988), and larvae of *Chilades lajus* Cr. (Polyommatini) have been observed to eat aphids (Agarwala & Saha 1984). In the subfamily Riodininae, *Setabis lagus* Butler is known to consume scale insects (DeVries et al. 1992).

Of the species that feed on ants, the habit of feeding on ant regurgitations either instead of, or in addition to, feeding on the ant brood itself also appears in disparate groups. Species of *Spindasis* (Aphnaeini), *Shirozua* (Theclini), and *Niphanda, Maculinea* and possibly *Anthene* (Polyommatini) feed by trophallaxis, as does *Audre aurina* Hewitson among the Riodininae (Table 2). *Acrodipsas* (Theclini) in Australia appears to be an exclusively myrmecophagous genus, whereas species in both *Lepidopchrysops* in Africa and *Maculinea* in the Palearctic (Polyommatini) are phyto-predatory in the sense that they begin life on specific host plant taxa, but spend their later instar(s) as predators in ant nests. *Lepidochysops* has over 100 species, but details of the life histories of only a handful of these have been described (Cottrell 1984, Table 2). All are thought to parasitize species of *Camponotus* ants in the third and fourth instars (Cripps 1947, Clark & Dickson 1971, Henning 1983).

Myrmecophagy in the genus *Maculinea*. The biology of the large blue, *Maculinea arion* Schiff. has long been of interest to lepidopterists (e.g., Frohawk 1906, 1916, Chapman 1916a, 1916b), but advances in our understanding of the ecology of the species of this genus have only come in the past ten years. Jeremy Thomas, Graham Elmes and their colleagues have been systematically identifying factors that influence the development, survival and reproductive success of different species of *Maculinea,* and have used these variables, measured in the field, to construct models that predict their population dynamics (Thomas 1981, 1984, Thomas et al. 1989, 1991, 1993, Thomas & Elmes 1993, Thomas & Wardlaw 1990, 1992, Elmes & Thomas 1985, 1992, Elmes & Wardlaw 1982, 1983, Elmes et al. 1991a, 1991b, 1994, Hochberg et al. 1992, 1994, DeVries et al. 1993).

All five species of European *Maculinea* (*arion, teleius* Bergs., *nausithous* Bergs., *alcon* Schiff. and *rebeli* Hirschke) are univoltine, and lay their eggs on flower heads of one or two plant species (Elmes & Thomas 1987), which are the hosts for the developing larvae until they reach the third instar, two or three weeks after hatching. At this point, they undergo a dramatic life history change—the final instar occurs in the nests of host ants, where larvae obtain more than 90% of their ultimate biomass by feeding on the ant brood, trophic eggs, prey, or regurgitations from their host ants. The exact nature of the food consumed varies depending upon the species involved (Elmes et al. 1991a, 1991b, Thomas & Wardlaw 1992).

Species of *Maculinea* live in highly restricted populations which are particularly sensitive to environmental perturbations, and the extinction of British populations of *Maculinea arion* has served as a model invertebrate system for conservation biologists (Thomas 1983). Key variables that have been shown to affect mortality in ant nests include: the species of ant adopting the caterpillars (Thomas et al. 1989); the condition of the host ant colony, such as its size, and whether or not it contains a queen (Elmes & Wardlaw 1982, 1983, Thomas & Wardlaw 1990); as well as the presence or absence of specialized parasites (Thomas & Elmes 1993).

By examining no less than 994 host ant nests, Thomas et al. (1989) firmly established that, although larvae of different *Maculinea* species will readily be adopted into the nests of a number of different species of *Myrmica* ants, each species of *Maculinea* survives well only in the nests of one particular ant partner (Table 2). This discovery was important from both an ecological and conservation point of view because it demonstrated how remarkably narrow the ecological niche is for species of *Maculinea*—not only do the larvae of each species require appropriate host plants to begin their development, but they also require the appropriate host ant species in order to survive. Habitats that appear to be suitable because they contain host plants and colonies of *Myrmica* are not necessarily acceptable unless they contain the correct species of *Myrmica*.

The life histories of two species of *Maculinea* found in Japan, *M. teleius* and *M. arionides* Staud., are not as well studied as their European counterparts. However, one distinctive facet of the biology of these species is that, in addition to parasitizing colonies of the ant *Myrmica ruginodis* Nylander, as in Europe, both *M. teleius* and *M. arionides* in Japan enter and survive successfully in nests of the ant *Aphaenogaster japonica* Forel (Fukuda et al. 1984, Yamaguchi 1988).

Given the high degree of host specificity involved in survival, it is surprising that females of each species of *Maculinea* do not generally appear to use ants as cues in laying eggs. Although some phytophagous species of Lycaenidae lay eggs in response to the presence of associated ant taxa (e.g., Atsatt 1981b, Pierce & Elgar 1985, Jordano et al. 1992), females of several species of *Maculinea*, including *M. arion* and *M. teleius*, do not respond to the presence of appropriate *Myrmica* colonies (Thomas 1977, 1984a, Elmes & Thomas 1987, van der Heijden et al. 1995). However, the density of females of *Maculinea nausithous* is correlated with the nest density of its host ant, *Myrmica rubra* L., as is its number of ovipositions. Thus, *M. nausithous* has behavioral mechanisms, perhaps including low vagility and fidelity to a particular habitat, that insure appropriate ant association by ovipositing females (van der Heijden et al. 1995).

Maculinea species have at least two strategies for parasitizing ant colonies. Most of the species, including *Maculinea arion*, are predators that feed directly on the ant brood. They forage in an adaptive manner, selecting the largest larvae and prepupae first, and sparing the eggs and younger brood that are still developing and will presumably provide more profitable food later on (Thomas & Wardlaw 1992). In contrast, two species, *Maculinea rebeli* and *M. alcon*, do not eat the ants themselves, but feed instead on regurgitations obtained through trophallaxis with their host ants (Elmes & Thomas 1987, Elmes et al. 1991). Thomas and Wardlaw (1992) proposed that feeding on regurgitations represents an evolutionarily derived condition within the genus, with simple predation representing the ancestral state.

Predation in the Miletinae. All the known members of the lycaenid subfamily Miletinae are aphytophagous, and the diversity of different feeding strategies is greatest in this group (Corbet & Pendlebury 1978, Cottrell 1984, Maschwitz et al. 1988). Much of our knowledge of the ecology of the Miletinae comes from recent work on South East Asian taxa, particularly *Logania* and the species-rich genera *Miletus* and *Allotinus*, by Ulrich Maschwitz, Konrad Fiedler and their colleagues (Maschwitz et al. 1985a, 1985b, Maschwitz et al. 1988, Fiedler 1992, 1993, Fiedler & Maschwitz 1989, see also Kitching 1987, Banno 1990). We now have life history data for about 30% of the approximately 120 species of miletines (Table 3). Unlike other lycaenid subfamilies, whose predatory members feed primarily on ants, most of the miletines are specialized to feed on homopterans. Homoptera commonly taken by miletine larvae include coccids, jassids, psyllids, membracids and aphids, particularly those in the closely related aphid families Hormaphididae and Pemphigidae (Table 2).

Maschwitz et al. (1988) proposed that feeding on Auchenorrhyncha is a derived condition with respect to preying on the Sternorrhyncha. They suggested that species such as *Logania malayica* Distant represent the ancestral pattern, feeding primarily on ant-attended aphids, whereas species of *Miletus* and *Allotinus* show greater feeding specializations. They identified three derived strategies among the latter taxa: (1) feeding on a broad spectrum of homopteran prey, and possibly using ants as cues in finding these homopterans (e.g., *Miletus biggsii*); (2) feeding on ants or ant regurgitations as a form of kleptoparasitism (e.g., *Allotinus apries*); and (3) feeding on members of the suborder Auchenorrhyncha in addition to or as an alternative to Stennorrhyncha (e.g., *Allotinus subviolaceus* C. & R. Felder).

III. THE EVOLUTION OF CARNIVORY

Although several patterns emerge from the distribution of carnivory in the Lepidoptera and from the limited information we have on the life histories of carnivorous species, we can make few strong inferences about the evolution of predatory behavior. While considerable advances have been made in recent years in reconstructing the phylogeny of Lepidoptera, particularly basal groups, we are handicapped in any such analysis by our lack of reliable phylogenies in many cases, and this discussion must accordingly start with both a caveat and an exhortation: (1) that the following conclusions are inevitably tentative; and (2) that generating phylogenies for these groups should be a high priority. Not only will phylogenetic analysis confirm or reject evolutionary-transition hypotheses such as those of Thomas and Wardlaw (1989) on the shift from myrmecophagy to kleptoparasitic trophallaxis, or of Maschwitz et al. (1988) on the shifts in prey niche of species of *Miletus* and *Allotinus*, but it also will throw light on a number of other evolutionary and ecological issues. For example, I noted earlier the apparent phylogenetic clustering of taxa that are carnivores, scavengers, and/or lichen feeders. In physiological terms, this is not surprising, because these lifestyles probably make similar demands on, for example, aspects of foraging and digestion. Phylogenetic information, however, will determine whether there is any consistent polarity to shifts between them. Does scavenging and/or fungivory or lichen feeding give rise to predation? Is scavenging typically an intermediate lifestyle between phytophagy and predation? Is predatory behavior more likely to evolve in taxa prone to cannibalism and the kind of incidental predation exhibited by many scavengers?

Predatory feeding strategies appear to have evolved repeatedly within the Lepidoptera. This we can surmise even without a full phylogeny. As discussed earlier, given that the Micropterigidae are likely to be the sister group to the rest of the Lepidoptera, and that these moths feed on detritus or plants, it is reasonable to conclude that predation is an evolutionarily derived state with respect to either detritus feeding or phytophagy in the Lepidoptera (Common 1990, Nielsen & Common 1992). Moreover, we see carnivory in groups that are so disparate taxonomically that parsimony would argue the trait to be homoplastic. Indeed, once we have reliable phylogenetic information, it is likely that the number of instances of the independent evolution of carnivory will be found to be greater rather than less than current estimates—in other words, existing carnivorous taxa that are regarded as monophyletic may well be found to be polyphyletic. After all, the convergent (or parallel) acquisition of carnivory in a number of related taxa might result in the concomitant acquisition of a set of lifestyle-associated traits which might well mislead the systematist into classifying them as constituting a monophyletic group.

The multiple origins of carnivory within the order suggest that (1) in teleological terms, carnivory is a relatively "desirable" life history trait, and (2) the physiological, behavioral and ecological hurdles that must be cleared in the course of the transition from herbivore to carnivore are easily overcome (indeed, most studies of lepidopteran feeding behavior are concerned with the hurdles faced by phytophagy, rather than the other way around.) Nevertheless, despite its desirability and the apparent ease with which carnivory can be acquired, lepidopteran predators are comparatively rare. This pattern is reflected generally throughout the insects (Mitter et al. 1988), although from the numbers of species involved, it is especially dramatic in the Lepidoptera. Weigmann et al. (1993) noted that carnivorous parasitism appears to have originated more than 60 times among insects, but in the 19 sister-group comparisons that they were able to perform with reliable phylogenies, they found no evidence that these insects with their highly specialized feeding habits diversify more rapidly than their more generalist relatives, including predators, saprophages and herbivores. If anything, their results indicate an opposite trend, and they suggested that one explanation for the great evolutionary success of phytophagous relative to carnivorous insect parasites is simply the trophic pyramid, with its differences in the quantity and availability of resources at each level.

Predatory behavior in the Lepidoptera seems to lack evolutionary staying power, suggesting that it is in some way evolutionarily unstable. This argument is analogous to the conundrum regarding the mysterious evolutionary disadvantage of asexuality—although it arises in evolution regularly, most instances are apparently recent, inasmuch as the taxonomic distribution of asexuality seldom creeps beyond the generic level. The same, broadly speaking, is true for predatory behavior in the Lepidoptera. There are numerous genera in which one or a few species are carnivorous while the others remain phytophagous. Given the assumption that carnivory is the derived state, we conclude that carnivory in these cases has arisen recently, after the origin of the genus.

There are a few notable exceptions to this pattern. The Epipyropidae and Cyclotornidae are small families which, perhaps significantly, both share the trait of parasitizing auchenorrhynchine Homoptera such as Fulgoroidea during some portion of their lifetimes. The Miletinae is a well-developed group, considered widely to have originated early on in the evolution of the Lycaenidae (Eliot 1973, Scott & Wright 1990), all of whose members are carnivorous, and whose phylogenetic depth goes well beyond the genus level. More detailed analysis, both phylogenetic and ecological, of the miletines and related taxa will help to determine why they have apparently succeeded where others have failed. Our analysis here, however, indicates a number of possible causes for the general failure of this evolutionary experiment.

It is for good evolutionary reasons that *Maculinea arion* has become the symbol of conservation in the United Kingdom. Because of the complexity (and specificity) of their life cycles, species of *Maculinea* are extremely sensitive to environmental perturbations. These perturbations are currently especially traumatic and rapid because they are human-caused; but, from an evolutionary viewpoint, life history "brittleness" in terms of overspecialization could also be costly in the long run. For example, *M. arion* is at best a rather inefficient predator. Whereas a single *Myrmica* nest of some 350 workers can accommodate only one carnivorous *Maculinea arion* larva, a similar sized nest can accommodate as many as six larva of the "cuckoo" species, *Maculinea rebeli,* which feeds on ant regurgitations (Thomas & Wardlaw 1992). Thomas & Wardlaw (1992) propose that feeding on regurgitations represents an evolutionarily derived condition within the genus, with simple predation representing the ancestral state. This hypothesis requires phylogenetic verification but, if we assume it to be correct, argues strongly that predation is evolutionarily unstable—so unstable in fact that it can readily be displaced by an alternative, ecologically complex lifestyle.

Maculinea illustrates well the problems of being a lepidopteran predator. Like other phytophages, Lepidoptera are entrenched not only in feeding on plants, but also in living on them (Southwood 1973). The evolutionary acquisition of carnivory, while representing a substantial diet shift, is rarely accompanied by a concomitant shift in habitat away from a plant-based existence. In essence, it often seems to involve the *addition* of a trophic level rather than the *replacement* of one. The simple case of this is *Maculinea,* where herbivory is retained in the early instars prior to the switch over to carnivory, but other predatory species, strictly carnivores, are also jointly plant- and prey-dependent. This is because of the nature of lepidopteran carnivory: with the single exception of the sit-and-wait geometrids in the genus *Eupithecia,* lepidopteran predators are sluggish browsers that are severely restricted in their ability to seek prey. This results in two strategies: (1) ant deception whereby the caterpillar induces its own import into an ant nest; and (2) oviposition on a plant populated by the prey species (usually Homoptera). Except for a few cases where caterpillars are myrmecophagous throughout their life cycles (e.g., *Liphyra brassolis*), both

TABLE 1. Moths that eat other insects as their primary food source. Moth species are grouped by family, following Common 1990, Nielsen & Common 1991, and Scoble 1992. Under feeding type: PRF = facultative predator, PRO = obligate predator, PA = parasite and/or parasitoid. Under food: homopteran taxa in Sternorrhyncha begin with S (Sal = Aleyrodoidea, Sap = Aphidoidea, Sc = Coccoidea, Sp = Psylloidea); homopteran taxa in Auchenorrhyncha begin with A (Acl = Cicadelloidea, Aci = Cicadoidea, Af = Fulgoroidea); F = ants (Formicidae).

Taxon	Type	Food	Notes	References
Tineoidea				
Tineidae				
Atticonviva sp.	PRO	F?	may consume ant brood	Busck 1935, Hinton 1951
Ereunetis miniuscula	PRO	Sc	*Icerya purchasi* and other scales	Leonard 1932
Hypophrictis dolichoderella	PRO	F	mature larvae form cases, eat brood of *Dolichoderus bituberculatus* and *Plagiolepis longipes*	Roepke 1925, Robinson et al. 1994
Hypophrictis (23 spp.)	PRO	F?	eat ant brood?	Robinson et al. 1994
Monopsis hemicitra	PRF	other	mantid egg masses	Fletcher 1920
Myrmecozela ochraceella	PRF	F?	may eat ant brood in *Formica* nests, scavengers in nests	Hinton 1951
Pringleophaga marioni	PRO	other	earthworms in captivity	French & Smith 1983, Scoble 1992
Tineola bisselliella	PRF	other	animal fibers, occasionally mites, conspecifics	Webster 1912, Illingworth 1917
Psychidae				
Ardiosteres moretonella	PRF	F?	scavenger in ant nests	Hinton 1951, Common 1990
A. dryophracta	PRF	F?	collected from "small tree ant nest"	Dodd in Common 1990
Iphierga macarista	PRF	F?	scavenger in *Iridomyrmex purpureus* nests	Hinton 1951, Common 1990
Cryptothelea (Platoeceticus) gloverii	PRF	Sc	*Pseudoaonidia duplex*	Plank & Cressman 1934, Clausen 1940
Gelechioidea				
Oecophoridae				
Stathmopoda arachnophthora	PRO	other	spider eggs	Clausen 1940
S. basiplectra	PRO	Sc	*Kerria (Laccifer)*	Imms & Chatterjee 1915, Beeson 1941, Hinton 1981
S. callichrysa	PRO	Sc	galls, mealybugs	Tillyard 1929, Hinton 1981, Common 1990
S. coccophanes	PRO	Sc	mealybugs	Tillyard 1929, Hinton 1981
S. conioma	PRO	Sc	coccids	Hinton 1981
S. cypris	PRO	Sc	*Kerria (Laccifer) lacca*	Fletcher 1933
S. melanochra	PRO	Sc	*Ceroplastes, Coccus baccatum, Eriococcus coriaceus, Icerya purchasi*	Hinton 1981, Common 1990, Fletcher 1933
S. oesteetis	PRO	Sc	*Kerria (Laccifer) decorella*	Gowdy 1917
S. ovigera	PRO	Sc	coccids	Fletcher 1920, Hinton 1981
S. theoris	PRO	Sc	*Kerria (Laccifer)*, coccids	Imms & Chatterjee 1915, Clausen 1940, Hinton 1981
Oedematopoda cypris	PRO	Sc	*Kerria (Laccifer) lacca*	Imms & Chatterjee 1915, Fletcher 1933, Hinton 1981
O. pyromyia	PRO	Sap	*Oregma* spp.	Fletcher 1933
O. semirubra	PRO	Sap	*Ceratovacuna japonica*	S. Aoki, pers. comm.

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
O. venusta	PRO	Sc	*Kerria (Laccifer) lacca*	Fletcher 1920, Hinton 1981
Cynarmostis vectigalis	PRO	Sc	*Eulecanium*	Silvestri 1943, Hinton 1981
Coleophoridae				
Batrachedra arenosella	PRO	Sc	*Poliaspis*, scale insects	Hudson 1928, Hinton 1981, Common 1990, Scoble 1992
B. myrmecophila	PRO	F	ant brood (*Polyrachis dives*)	Hinton 1951
B. silvatica	PRO	Sc	*Pseudococcus*	Fletcher 1921, Hudson 1928, Hinton 1981
Eustaintonia phragmatella	PRO	Sc	*Alcerda*	Silvestri 1943, Hinton 1981
Blastobasidae				
Blastobasis coccivorella	PRO	Sc	*Kermes*	Walsingham 1907, Glover 1933, Comstock in Clausen 1940, Hinton 1981
B. lecaniella	PRO	Sc	*Lecanium, Ceroplastes floridensis, Saissetia nigra, S. oleae, S. coffeae (hemisphaerica)*	Busck 1913, Bodkin 1917, Balduf 1939
B. thelymorpha	PRO	Sc	*Lac*	Stebbing 1910, Clausen 1940, Hinton 1981
B. transcripta	PRO	Sc	*Ripersia*	Fletcher 1920, Glover 1933, Clausen 1940
Holcocera iceryaella	PRO	Sc	*Lecanium persicae, Icerya purchassi, Saissetia oleae, Parthenolecanium (Eulecanium) persicae, Pseudococcus bakeri*	Dietz 1910, Essig 1916, Bassinger 1928, Clausen 1940, Hinton 1981
H. phenacocci	PRO	Sc	*Coccus (Phenacoccus) colemani*	Braun 1927, Hinton 1981
H. pulverea	PRO	Sc	*Kerria (Laccifer) lacca*	Misra & Gupta 1934, Glover 1933, Clausen 1940, Hinton 1981
Zenodochium coccivorella	PAo	Sc	*Kermes*	Glover 1933, Clausen 1940
Momphidae				
Coccidiphlia gerasimovi	PRO	Sc	*Sphaerolecanium (Eulecanium) prunastri*	Danilevskii 1950, Hinton 1981
C. ledereriella	PRO	Sc	*Trabutina, Pseudococcus*	Danilevskii 1950, Hinton 1981
Lacciferophaga yunnanea	PRO	Sc	scales	Zagulyaev & Din-si 1959, Hinton 1981
Cosmopterigidae				
Euclemensia bassettella	PRO	Sc	*Kermes galliformis, Kermes* spp.	Hollinger & Parks 1919, Clausen 1940
Limnoecia peranodes	PRO	Sc	*Saissetia* spp.	Fletcher 1920
Pyroderces bicincta	PRO	Sc	scales	Glover 1937, Beeson 1941, Hinton 1981
P. falcatella	PRO	Sc	*Kerria (Laccifer) lacca, K. (L.) lobata, K. (L.) albizziae, Ceroplastes (Lakshadia) communis, Dactylopius*	Norris 1931, Fletcher 1920, 1933, Glover 1937, Beeson 1941, Hinton 1981
P. gymnocentra	PRO	Sc	scales	Glover 1937, Beeson 1941, Hinton 1981
P. holoterma	PRO	Sc	scales	Glover 1937, Beeson 1941, Hinton 1981

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
P. philogeorgia	PRF	Sc	*Pseudococcus perniciosus, Coccus*	Meyrick 1933, Glover 1937, Beeson 1941, Hinton 1981
P. rileyi	PRO	S	*Icerya purchasi, Pulvinaria psidii*	Berger 1917, Hinton 1981
Gelechiidae				
Brachmia spp.	PRF	other	spider eggs, insect prey in spider webs	Meyrick 1912, Scoble 1992
Tortricoidea				
Tortricidae				
Tortrix callopista	PRO	Sc	*Strictococcus sjostedti*	Lamborn 1914, Clausen 1940, Hinton 1981
T. podana	PRO	other	*Eriophyes ribis* (gall-mite)	Mumford 1931
Russograptis spp.	PRO	Sc	coccids	Scoble 1992
Pammene isocampta	PRO	Sc	*Lecanium*	Ayyar 1929, Hinton 1981
Cnephasia spp.	PRO	Sc	*Pseudococcus*	Edwards et al. 1934, Hinton 1981
Coccothera spissana	PA	Sc	*Waxiella egbara* (*Ceroplastes egbarium*)	Bevis 1923, Clausen 1940
Zygaenoidea				
Epipyropidae				
Agamopsyche threnodes	PA	Af	*Perkinsiella saccharicida* and related species	Perkins 1905, Kato 1940, Common 1990
Epieurybrachys eurybrachidis	PA	Af	*Eurybrachys tomentosa, E. spinosa*	Fletcher 1920, Krishnamurti 1933, Clausen 1940
Epimesophantia dlabolai	PA	Af	*Mesophantia kanganica*	Fletcher 1939, Krishnamurti 1933, Krampl & Dlabola 1983
E. schawerdae	PA	Af	*Mesophantia kanganica*	Fletcher 1939, Krishnamurti 1933, Krampl & Dlabola 1983
Epipomponia nawai	PA	Af, Aci	*Tanna japonensis, Oncotympana maculaticollis, Meimuna opalifera, Macrosemia kareisana, Graptosaltria nigrofascata, Ricania japonica*	Nawa 1903, Kirkaldy 1903, Dyar 1904, Balduf 1938, Kato 1940, Ohgushi 1953
E. multipunctata group	PA	Af	*Laternaria lucifera*	Jordan 1928, Krampl & Dlabola 1983
E. elongata	PA	Af	*Laternaria lucifera*	Jordan 1928, Krampl & Dlabola 1983
Epiricania hagomoro	PA	Af	*Ricania japonica, Euricania ocellus, Dictyophara patruelis, Oliarus subnubilus*	Kato 1940
E. melanoleuca	PA	Af	*Pyrilla* sp.	Fletcher 1939
Fulgoraecia barberiana	PA	Af	*Metacalfa pruinosa, Hysteropterum auroreum, Theonia bullata, T. elliptica, Acalonia conica*	Kato 1940, Wilson & McPherson 1979
F. bowringi	PA	Af	*Laternaria candelaria* (waxy secretions)	Bowring 1876, Westwood 1876, Kato 1940
F. cerolestes	PA	Af	*Metaphaena cruenta, M. militarus*	Tams 1947
F. epityraea	PA	Af	*Ityraea nigrocincta patricia*	Sheven 1974
F. (*Epipyrops*) *fuliginosa*	PA	Acl	*Idiocerus niveosparsus, I. atkinsoni, I. clypealis* (waxy secretions)	Subramaniam 1922, Clausen 1940
F. (*E.*) *fulvipunctata*	PA	Af	*Rhinortha guttata*	Bell-Marley 1913
F. (*E.*) *poliographa*	PA	Af	*Eurybrachys tomentosa*	Ayyar 1929

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
Heteropsyche aenea	PA	Af	*Platybrachys* spp., *Scolypopa australis*	Rothschild 1906, Common 1990
H. doddi	PA	Af	*Dictyophora praeferrata*, *Olonia*, Flatidae	Rothschild 1906, Clausen 1940
H. dyscrita	PA	Af	Fulgoridae	Perkins 1905
H. melanochroma	PA	Af	*Scolypopa australis*	Perkins 1905, Common 1990
H. micromorpha	PA	Af	*Platybrachys* spp., *Scolypopa australis*	Rothschild 1906, Common 1990
H. poecilochroma	PA	Af	Fulgoridae	Perkins 1905
H. stenomorpha	PA	Af	*Platybrachys* spp., *Scolypopa australis*	Rothschild 1906, Common 1990
Paleopsyche melanias	PA	Acl	Cicadellidae	Kato 1940
Cyclotornidae				
Cyclotorna egena	PA	Sp, F	Psyllidae for first instar, then ants	Dodd 1912, Common 1990
C. monocentra	PA	Acl, F	*Iridomyrmex purpureus*	Dodd 1912, Clausen 1940, Common 1990
Cyclotorna spp.	PA	Sc, F, Acl	*Eriococcus coriaceus*, *Iridomyrmex purpureus*, Eurymelidae, ants	Common 1990
Pyraloidea				
Pyralidae				
Chalcoela pegasalis	PRF	other	larvae of vespid wasp, *Polistes annularis*	Ballou in Balduf 1939
Creobota coccophthora	PRO	Sc	*Eriococcus coriaceus*	Common 1990, Scoble 1992
Cryptoblabes gnidiella	PRF	Sal	*Aleurocanthus* spp. (also a plant feeder)	Clausen 1940
C. proleucella	PRO	Sc	*Coccus viridis*	Rutherford in Balduf 1939
Dicymolomia julianalis	PRF	other	eggs of *Thyridopteryx ephemeraeformis*, heads of *Typha*	Gahan 1909, Balduf 1938, Clausen 1940
Dipha (Conobathra) aphidovora (= Thiallela sp.)	PRO	Sap	*Ceratovacuna japonica*, *Pseudoregma bambucicola*, *P. alexanderi*	Lopez 1930, Takano 1941, Arakaki & Yoshiyasu 1988
Ephestia cautella	PRO	Sc	*Coccus*, *Tachardia lacca*, *Eublemma*, *Holcocera* spp.	Keuchenius 1915, Balduf 1939, but see Hinton 1981
Euzophera cocciphaga	PA	Sc	*Aspidoproctus xyliae*	Jordan 1926, Ayyar 1929, Clausen 1940
Laetilia coccidivora	PRO	Sc	*Icerya purchasi*, *Dactylopius* spp., *Trionymus*, *Pseudococcus* spp., *Eriococcus*, *Coccus hesperidum*, *Lecanium nigrofasciatum*, *Toumeyella liriodendri*, *Pulvinaria innumerabilis*, *P. psidii*, *Kermes* spp., Lepidoptera	Ayyar 1929, Berger 1917, Chaffin 1921, Comstock 1924, Douglas 1888, Felt 1933, Howard 1895, Parks 1919, van der Merwe 1921, Simanton 1916
L. obscura	PRO	Sc	*Saissetia hemisphaerica*	Blahutiak & Alayo Soto 1982
Macrotheca unipunctata	PRO	Sc	scales	Forbes 1923, Hinton 1981
Myelois grossipunctella	PRF	Sc	*Icerya* sp.	Ragonot 1893, Hinton 1981
Niphopyralis aurivillii	PRO	F	ant eggs and larvae (*Polyrachis bicolor*)	Kemner 1923, Robinson et al. 1994
N. chionesis	PRF	F?	scavenger in ant nests (*Oecophylla smaragdina*)	Common 1990

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
N. myrmecophila	PRO	F	ant brood (*Oecophylla smaragdina*)	Roepke 1916, Robinson et al. 1994
Niphopyralis (28 spp.)	PRO	F?	may all be myrmecophages	Robinson et al. 1994
Pachypodistes goeldii	PRF	F?	may eat brood of *Dolichoderus gibbosoanalis*, eats nest carton	Hagmann 1907, Hinton 1951
Phycita dentilinella	PA	Sc, other	scales, other insects, *Parasa lepida* (larvae and pupae), *Cricula trifenesetrata*	Ayyar 1929, Clausen 1940
Stenachroia myrmecophila	PRO	F?	may consume brood of *Crematogaster*	Turner 1912, Hinton 1951
Sthenobaea (*Stenauge*) *parasitus*	PA	other	*Automeris* and *Dirphia* (Saturniidae)	Jordan 1926, Clausen 1940, Scoble 1992
Titanoceros thermoptera	PRO	other	eggs of *Ochrogaster lunifer* (Thaumetopoeidae)	Common 1990
Tirathaba parasitica	PRF	other	dead insects, hepialid larvae	Common 1990, Scoble 1992
Vitula bodkini	PRO	Sc	*Saissetia oleae, S. nigra, S. coffeae* (*hemisphaerica*), *Ceroplastes floridensis*	Bodkin 1917
V. saissetiae	PRO	Sc	*Saissetia* sp.	Simanton 1916, Dyar 1929, Clausen 1940, Hinton 1981
V. toboga	PRO	Sc	*Saissetia oleae, S. nigra, S. coffeae* (*hemisphaerica*), *Ceroplastes floridensis*	Bodkin 1917
Geometroidea				
Geometridae				
Biston zonarius	PRF	other	larvae of ichneumonid parasitoids that emerged from conspecifics	Sorhagen 1899
Eupithecia craterias	PRO	other	small insects, spiders	Montgomery 1982
E. niphorias	PRO	other	small insects, spiders	Montgomery 1982
E. oblongata	PRO	Sap	aphids	Hawkins 1942
E. orichloris	PRO	other	small insects, spiders	Montgomery 1982
E. prasinombra	PRO	other	small insects, spiders	Montgomery 1982
E. rhodopyra	PRO	other	small insects, spiders	Montgomery 1982
E. scoriodes	PRO	other	small insects, spiders	Montgomery 1982
E. staurophragma	PRO	other	small insects, spiders	Montgomery 1982
Eupithecia (8 spp.)	PRO	other	small insects, spiders	Montgomery 1982
Noctuoidea				
Noctuidae				
Aglossa dimidiata	PRF	other	stored eggs of *Bombyx mori*	Nishikawa in Balduf 1939
Calymnia tapezena	PRF	other	forms rolled leaf hiding place and emerges to attack other insects	Sorhagen 1919, Gauckler 1911, Balduf 1939
Calyptra eustrigata	PA	other	blood of ungulates (adults have piercing mouthparts)	Common 1990
Catoblemma dubia	PRO	Sc	*Coccus hesperidum, Eriococcus coriaceus, Parthenolecanium, Saissetia oleae, Ceroplastes rubens*	Blumberg 1935, Flanders 1932, Common 1990
C. mesotaenia	PRO	Sc	*Eriococcus coriaceus*	Common 1990
C. sumbavensis	PRO	Sc	*Kerria* (*Laccifer*) *aurantica*	Jacobson 1913, Clausen 1940, Hinton 1981
Coccidophaga (*Erastria*) *scitula*	PRO	Sc	black olive scale and others	Rouzaud 1893, Balduf 1931
Eublemma amabilis	PRO	Sc	*Kerria* (*Laccifer*) *lacca, K.* (*L.*) *javanus*	Rouzaud 1893, Misra 1924, Balachowsky 1928, Misra et al. 1930, Mahdihassen 1934, Glover & Negi 1935, Miller 1933

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
E. coccophaga	PRO	Sc	*Coccus* spp., *Saissetia oleae*, esp. eggs	Douglas 1988, Balachowsky 1928, Clausen 1940, Froggatt 1922, Vosler 1919
E. communimacula	PRO	Sc	*Parthenolacanium (Lecanium) persicae, Sphaerolecanium (L.) prunastri*	Hampson 1910, Hinton 1981
E. costimacula	PRO	Sc	*Ferrisia virgata, Pseudococcus perniciosus, Coccus viridis, Strictococcus diversiseta, S. dimorphus*	Hampson 1910, Fiedler 1950, Hinton 1981, Ritchie 1926, Ritchie 1929, Gowdy 1915, Gowdy 1917
E. deserta	PRO	Sc	*Margarodes* spp.	Balachowsky 1929
E. dubia	PRO	Sc	scales	Froggatt 1910, Hinton 1981
E. gayneri	PRO	Sc	*Phenacoccus hirsutus*	Hall in Ayyar 1929, Hinton 1981
E. ochrochroa	PRO	Sc	*Stictococcus sjostedti*	Lamborn 1914, Hinton 1981
E. pulvinariae	PRO	Sc	scales	Hampson 1910, Hinton 1981
E. roseonivea	PRO	Sc	*Kerria (Laccifer) javanus*	Miller in Balduf 1939
E. rubra	PRO	Sc	*Coccus optimum, C. africanus*	Rouzaud 1893, Jacobson 1913, Balachowsky 1928, Clausen 1940
E. rufiplaga	PRO	Sc	scales	Ayyar 1929, Hinton 1981
E. scitula	PRO	Sc, Sal	*Parthenolecanium (Aspidiotus) orientalis, Saissetia oleae, Inglisia conchiformis, Megapulvinaria (Pulvinaria) maxima, M. (P.) psidii, Kerria (Laccifer) lacca, Anomalococcus indicus, Saessetia coffeae (hemisphaerica), Bodenmeimera racheli, Pseudococcus lilacinus, Ceroplastes rusci, C. actinoformis, C. lecanium, C. ceriferus, C. rubens, Ceroplastes (Lakshaida) communis, Coccus (Lecanium) cajani, Aleurodes africanus*	Misra 1924, Ayyar 1929, Panis 1974, Hinton 1981, Glover 1933, Widiez 1932, Gowdy 1917, Farquharson 1921, Bodenheimer 1924, Rousaud 1893, Douglas 1888, Mahdihassan 1925
E. trifasciata	PRO	Sc	*Phenacoccus hirsutus*	Fletcher 1919
E. versicolora	PRO	Sc	coccids	Jacobson 1913, Clausen 1940
E. virginalis	PRO	Sc	*Margarodes* spp.	Balachowsky 1928
E. vinotincta	PRO	Sc	scales, *Lecanium* spp.	Ayyar 1929, Hinton 1981
Cosmia trapezina	PRF	other	other Lepidoptera	Crawley 1983
Cosmia spp.	PRF	other	other Lepidoptera	Forbes 1954, Hinton 1981, Scoble 1992
Enargia spp.	PRF	other	other Lepidoptera	Forbes 1954, Schweitzer 1979
Erastria venustula	PRO	Sc	scales	Wolff & Krausse 1922, Hinton 1981
Eupsilia transversa	PRF	other	other Lepidoptera	Stokoe & Stovin 1948, South 1948, Schweitzer 1979
Heliothis dispaceus	PRF	other	*Pieris rapae* pupae	Huguenin 1914
Lithophane querquera	PRF	other	*Tenebrio* (in lab)	Schweitzger 1979
L. bethunei	PRF	other	*Malacosoma* pupae	Sanders & Dustan 1919, Schweitzer 1979
Nola innocua	PRF	Sap	kleptoparasite of gall aphids, *Nipponaphis distyliicola, Monzenia globuli*	Ito & Hattori 1982, 1983

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
N. sorghiella	PRF	other	*Chrysops* sp. eggs (tabanid fly)	Johnson & Hays 1973, Hinton 1981
Ozopteryx basalis	PRO	Sc	*Coccus* spp.	Hargreaves 1928
Selepta leucogonia	PRO	Sc	wine palm scale	Farquharson 1921, Hinton 1981
Senta maritima	PRF	other	eats conspecifics and braconid parasitoids emerging from conspecifics	Rangnow 1909

these strategies are plant-dependent because they entail either early-instar phytophagy, or oviposition and subsequent habitation on the host plant of the prey insect. Thus, the life cycles of predatory Lepidoptera are typically more complex in terms of the number of factors contributing to them than those of phytophagous Lepidoptera. Such complexity, as is apparently the case for *Maculinea,* can result in enhanced sensitivity to environmental perturbation because there is simply more that can go wrong. Perhaps such life cycle complexity is, over evolutionary time, correlated with a relatively high extinction rate (discussed below).

A second possible reason for the lack of evolutionary persistence of carnivory in the Lepidoptera may be related to phylogenetic constraints (*sensu* Gould & Lewontin 1979). The lepidopteran larva is a well designed plant-eating machine that apparently has been modified by evolution only to a minor extent in the course of the acquisition of predatory habits. The result is a somewhat limited predator. We see this in the range of prey choice of predatory Lepidoptera. They consume sedentary, poorly defended insects, and this has resulted in their specialization on the sternorrhynchine Homoptera such as aphids and coccids. In keeping with this view of historical constraint, it is not surprising that the only ambush predators that have evolved among the Lepidoptera, the *Eupithecia* of Hawaii, are "inchworm" geometrids, whose particular morphology enables them to rear up on their hind claspers and strike at passing prey. Species of Epipyropidae and Cyclotornidae whose first instar larvae parasitize auchenorrhynchine Homoptera also have unusual, hypermetamorphic larvae—the first instars have a tapered body plan, and can stand up on their claspers and wave their heads about in a leech-like fashion when seeking a new host. These then molt into a more customary, slug-like morphology in later instars.

Myrmecophagy, especially in the lycaenids, also may be largely an heirloom from the phytophagous past, in which lycaenids evolved the ability to interact with ants, usually in a mutualistic way. Once the wherewithal, such as specialized exocrine glands for ant appeasement

TABLE 2. Feeding specializations in the Lycaenidae, not including Miletinae. HO = Homoptera, AR = ant regurgitations, AB = ant brood; X = direct observation, V = inferred. In the Polyommatinae, an additional 32 species of *Lepidochrysops* are thought to feed on ant brood (see e.g., Clark & Dickson 1971).

Taxon	HO	AR	AB	References
Lycaeninae				
Aphaeini				
Aphnaeus adamsi		x		Callaghan 1993
Argyrocupha malagrida			v	Clark & Dickson 1971, Henning & Henning 1989
Axiocerses harpax		x		Jackson 1947, Larsen 1983, Ackery & Rajan 1990
A. (Chloroselas) umbrosa		x		Jackson 1937, Larsen 1991
Cigaritis (Apharitis) acamas		x	x	Larsen & Pittaway 1982
Oxychaeta dicksoni			x	Clark & Dickson 1971
Spindasis nyassae		x		Hinton 1951, Sevastopulo 1975
S. takanonis		x	x	Iwase 1955, Yamaguchi 1988
Trimenia argyroplaga			v	Clark & Dickson 1971
T. wallengrenii			v	Clark & Dickson 1971
Theclini				
Acrodipsas cuprea			x	Common & Waterhouse 1981
A. illidgei			x	Samson 1989
A. myrmecophila			x	Common & Waterhouse 1981
Arhopala wildei			x	Dunn, pers. comm.
Shirozua jonasi	x			Shirozu 1961, Fukuda et al. 1984, Yamaguchi 1988
Polyommatini				
Anthene levis		v		Jackson 1937, Hinton 1951
Athsanota ornata			x	Kielland 1990
Chilades lajus	x			Bell 1915, Agarwala & Saha 1984
Lepidochrysops ignota			x	Henning 1983
L. longifalces			x	Cottrell 1984
L. methymna			x	Cottrell 1965
L. niobe			x	Henning & Henning 1989
L. oreas			x	Claassens & Dickson 1980
L. patricia			x	Clark & Dickson 1971
L. pephredo			x	Pennington et al. 1978
L. phasma			x	Farquharson 1922, Chapman 1922
L. robertsoni			x	Claasens & Dickson 1980
L. trimeni			x	Clark & Dickson 1971
L. variabilis			x	Cottrell 1965
L. victoriae			x	Cripps 1947
Maculinea alcon		x	x	Thomas et al. 1989
M. arion			x	Chapman 1916a, 1916b, Thomas et al. 1989
M. arionides			x	Fukuda et al. 1984
M. nausithous			x	Thomas et al. 1989
M. rebeli		x	x	Thomas et al. 1989
M. teleius			x	Thomas et al. 1989, Fukuda et al. 1984
Niphanda fusca		x		Fukuda et al. 1984, Hama et al. 1989
Oboronia punctatus			x	Lamborn 1914
Riodininae				
Setabis lagus	x			DeVries et al. 1992
Audre aurina		x		DeVries pers. comm.

TABLE 3. Feeding specializations in the Miletinae. HD = honeydew, HO = Homoptera, AR = ant regurgitations, AB = ant brood; X = direct observation, V = inferred.

Taxon	HD	HO	AR	AB	References
Miletinae					
Miletini					
Spalgiti					
Feniseca tarquinius		x			Riley 1886, Edwards 1886, Scott 1986
Spalgis epius		x			Aitken 1894, Green 1902, Misra 1920, Cottrell 1984
S. lemolea		x			Lamborn 1914, Cottrell 1984
S. substrigata		x			Smith 1914
Taraka hamada	x	x			Banno 1990
Miletiti					
Allotinus apries		x		v	Maschwitz et al. 1988
A. davidis		x			Maschwitz et al. 1985
A. major		x			Kitching 1987
A. substrigosus		x			Maschwitz et al. 1988
A. subviolaceus		x			Maschwitz et al. 1988
A. unicolor	x	x			Maschwitz et al. 1985
Logania hampsoni	v	v	v		Parsons 1991
L. malayica	x	x	x		Maschwitz et al. 1988, Fiedler 1993
L. marmorata	x	x	v		Fiedler 1993
Megalopalpus zymna		x			Lamborn 1914, Cottrell 1984
M. biggsii		x			Maschwitz et al. 1988
M. boisduvali		x			Roepke 1918, Cottrell 1984
Miletus chinensis		x			Kershaw 1905, Cottrell 1984
M. nymphis		x			Maschwitz et al. 1988
M. symethus		x		v	Roepke 1918, Eliot 1980
Lachnocnemiti					
Lachnocnema bibulus	x	x	x		Cripps & Jackson 1940, van Someren 1974, Cottrell 1984
L. brimo		x			Ackery 1990
L. durbani		x			Ackery & Rajan 1990, Larsen 1991
Thestor basutus				v	Clark & Dickson 1971
T. brachycerus				v	Clark & Dickson 1971
T. dicksoni				v	Clark & Dickson 1971
T. dukei				v	Clark & Dickson 1971
T. holmesi				v	Clark & Dickson 1971
T. protumnus				v	Clark & Dickson 1971, Migdoll 1988
T. rileyi		x		v	Clark & Dickson 1971
T. yildizae (as *obscurus*)				v	Claassens & Dickson 1980, Henning & Henning 1989
Liphyrini					
Aslauga atrophifurca		x			Cottrell 1984, Villet 1986
A. lamborni		x			Lamborn 1914, van Someren 1974, Cottrell 1984
A. latifurca		x			Jackson 1937, Cottrell 1981, Ackery & Rajan 1990
A. orientalis		x			Cottrell 1981
A. purpurascens		x			Boulard 1968, Cottrell 1981
A. vininga		x			Lamborn 1914, Cottrell 1984, Ackery & Rajan 1990
Euliphyra leucyania			x		Kielland 1990, Dejean 1991
E. mirifica			x		Hinton 1951, Dejean 1991
Liphyra brassolis				x	Dodd 1902, Johnson & Valentine 1986, Cottrell 1987
L. grandis				x	Parsons 1991

and communication, had evolved, however, evolutionary opportunities for exploiting ants as prey became available. Myrmecophagy (and exploitation through trophallaxis) is likely therefore to be a derived trait in the otherwise myrmecophilic lycaenids, although this claim requires rigorous phylogenetic corroboration.

It also is possible that phylogenetic constraints operate in this system at levels other than the actual acquisition of predatory habits. It is notable that a large proportion of the miletine lycaenids prey on aphids of the closely related families Hormaphididae and Pemphigidae, whereas the Aphididae, for example, are seldom consumed by this group. Is this failure to exploit the entire range of potential aphid prey the product of a phylogenetic constraint in which the biology of the entire predatory miletine lineage became locked into the exploitation of the Hormaphidine/Pemphigidine group? Such a hypothesis would be refuted if it were found that Hormaphidine/Pemphigine feeding had arisen independently in separate miletine groups, suggesting that they are particularly amenable to such exploitation while other groups of aphids are not. For example, it may be somehow easier for carnivorous miletines to feed on woolly aphids than on other kinds of aphids, in which case the constraint would be functional, rather than phylogenetic. Alternatively, the Hormaphididae and Pemphigidae may happen to feed on the same host plants as those favored by phytophagous miletine-ancestors.

A discussion of "phylogenetic constraint" addresses a familiar topic in evolutionary biology: the assumption that specialized life history strategies represent more highly derived conditions than generalist interactions (Futuyma & Moreno 1988, Thompson 1994). Having once accumulated adaptations necessary to exploit a particular resource or survive in a special habitat, reversion to more general resource or habitat use is increasingly difficult. For example, specializations may include modifications such as the loss of eyes, or chewing mouthparts, making reversals unlikely.

However, generalizations about the evolutionary trajectory of specialization remain problematic. A phylogeny of the Papilionidae shows a generalist strategy, polyphagy in *Papilio glaucus* L., evolving from specialist ancestors (Miller 1987). The phylogeny of yucca moths and their related genera shows transitions in both directions (Thompson 1994). Futuyma & Moreno (1988:222) conclude: "Far more phylogenetic analysis is required than has been done, to document patterns of evolution of generalized and specialized habits" In the same vein, Thompson (1994:64) advocates: "The ideal analysis for understanding whether extreme specialization is generally a phylogenetically derived condition would be to take a group of fairly large monophyletic lineages and determine the proportion of times that specialization is the evolutionarily derived condition within each lineage." Further research on the evolution of predatory Lepidoptera, and particularly the phylogeny of groups such as the Lycaenidae, provide an ideal opportunity to do just that.

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