Insect Parasitoids: An Evolutionary Overview

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SUMMARY

This paper reviews the biology of insect parasitoids and cleptoparasitoids and places them in an evolutionary context. Available biological data are reviewed and tabulated (at the family level) with an emphasis on non-hymenopteran parasitoids. Existing cladistic or near-cladistic treatments of the parasitoid groups are used to make outgroup comparisons, and pathways to and from the parasitoid lifeway are estimated. Approximately 10% of all described insect species are parasitoids or cleptoparasitoids. Of these about three-quarters are Hymenoptera, and one-quarter are either Diptera or Coleoptera. The parasitoid lifeway has arisen most commonly in the Diptera, where it has evolved independently in 21 families (probably over 100 times). It has arisen in 11 coleopteran families but probably only once in the Hymenoptera. In most cases host searching is by the adult female parasitoid but in a significant minority of cases host-searching is by the first instar larva of the parasitoid, or (more rarely) by the host ingesting the parasitoid's egg. Dipteran parasitoids (as a whole) have a wider host range than hymenopteran or coleopteran parasitoids. The most common pathways to parasitoidism are from mycophagy, saprophagy and predation. In contrast, evolutionary shifts away from parasitoidism are relatively rare. Possible evolutionary explanations for these pathways are reviewed and others are suggested. A possible (evolutionary) explanation of the common evolutionary association of parasitoids with specialized egg predators is also discussed.

1. INTRODUCTION

Insect parasitoids have attracted considerable attention from biologists. This interest stems primarily from their importance in biological control where for many years they have been used in attempts to control pest insects on food crops (Greathead 1986). This economic importance has meant that many species have been brought into laboratory culture (Waage *et al.* 1985) focusing attention upon aspects of their biology and ecology. Areas of interest include: life-history strategies (Blackburn 1991); clutch size (Waage &

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Godfray 1985; Godfray 1987; Waage 1988); sex ratios (Waage 1986; Cornell 1988); population dynamics (Hassell 1986; Godfray & Hassell 1988; Hassell & May 1988; Strong 1988); physiology (Strand 1986); optimal foraging models (Speirs *et al.* 1991) and the evolution of host preferences (Gauld 1988). Recently workers have studied parasitoid communities as important ecological systems in their own right (see, for example, Hawkins (1990)), with an emphasis on their role in determining patterns of phytophagy (Lawton 1986). Attempts to find correlates of host ranges have led to the elaboration of sophisticated concepts of attack strategies (Askew & Shaw 1986; Sheehan & Hawkins 1990). In addition the apparent relative drop in diversity of certain parasitoid taxa towards the tropics has attracted considerable attention (Janzen 1981; Gauld 1986).

Although the biological literature abounds with information on 'insect parasitoids' nearly all of this deals with a single group, the 'parasitic' Hymenoptera. A recent symposium on insect parasitoids (Waage & Greathead 1986) contained no contributions dealing with non-Hymenopteran parasitoids (an omission noted in the preface). Attempts to examine patterns in parasitoid communities invariably deal only with species of Hymenoptera (Eggleton & Gaston 1990). Although this bias is understandable, derived ultimately from the high diversity of hymenopteran parasitoids attacking pests of food crops, it is a poor reflection of the true biological diversity that exists among insect parasitoids.

In this paper we review the wide range of parasitoid associations found within the insects. We place those associations in an evolutionary context by attempting to reconstruct the pathways leading to and from the parasitoid lifeway. In addition we review the evolutionary explanations that have been proposed for these pathways and propose some provisional explanations ourselves. These explanations are mostly uncorroborated by cladistic analyses and are intended to stimulate further work.

Our overview is consciously biased towards non-hymenopteran parasitoids. A great deal has been written about hymenopteran parasitoids, and an excellent general account exists of their biology (Gauld & Bolton 1988). For this reason we present a less detailed account of hymenopteran parasitoid biology than that of the other groups. Non-hymenopteran groups are discussed comprehensively only in Clausen (1940) and Askew (1971). Many papers on non-hymenopteran parasitoids have appeared since those works and part of our purpose is to gather together some of these new data.

2. DEFINITIONS

Many of the terms used in parasitoid biology are poorly defined and used very loosely. The term 'parasitoid' has been defined in several ways, and always with taxonomic constraints which have no functional significance (for a detailed discussion of this see Eggleton & Gaston (1990)). Our aim is to define terms which represent broad functional discontinuities.

Our definition of the term 'parasitoid' differs from that in common usage by entomologists. We include groups that attack non-arthropod hosts and solitary wasps that move their host after oviposition. However, we feel this is justified on functional grounds, especially as several authors have used the term for non-arthropod groups attacking non-arthropod hosts (Kuris 1974; Newell *et al.* 1977; Laval 1980) and even groups attacking individual seeds (Janzen, 1975).

We adopt the following general definitions of 'parasitoid' and 'cleptoparasitoid':

A *parasitoid* is 'an organism which develops on or in another single ("host") organism, extracts nourishment from it, and kills it as a direct or indirect result of that development'. (Eggleton & Gaston 1990, following Kuris 1974).

A *cleptoparasitoid* is 'an organism which develops at the expense of another single ("host") organism by (at least partial) usurpation of its food supply, killing the host as a direct or indirect result of that usurpation'.

The food stuff in the above definition is commonly the provision provided for the offspring by the adult female host. The nature of this provisioning distinguishes between provisioning parasitoids and provisioning predators (e.g. some aculeate wasps), omnivores (e.g. ants) and phytophages (e.g. bees). Provisioning can include leaf rolls, galls, or the hosts made available by other parasitoid species. We use the term 'host' to refer to the individual killed by the parasitoid. If that individual is a parasitoid then it will have its own (separate) 'host' which is referred to as the 'provision'.

Our definition of 'parasitoid' excludes the following groups.

1. Facultative relationships, where a species may develop as a parasitoid or as a predator, sarcophage, parasite, etc. This excludes many primarily sarcophagous species, e.g. many Sarcophagidae, Muscidae and Phoridae (all Diptera) which develop upon dead, dying or (apparently) healthy 'host' individuals. The results of single rearings can be misleading in these cases. Robinson (1971) lists rearing records of *Megaselia* species (Diptera: Phoridae) where the number of species which appear to be obligate parasitoids drops dramatically as the number of records for individual species increases. Also excluded are many primarily parasitic species which only occasionally kill their host, e.g. several Diptera whose larvae cause myiasis in vertebrates may (depending on several factors) cause the death of the host. However, this is rarely an inevitable result of the attack (although it is possible that in small mammals mortality is often the norm (Erzinçlioğlu, personal communication)).

Conversely, species which only occasionally fail to kill their host have been included. Individual hosts of the Anthomyiidae and Tachinidae (Diptera) have been noted occasionally to survive emergence of the attacker (Clausen 1940), and even to complete their life cycles apparently normally (e.g. earwigs (Phillips 1983) and Lepidoptera larvae attacked by Tachinidae (Richards & Waloff 1948; DeVries 1984; English-Loeb *et al.* 1990)).

2. Species which develop within the protective

covering of an egg mass (e.g. Orthoptera egg-cases or spider egg-sacs) and consume a number of eggs. Such species are referred to here as specialized egg predators. They share many features of true parasitoids however and are discussed below.

3. Species where an individual destroys a single colony of a social insect. An example is *Psithyrus* (Hymenoptera: Apidae), where the female enters a host colony, kills the host queen, and manipulates the host workers so that they rear her own offspring. Although falling outside the definition used here, a single unit of selection is destroyed by each individual, and such species (the permanent social parasites of Gauld & Bolton (1988)), may be thought of as colony parasitoids.

4. Species which castrate but do not kill their host (parasitic castrators). These differ from typical parasites in that, although the host is not killed, its fitness is reduced to zero (Kuris 1974). Castrated individuals are still free to compete for resources with other host individuals and may be subject to parasitoid attack after castration (Eggleton & Gaston 1990). For these reasons, we exclude them.

5. Species which feed on plants. Price (1980) has expanded the term parasite to include phytophagous groups such as Homoptera. These commonly complete their life cycle on a single individual plant and reduce its fitness, in a similar fashion to an typical parasite of an animal host. Such a classification ignores the different trophic levels occupied by taxa and for this reason we reject it. However, the similarities between the two systems are certainly worthy of further investigation (Janzen 1975), and we recognize that the exclusion is somewhat arbitrary.

3. METHODS OF PHYLOGENETIC ESTIMATION

We have employed a cladistic methodology to reconstruct pathways to and from the parasitoid lifeway within the insects. The recent cladistic (or near-cladistic treatments) of the arrangement of families within insect orders provide the framework for these reconstructions (see Boudreaux (1979) and Hennig (1981), for the whole Insecta; Crowson (1967, 1981) for Coleoptera; Rasnitsyn (1988), Konigsman (1976) and Brothers (1975) for Hymenoptera; McAlpine (1989) for Diptera; Nielsen (1989) for Lepidoptera; New (1989) for Neuroptera). Using the results of these analyses we have attempted to estimate the polarity of lifeway shifts by outgroup comparison (Madison *et al.* 1984). One example will suffice to explain the method. Rasnitsyn (1988) proposes a cladogram (which we accept here, figure 1) for the Hymenoptera which places the parasitoid taxa, the Apocrita and the Orussidae, as sister groups (i.e. a monophyletic lineage). The outgroups in this case are the Anaxyleidae, Siricidae and Xiphydriidae, all of which are mycophages in dead wood, and so we chose that lifeway as the ancestral (plesiomorphic) condition.

This method assumes that the cladogram used to identify the outgroups represents a good estimation of phylogeny. This may not be so in all cases, and therefore our pathways of lifeway evolution will mirror errors in the original cladograms.

Two other methods of estimating evolutionary pathways (plausibility and commonality) are often used, but they have several weaknesses. As these methods have been used to propose evolutionary pathways to the parasitoid lifeway we discuss their shortcomings here.

(*i*) *Plausibility*. The occurrence of evolutionary changes are often inferred by their apparent likelihood. This is usually judged by the ease with which selective forces can be imagined which could produce or inhibit any particular shift. This approach is, despite cladistics, the predominant one employed when considering evolutionary changes.

Coddington (1988) gives good examples of plausibility explanations which have been shown to be incorrect after cladistic analysis.

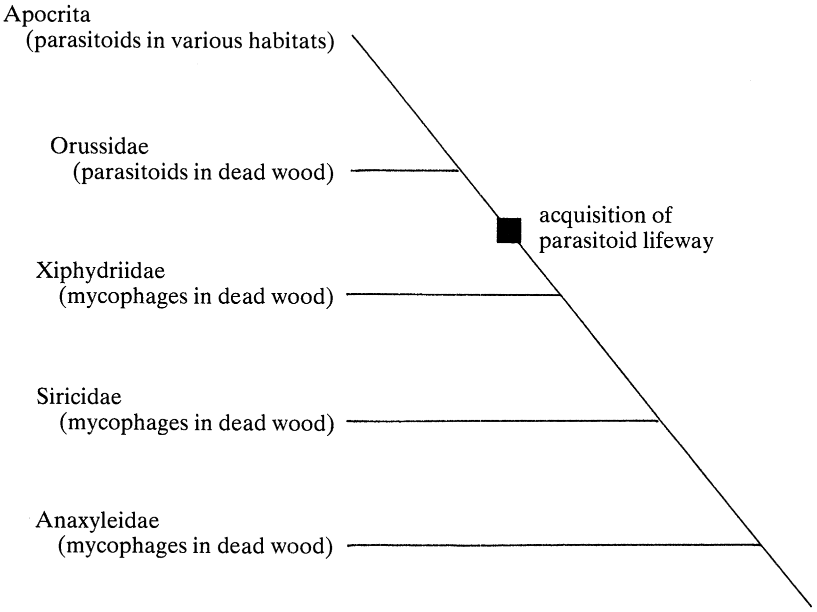

Figure 1. Simplified cladogram of relationships in the Siricoidea plus Orussidae plus Apocrita clade (after Rasnitsyn 1988) showing method of outgroup comparison.

Table 1. *Insect families with parasitoid members*

(Figures for the total number of species within each family are the number of described species. Unless otherwise stated, all evolutionary shifts have been inferred by outgroup comparison (Madison *et al.* 1984), using the phylogenies from Crowson (1981), Rasnitsyn (1978) and McAlpine (1989). Note that, a very much more general overview of the Hymenoptera is given than for the other orders (see Introduction).

Where the parasitoid lifeway is rare within the family, the total number of known parasitoid species are given. Where all species whose biology is known in a family are parasitoids it is assumed that the lifeway occurs throughout the family. In intermediate situations an estimate of the number of parasitoid species has been made, extrapolating from the number of species whose biology is known.

The term 'many' is used where the parasitoid lifeway appears to have been acquired repeatedly within a family but no figure for the number of times can be obtained.

Sources of biological data given in Appendix 1. These are heavily biased towards the Holarctic region.

No. acq. = number of acquisitions.)

taxon	no. acq.	no. spp.	biologies and evolutionary shifts
Lepidoptera			
Pyralidae (20 000 spp.)	1	1	*Sthenauge parasitus* is an ectoparasitoid of *Aplomerus* larvae (Saturnidae); feeding on host spines. Host locating process unknown. *Evolved from*: unknown.
Epipyropidae (20 spp.)	many	10	Ectoparasitoids of Hemiptera (and occasionally Lepidoptera larvae) on plant surfaces (only *Epiricania melanoleuca* attacking *Pyrilla perpusilla* is undoubtedly a parasitoid[a]). Host-searching first instar larvae. Once attached to host it pierces its cuticle and sucks the haemolymph. *Evolved from*: parasites of Hemiptera on plant surfaces (plausibility).
Neuroptera			
Mantispidae (250 spp.)	1	50	Symphrasinae are ectoparasitoids of insect larvae and pupae in cells in the soil; Scarabaeidae (Coleoptera), Apidae (Hymenoptera) and pupal cocoons of Noctuiidae (Lepidoptera). Host-searching first instar larvae. *Evolved from*: predators in the soil (plausibility[b]). *Evolved into*: specialized egg predators; attacking spider egg sacs, females with reduced ovipositors, host-searching first instar larvae may be parasitic and phoretic on the adult female spider (200 spp.).
Diptera			
Mycetophilidae (3400 spp.)	1	4	*Planarivora insignis* is an endoparasitoid of terrestrial flatworms (Platyheminthes). Host-searching first instar larva. *Evolved from*: mycophages (commonality within family).
Cecidomyiidae (4500 spp.)	?4	6	Endoparasitoids of Hemiptera on plants; larval Tingidae (*Endopsylla endogena*), adult aphids (*Endaphis perfidus*, *E. gregaria*, *Occuloxenium compitale* & *Pseudendaphis maculans*) and adult Psyllidae (*Endopsylla agilis*). Eggs laid on host. *Evolved from*: predators of the same taxon (plausibility and commonality).
Chironomidae (5000 spp.)	2	2	*Tendipes varus* is an ectoparasitoid, and an unidentified species is an endoparasitoid, of fresh-water gastropods. Host-searching first instar larva. *Evolved from*: microphages; although family contains a few unrelated phoretic and parasitic[c] species.
Nemestrinidae (300 spp., 7 known)	1	300	Endoparasitoids of Scarabaeidae (Coleoptera) larvae (1 sp.) and adult grasshoppers (6 spp.) in soil and ground. Host-searching first instar larvae. Eggs laid in openings in wood and larvae drop to ground. *Evolved from*: predators in soil/ground; in shared ancestor of Nemestrinidae and Acroceridae.
Acroceridae (= Cyrtidae) (475 spp.)	1	475	Endoparasitoids of adult spiders (mostly non-web spinning) on the ground and on plants Host-searching first-instar larvae *Evolved from*: predators in soil/ground; in shared ancestor of Acroceridae and Nemestrinidae.
Bombyliidae (3980 spp., 144 known)	1	3000	Ectoparasitoids of insect larvae and pupae, predominantly in burrows with the female laying eggs at the burrow entrance and the host contacted by the first instar larva. (i) From nests of aculeate Hymenoptera (in soil, stems and mud nests); where known ectoparasitoids of larvae and pupae (51 spp.). Feeding on the provisioning (host-directed cleptoparasitoidism) recorded in two, and its absence noted in five, species. (ii) From cocoons of hymenopteran parasitoids in soil (9 spp.). (iii) Endoparasitoids of Lepidoptera larvae and pupae (31 spp.); predominantly soil-dwelling species (although may feed above ground nocturnally). Also one species from sawfly cocoon in the soil. (iv) From within Diptera puparia in soil (Glossinidae and Tachinidae) (15 spp.). (v) Wood-boring or soil-dwelling Coleoptera larvae and pupae (6 spp.). *Evolved from*: predators in soil/ground.

Table 1 (*continued*)

taxon	no. acq.	no. spp.	biologies and evolutionary shifts
			Evolved into: (i) Grasshopper egg pod predators (32 spp.; scattered through family, some may be parasitoids of egg pod predators) (commonality). (ii) In *Lepidophora lepidocera* the provisioning in several cells of its sphecid (Hymenoptera) host are necessary for development (= a provision-directed cleptopredator) (commonality).
Asilidae (5000 spp.)	many	1000	(i) *Hyperechia bomboides* is an ectoparasitoid of Xylocopidae (Hymenoptera) in dead wood (inconclusive evidence for the same habit in other *Hyperechia* spp.). (ii) At least 30 other species recorded as carnivorous on insect larvae in the soil. In only three is it known if the species is a predator or a parasitoid; *Mallophaga ruficauda* is an ectoparasitoid, *Promachus yesonicus* is predacious, and *M. media* appears to be capable of developing as either (all attack Scarabaeidae (Coleoptera) larvae). Host-searching first instar larvae. *Evolved from*: predators in soil/ground.
Empididae (2000 spp.)	?4	4	Endo- and ectoparasitoids of aquatic immature caddisflies (Trichoptera); found attacking prepupal and pupal stages. Host locating process unknown. *Evolved from*: predators in soil/ground (commonality within family).
Phoridae (3000 spp.)	many	300	Endoparasitoids of arthropods in soil, eggs laid on or (more rarely) inserted into host. Most attack larval or adult ants. Also attacked are other provisioning aculeate Hymenoptera and termites, and (more rarely) other arthropods in the soil[d]: Coccinellidae pupae and adult Lampyridae (Coleoptera); Sciaridae, Tipulidae and Bibionidae larvae (Diptera); earthworms; millipedes; and snails. Some phorid females oviposit into adult bees in flight. Many other host records may be of facultative parasitoids. *Evolved from*: saprophages; probably often via commensalism with burrowing social insects (most genera contain species associated with social insects (plausibility)).
Pipunculidae (600 spp.)	1	600	Endoparasitoids of Homoptera nymphs (mostly Delphacidae and Cicadellidae) on plants. Eggs inserted into host using piercing ovipositor. *Evolved from*: saprophages; a direct transition however is implausible, possibly an extinct ancestral taxon was a parasitoid of a soil/ground host taxon or predacious on Homoptera[e].
Conopidae (800 spp.)	1	800	(i) Endoparasitoids of adult bees and aculeate wasps (all species excluding *Stylogaster*). Egg inserted into host during flight using piercing ovipositor. Also two questionable records from grasshopper egg pods. (ii) *Stylogaster* recorded as an endoparasitoid of crickets and cockroaches[f], its eggs also found on adult calyptrate flies. Commonly attacks insects flushed out by army ants. Given family status by some authors (*ca.* 30 spp.). *Evolved from*: saprophages; a direct transition however is implausible, possibly an extinct ancestral taxon was a parasitoid of larval aculeates.
Pyrgotidae[g] (330 spp., 7 known)	1	330	Endoparasitoids of adult Scarabaeidae (Coleoptera). Eggs inserted into host, at least in some cases during flight using piercing ovipositor. *Evolved from*: saprophages; possibly an extinct ancestral taxon was a parasitoid of larval Scarabaeidae, however a direct transition seems implausible.
Sciomyzidae (550 spp. *ca.* 200 known)	?4	6	*Sciomyza aristalis*, *S. varia*, *Pteromicra inermis*, *Colobaea bifasciella* and *Oidematops ferrugineus* are endoparasitoids of terrestrial or stranded/aestivating aquatic Gastropoda (Mollusca). *Sciomyza testacea* may also be a parasitoid. Eggs laid on host or (*Oidematops*) with a host-searching first instar larva. *Evolved from*: predators of gastropods (plausibility).
Phaeomyiidae[h] (4 spp.)	1	4	*Pelidnoptera nigripennis* is an endoparasitoid of millipedes (Diplopoda). Eggs laid on host. *Evolved from*: saprophages.
Cryptochetidae (25 spp.)	1	25	Endoparasitoids of Coccoidea (Homoptera) nymphs on plants. Eggs inserted into the host using piercing ovipositor. *Evolved from*: saprophages (outgroup comparison within Carnoidea); a direct transition however is implausible, possibly an extinct ancestral taxon was a parasitoid of a soil/ground host taxon or predacious on Homoptera.
Chloropidae[i] (2000 spp.)	?6	6	Scattered single records of parasitoidism, usually on insect larvae in plant tissue. *Oscinisoma confluens* in Chrysomelidae (Coleoptera) eggs, and *Polyodaspis endogena* in Tortricidae (Lepidoptera) larvae. Also questionable records from *O.* sp. near *confluens*, *Anacamptoneura* sp. and two species of *Conioscinella*. Facultative parasitoids found in other species. Method of host-location unknown. *Evolved from*: saprophages; probably as a commensal in plant tissue (plausibility).
Anthomyiidae[j] (1200 spp.)	?5	43	(i) Endoparasitoids of adult or late nymph Orthoptera. Eggs inserted into host through hole made by female mouthparts. Group comprises all (four) species of *Acridomyia*, *Acyglossa* and *Tettigoniomyia*). (ii) Provision-directed cleptoparasitoids of Sphecidae and Andrenidae (Hymenoptera)

Table 1 (*continued*)

taxon	no. acq.	no. spp.	biologies and evolutionary shifts
			larvae in soil. Group probably comprises all (*ca.* 39) members of *Eustalomyia* and *Leucophora*. *Evolved from*: saprophages.
Muscidae[k] (3900 spp.)	1	13	The aberrant Eginiini (sometimes given family status) are probably all endoparasitoids of millipedes (Diplopoda); four known. Eggs laid on host. *Evolved from*: saprophages.
Calliphoridae[l] (1100 spp.)	6	240	Endoparasitoids of soft-bodied organisms in the soil/ground. Eggs laid on host, or host-searching first instar larvae. Some species with varying degrees of uterine incubation. (i) Polleniini, *Onesia*, *Bellardia* and five Australian *Calliphora* attack earthworms (179 spp.). (ii) Ameniinae and Melanomyinae (inc. *Eggisops*, *Melinda*, *Angioneura* and *Melanomya*) attack terrestrial Gastropoda (Mollusca) (60 spp.). (iii) *Lucilia bufonivora* is an endoparasitoid of frogs and toads (gregarious, feeding in nasal and other head cavities). *Evolved from*: saprophages.
Rhinophoridae (90 spp.)	1	90	Endoparasitoids of woodlice (Isopoda). Host-seaching first instar larva. *Evolved from*: saprophages.
Sarcophagidae (2500 spp.)	Many	1250	Parasitoids of animals in the soil/ground. Larva laid on or (more rarely) inserted into host, except in *Sarcophaga s.s.* where contact apparently is by first instar larvae. Entire family with uterine incubation. (i) Provision-directed cleptoparasitoids of soil-nesting Aculeata (Miltogrammini – 500 spp). (ii) Endoparasitoids chiefly of terrestrial gastropods (*Johnsonia* sp., *Microcerella* sp., *Nyctia halterata*[m] and many Sarcophagini) and Orthoptera (*Taxigramma heteroneura*, *Hilarella hilarella*, most Protodexiini – inc. *Blaesoxipha*.). Also a few parasitoids of earthworms (*Sarcophaga s.s.*[n]) and other arthropods: e.g. adult Diptera (*Macronychia* sp.), larvae & pupae of *Bombus* (*Brachycoma* spp.), cicadas (*Emblemosoma* sp. and *Colcondamyia* spp.), termites (*Noditermitomyia arabops*), Lepidoptera larvae (*Agria*), millipedes (*Spirobolomyia*). Estimated 750 spp. (iii) *Notochaeta bufonivora* appears to be an ectoparasitoid of toads; two records. Many other, primarily sarcophagous, species are also facultative parasitoids. *Evolved from*: saprophages. *Evolved into*: *Senotainia tricuspis* develops as an internal parasite in bees, consuming host only when it has died naturally (= parasite or sarcophage) (plausibility). Possible that rearings from adult Scarabaeidae (Coleoptera) and adult *Bombus* (Hymenoptera) represent parasitic rather than parasitoid associations.
Tachinidae (8000 spp.)	1	8000	Endoparasitoids of arthropods; mostly of insects. Eggs laid on or inserted into host; laid on plant and ingested by host (larvae entering host via gut); or host-seaching first instar larvae. Latter two strategies allow access to hosts otherwise inaccessible to female. Some groups with uterine incubation. (i) Insects exposed on plants. Estimated 5800 spp; mostly Lepidoptera larvae, also sawfly larvae (Hymenoptera: Symphyta), Heteroptera and Chrysomelidae (Coleoptera) larvae and adults. (ii) Insects concealed in plants or within leaf-rolls etc. Estimated 1400 spp; predominantly microlepidoptera larvae, also some boring Coleoptera and macrolepidoptera larvae. (iii) Arthropods in soil/ground. Estimated 800 spp; adult and larval Coleoptera (commonly larval Scarabaeidae), Tipulidae (Diptera) larvae, Dermaptera, Orthoptera, and Chilopoda. The genus *Strongygaster* attacks adult ants and a few genera attack the immature stages of social wasps. Single species also attack scorpions, spiders, Embioptera, adult Tabanidae and adult Calliphoridae (Diptera). *Evolved from*: saprophages.
Coleoptera[o]			
Carabidae[p] (30 000 spp.)	3	470	(i) Ectoparasitoids of arthropods in the soil; Coleoptera pupae and millipedes (*Pelecium*: 15 spp.); Hydrophilidae (Coleoptera) pupae in their (terrestrial) pupal cells (*Brachinus*: 150 spp.). (ii) Ectoparasitoids of Chrysomelidae (Coleoptera) pupae on aerial parts of plants (*Lebia*: 300 spp.). All groups with host-searching first instar larvae. *Evolved from*: predators of other insects; mostly on ground and in dead wood. *Brachinus* in same subfamily (Brachininae) as *Pheropsophus*, a specialized egg predator of mole crickets.
Staphylinidae (30 000 spp.)	1	500	Ectoparasitoids of Diptera puparia in mostly moist ephemeral habitats (dung, carrion, vegetable refuse, seaweed, fungi, vertebrate nests & ant's nests). Host-searching first instar larvae. *Evolved from*: predators of Diptera or other prey in the same habitats (plausibility).
Scarabaeidae[q] (25 000 spp.)	many	10+	Provision-directed cleptoparasitoids of other scarabaeid and geotrupid (Coleoptera) brood dung balls (some *Aphodius* and *Onthophagus*). Adults penetrate into brood balls after they have

Table 1 (*continued*)

taxon	no. acq.	no. spp.	biologies and evolutionary shifts
			been made and lay eggs inside them. Host egg is eaten and brood ball is consumed by cleptoparasitoid *Evolved from*: provisioning saprophages.
Rhipiceridae (50 spp.)	1	50	Probably endoparasitoids of cicada nymphs; only one record. Eggs laid in bark crevices where cicadas oviposit, larvae may attach to the nymphs before they enter the soil. *Evolved from*: mycophages in dead wood.
Cleridae (4000 spp.)	2	26	(i) Host-directed cleptoparasitoids of Apidae (Hymenoptera) cells in soil and dead plant material (*Trichodes*: 25 spp.). Feeds for only a short time on provisioning. Host-searching first instar larvae; some phoretic. (ii) Parasitoids of gall-forming Lepidoptera larvae on aerial parts of plants (*Phyllobaenus*: 2 spp.). Host locating process unknown. *Evolved from*: predators of other insects, probably in dead wood. *Evolved into*: (i) Cleptopredators of Apidae cells in soil and dead plant material (a few *Trichodes* species). (ii) Grasshopper egg pod predators (one *Trichodes* species) (polarity by commonality within *Trichodes*: evidence rather weak).
Rhipiphoridae (400 spp.)	1	400	(i) *Rhipistena cryptartha* is an ectoparasitoid of Cerambycidae (Coleoptera) larvae in wood. (ii) Endoparasitoids of cockroach adults (Rhipidiinae). Eggs laid in host environment, first instar larvae phoretic; attaching when host passes. (iii) Endoparasitoids (possibly ectoparasitoids when older larvae) of scoliid, tiphiid and solitary vespid wasp larvae, and solitary and semi-solitary bee larvae (Rhipiphorinae). Eggs laid on foliage, in flowers or in cracks in wood. First instar larvae phoretic, attaching to adult host, dropping off after oviposition and attacking immature stage of host. *Evolved from*: (mordellid-like) mycophages in dead wood.
Meloidae (3000 spp.)	1	2000	Provision-directed cleptoparasitoids of provisioned bee cells in soil[r] (all groups except Mylabrina and Epicautina). Some lay eggs on vegetation, others in burrows in the soil from where the larvae climb onto flowers. In both groups the first instar larvae are phoretic: either searching for host bee nests in the soil or waiting for pollen-gathering bees. *Evolved from*: saprophages feeding in very old dead wood, possibly via a spore/pollen-feeding (in larval stage) ancestor. Flower visting in adults may also have been important. *Evolved into*: Grasshopper egg pod predators (Mylabrina and Epicautina: 1000 spp.), a few species may attack egg masses of other Meloidae.
Passandridae (50 spp.)	1	10	*Catogenus rufus* has been recorded as an ectoparasitoid of Cerambycidae (Coleoptera) pupae in dead wood and as a hyperparasitoid of a braconid (Hymenoptera). Host locating process unknown. *Evolved from*: predators of insects in dead wood (commonality within Passandridae).
Bothrideridae (200 spp.)	1	150+	Ectoparasitoids of the larvae and pupae of Coleoptera in dead wood (*Bothrideres*, *Deretaphrus*, *Dastarcus*, *Sosylus*, *Asosylus* and *Lophorus*); *Dastarcus* spp. also recorded as ectoparasitoids of Xylocopidae (Hymenoptera) larvae in dead wood. Host-searching first instar larvae. *Evolved from*: mycophages in dead wood.
Curculionidae (50 000 spp.)	1+	3+	Provision-directed cleptoparasitoids of other curculionid larvae within galls. Adult places e.g. inside gall by using a piercing rostrum. *Evolved from*: gall-forming species (plausibility).
Stylopoidea (400 spp.)	1	10	Mengeinae (10 spp.) are ectoparasitoids of leptismatid Thysanura in soil. Host-searching first instar larvae. *Evolved from*: mycophages in dead wood (outgroup comparison within Heteromera, assuming Strepistera is a coleopteran group). *Evolved into*: parasites and parasitic castrators of Heteroptera, Hemiptera, Blattodea, Orthoptera, Diptera, Mantodea and Aculeata. Females always castrators, males may be castrators, parasites or (at least in some Homoptera-attacking spp.) parasitoids (390 spp.)
Hymenoptera			
Orussidae (75 spp., 2 known)	1	75	Ectoparasitoids of larvae in dead wood. *Guiglia schaunslandi* recorded from *Sirex* (Hymenoptera: Siricoidea) larva; host finding by adult female with piercing ovipositor. *Orusses occidentalis* recorded from Buprestidae (Coleoptera) larvae; host locating process unknown. *Evolved from*: mycophages in dead wood in shared ancestor of Apocrita plus Orussidae.
Apocrita (95 000 spp.)	1	67 000	With very few exceptions[s], ecto- or endoparasitoids of other insects, attacking all developmental stages except for the adult stages of holometabolous insects. Eggs are laid on or in the host, often together with a paralysing venom. Most families attack taxa on or within living plants or dead wood[t], exceptions to this are listed below. (i) Scelionidae are endoparasitoids of arthropod eggs in most terrestrial habitats.

Table 1 (*continued*)

taxon	no. acq.	no. spp.	biologies and evolutionary shifts
			(ii) Parasitoids of aquatic insects. Endoparasitoids of eggs exposed on the water's edge (some Eulophidae) or underwater (some Trichogrammatidae, some Mymaridae, some Eulophidae). Some phygadeuontine Ichneumonidae are associated with pupal cocoons in semi-aquatic habitats. Agriotypine Ichneumonidae attack Trichoptera pupae and prepupae in fresh water. (iii) Endoparasitoids of Diptera puparia in decaying animal and plant matter (Figitidae; Eucoilidae; Diapriidae; some Chalcididae; some Pteromalidae; some Signiphoridae). Some Ichneumonidae and Braconidae are ectoparasitoids or endoparasitoids of larval Diptera. (iv) Endoparasitoids of Coleoptera and Diptera[u] larvae in damp secluded places (leaf litter, fungi, etc.) (Proctotrupidae; some Ichneumonidae; some Braconidae). (v) Ectoparasitoids of fleas within mammal and bird nests (some Pteromalidae). (vi) Ectoparasitoids of Scarabaeidae (Coleoptera) larvae in their cells in the soil (Pelecinidae; Tiphidae; Scoliidae). (vii) Ectoparasitoids of the larvae of soil- and wood-nesting aculeates (Hymenoptera) in their cells (Mutillidae; some Chrysididae; Leucospidae; some Torymidae; some Ichneumonidae). (viii) Parasitoids of ants, either attacking the larval stages via a host-searching first instar (some Eucharitidae) or the female attacks the adult (neoneurine Braconidae). (ix) Host-directed cleptoparasitoids of the larval stages of soil- and wood-nesting aculeates (Hymenoptera) in their cells (Chrysididae; Sapygidae; Gasteruptidae). (x) Provisioning ectoparasitoids of all stages of insects (Pompilidae; Bethylidae; some Sphecidae). *Evolved from*: mycophages in dead wood in shared ancestor of Orussidae and Apocrita; also secondary acquisitions from phytophagy: (*a*) Provision-directed cleptoparasitoids within galls (some Tanaostigmatidae; some Cynipidae; some Eurytomidae; some Pteromalidae; some Torymidae; some Eulophidae), or within figs (some Agaonidae). Secondary acquisition from (1) below. (*b*) Many Apidae (*ca.* 4000 spp) are provision-directed cleptoparasitoids of other bees. *Evolved into*: 1. Gall-forming and endophytic phytophages (Agaonidae; Cynipidae; some Tanaostigmatidae; some Eurytomidae; some Pteromalidae; some Eulophidae; some Torymidae); *ca.* 2000 spp. 2. Host-directed cleptopredators of immature aculeates in their cells (some Gasteuptidae; some Chrysididae); *ca.* 200 spp. Probably evolved from (ix) above (plausibility). 3. Predators of eggs and larvae of various insects and spiders (some Pteromalidae; some Eupelmidae; some Eurytomidae; some Eulophidae; some Encyrtidae); *ca.* 500 spp. 4. Specialized egg predators of Blattaria oothecae (Evaniidae; some Eulophidae); Mantoidea oothecae (*Podagrion* (Torymidae)); spider egg sacs (some Ichneumonidae; some Eulophidae), occasionally pseudoscorpion egg sacs (some Ichneumonidae); *ca.* 800 spp. 5. Provisioning predators of all stages of insects (some Sphecidae; Eumenidae; Vespidae; a few Masaridae); some eusocial (Vespidae). *ca.* 4000 spp.. Evolved from (x) above. 6. Provisioning omnivores (Formicidae); *ca.* 15 000 spp. Evolved from (x) above.

[a] Also possibly *Fulgoraecia cerolestes* (Epipyropidae) which 'apparently' causes death of Fulgoridae (Homoptera) host shortly after leaving it (Kirkpatrick 1947).

[b] Macleod & Redborg (1982) claim that primitive mantispids are generalist predators.

[c] At least one species is an ectoparasite of Ephemoptera nymphs (resulting in the castration of the adult host).

[d] Also possibly from Homoptera (R. H. L. Disney, personal communication).

[e] The sister group to the Pipunculidae, the Syrphidae, contain predators of Aphidae (Homoptera) but this is a derived condition within that family, with the most primitive syrphids phytophagous (Rotheray & Gilbert 1989; G. E. Rotheray, personal communication).

[f] The suggestion that this is a phoretic association by Ferrar (1987) predated recovery of immature stages within hosts.

[g] The closely related Tachiniscidae have been excluded. Their status as parasitoids rests on a single record (see Ferrar 1987).

[h] Formerly placed within the Sciomyzidae.

[i] The Australian genus *Batrachomyia* (10 species) causes myiasis in Amphibia but is not usually fatal. Several genera contain specialized egg predators, attacking those of spiders and a range of insects.

[j] Also a few facultative parasitoids of Lepidoptera and sawfly pupae in the soil. Two genera are Orthoptera egg pod predators.

[k] *Passeromyia* larvae attack and may kill nesting birds and most *Philornis* may cause myiasis.

[l] Common origin of parasitoid habit assumed for *Bellardia* and *Onesia*. Mesembrinellinae (treated as a subfamily of Calliphoridae by K. Rognes (personal communication)) may also be snail parasitoids. *Eurychaeta* (= *Helicobosca*) attacks dead or dying snails (Rognes 1986). There is also one record of a *Pollenia* sp. reared from adult honey bees (Ibrahim 1984). *Eumacronychia sternalis* and several Boettcheriini reared from turtle eggs and *E. nigricornis* from lizard eggs but they are

(*ii*) *Commonality*. It can be argued that the probability is low that a species with a rare biological character state is also coincidentally the most primitive species in a given taxon. The character state is therefore considered to be derived (apomorphic). Unfortunately this is precisely the case for several important character-states, e.g. egg-laying in mammals and winglessness in insects.

Both plausibility and commonality arguments are usually based on inspection of a single character. They are at best either weak (plausibility) or very weak (commonality) explanations.

We have adopted the terminology of O'Hara (1988) when discussing evolutionary events. He insists on a clear conceptual separation between (i) the order and direction in which evolutionary changes have occurred (an evolutionary chronicle), and (ii) causal explanations for these changes (an evolutionary narrative).

The importance of first constructing a chronicle before attempting a narrative cannot be overstressed: it is clearly essential to understand precisely what evolutionary changes have occurred, and in what order, before a meaningful explanation for them can be advanced. Most of the narratives discussed below lack a supporting chronicle, due to the paucity of phylogenetic reconstructions below the family level.

4. OVERVIEW

Table 1 shows the known occurrence of the parasitoid lifeway within all insect groups. We have derived a number of general points from this table (see table 2). We calculate that there are approximately 87000 described species of insect parasitoids, representing roughly 10% of described insects (based on Gaston's (1991) estimation of the number of described insect species). Roughly one quarter of insect parasitoids are non-hymenopteran (20000 species, table 2).

The parasitoid lifeway is found in all major holometabolous orders of insects (Diptera, Coleoptera, Hymenoptera, Lepidoptera and Neuroptera). Table 2 shows that the lifeway has evolved in 21 families of Diptera (and in most evolutionary subgroups of the order), 11 families of Coleoptera, but probably only once in the Hymenoptera (in the clade 'Apocrita plus Orussidae', although some secondarily phytophagous groups may have become cleptoparasitoids, see below). We feel sure that further studies will indicate that the lifeway has arisen well over 100 times in the Diptera.

The Diptera have by far the widest host range of the orders of parasitoid insects, attacking hosts in at least 22 orders of animals in five phyla. In contrast the Hymenoptera (probably at least four times as species-rich) attack approximately 19 orders of animals in one phylum. The Coleoptera have an even narrower host range, attacking about eight orders in one phylum.

In about 85% of all insect parasitoids the host searching is by the adult female. In the remainder, almost all of which are in the Diptera and Coleoptera, at least the final stage of host location is by the first instar larva. Some Diptera (some Tachinidae) and a very few Hymenoptera (Trigonalyidae) lay eggs that are ingested by their host.

These various differences between different orders of insect parasitoids are striking and in need of some explanation. They are discussed in detail in Eggleton & Belshaw (1992).

Figures 2, 3 and 4 show for the three main parasitoid orders the type and relative importance of estimated evolutionary shifts to and from the parasitoid lifeway. From these diagrams we conclude that

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probably egg predators. *Cistudinomyia cistudinis* causes myiasis in land turtles and *Notochaeta blakeae* has been reared from a chameleon, *Wolhfahrtia* is apparently an obligate myiasis-causer. *Protocalliphora* and *Trypocalliphora* are ectoparasites of nesting birds.

[m] Not a parasitoid of weevils as often listed (T. Pape, personal communication).

[n] Larvae deposited in or near the entrances of earthworm burrows and probably seek their prey actively (Pape 1987). Although larvae of several species have been reared in decaying meat in the laboratory, all species for which feeding habits are known are parasitoids or predators of earthworms (Pape 1987, personal communication).

[o] Some Colyiidae, Brentidae and Curculionidae may be cleptoparasitoids of Platypodidae and Scolytidae within tunnels in dead wood (Crowson 1981; Beeson 1925, 1941). In addition, some Curculionidae may be cleptoparasitoids of Tenthridinidae sawflies in galls (Sherf 1964), and certain Attelabidae may be cleptoparasitoids of other attelabids within leaf rolls (Sherf 1964). Paulian (1988) lists some Ptinidae as 'parasites' of solitary bees and wasps. However, the status of all these groups as parasitoids is uncertain.

[p] Paulian (1988) describes the following additional carabid genera as 'parasites': *Chaetodactyla* (on pupae of cetoniine Scarabaeidae); *Arsinoe* (on pupae of Tenebrionidae). Their actual status is uncertain.

[q] Paulian (1988) lists several other species of Scarabaeidae as 'cleptoparasites'. Their actual status is uncertain.

[r] A few species may kill more than one individual, possibly only when the host is very small (= facultative cleptopredators).

[s] Occasionally attacking spiders, also records of some encyrtids attacking mites and ticks and certain tetrastrichine eulophids attacking eriophyid mites and even nematodes (van den Berg *et al.* 1990). Some Pteromalidae attack adult beetles and several genera of euphorine Braconidae attack adult Coleoptera, Hymenoptera and Neuroptera. Perilampine Perilampidae and eucerotine Ichneumonidae have host-searching first instar larvae (some Eulophidae lays eggs in the immediate vicinity of the host). In the complex life cycle of the Trigonalyidae, its eggs are ingested by a caterpillar which is then itself attacked by the vespid, ichneumonid or tachinid host of the trygonalyid.

[t] Including galls, leaf-mines, inside stems and leaves, under bark, and occasionally on roots (some Pteromalidae).

[u] Also one record from a lithobiid centipede.

Table 2. *Summarized data from table 1*

(The numbers are approximate estimates based on described species. The numbers of acquisitions is a minimum figure based on the number of families with independent acquisitions. The estimates for the number of Diptera with host searching by adult female or larva are very rough estimates, based partially on extrapolations from the British tachinid fauna (from Belshaw 1992).)

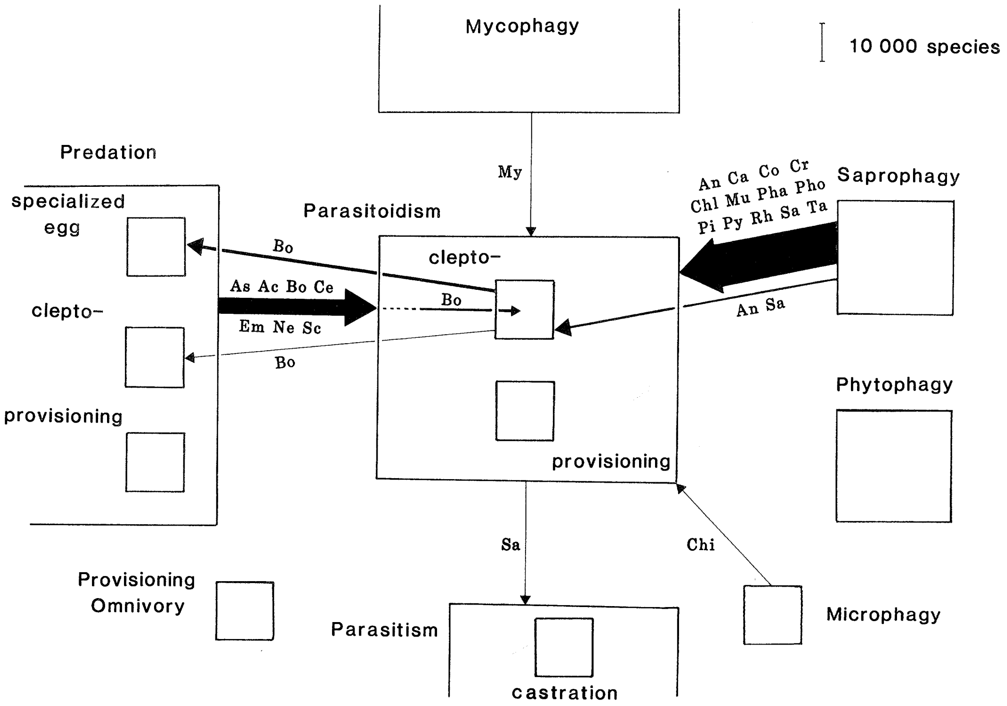
order	no. of parasitoids	no. of clepto parasitoids	minimum no. of acquisitions	host searching by larva	host searching by adult	no. of host orders
Hymenoptera	60 000	7000	1	500	66 500	19
Diptera	15 600	900	21	8600[a]	7900	22
Coleoptera	1600	2000	14	3590	10	8
Lepidoptera	10	—	2	10	—	2
Neuroptera	50	—	1	50	—	3
totals	77 260	9900	39	12 750	74 410	—

[a] Estimates for Diptera host-searching larvae include a number of tachinids where the host ingests the parasitoid egg (about 800 species).

most insect parasitoids have saprophagous, mycophagous or predatory ancestors. Mycophagy is clearly a very important precursor lifeway occurring in both the Hymenoptera and several Coleoptera groups. The shift from phytophagy to the parasitoid lifeway is unknown except in a few cleptoparasitoid groups (see below).

Shifts away from the parasitoid lifeway have been rare in the Diptera and Coleoptera, whereas in the Hymenoptera there have been shifts to cleptoparasitoidism, specialized egg predation, cleptopredation, provisioning predation, provisioning omnivory and phytophagy.

Cleptoparasitoids are present in all three groups (representing a majority of the coleopteran parasitoids) and the lifeway appears to be derived along a number of different pathways. In all three major parasitoid orders some cleptoparasitoid clades appear to have sister groups with the specialized egg predator or cleptopredator lifeway (see below.)



Figures 2. Evolutionary shifts to and from the parasitoid lifeway in the Diptera. The thickness of the arrow is directly proportional to the number of described parasitoid species in families which are derived from the ancestor making the shift. It does not indicate the number of times the shift has occured. Key: Ac, Acroceridae; An, Anthomyiidae; As, Asilidae; Bo, Bombyliidae; Ca, Calliphoridae; Ce, Cecidomyiidae; Chi, Chironomidae; Chl, Chloropidae; Co, Conopidae; Cr, Cryptochetidae; Em, Empididae; Mu, Muscidae; My, Mycetophilidae; Ne, Nemestrinidae; Pho, Phoridae; Pha, Phaeomyiidae; Pi, Pipunculidae; Py, Pyrgotidae; Rh, Rhinophoridae; Sa, Sarcophagidae; Sc, Sciomyzidae; Ta, Tachinidae.

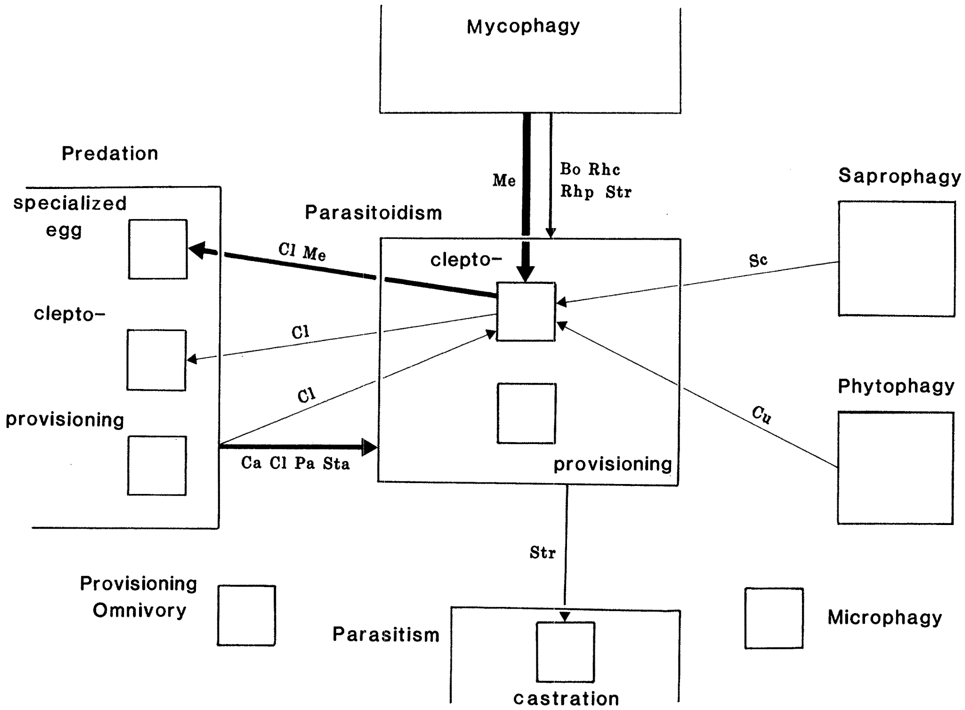


Figure 3. Evolutionary shifts to and from the parasitoid lifeway in the Coleoptera. The thickness of the arrrow is directly proportional to the number of described parasitoid species in the families which are derived from the ancestor making the shift. It does not indicate the number of times the shift has occured. Key: Bo, Bothrideridae; Ca, Carabidae; Cl, Cleridae; Cu, Curculionidae; Me, Meloidae; Pa, Passandridae; Rhc, Rhipiceridae; Rhp, Rhipiphoridae; Sc, Scarabaeidae; Sta, Staphylinidae; Str, Stylopoidea.

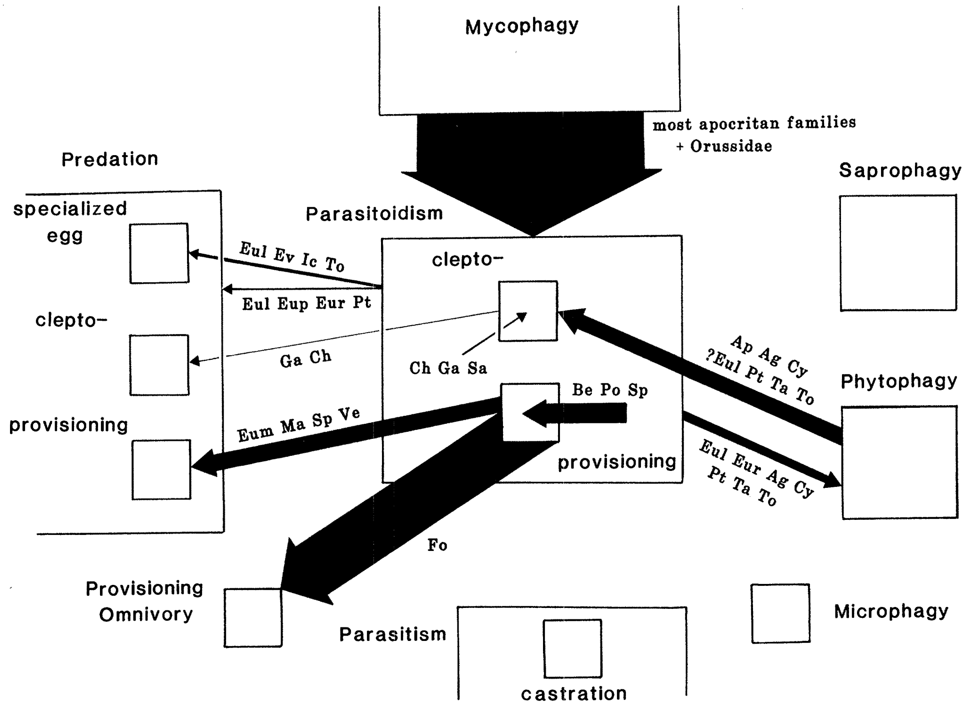


Figure 4. Evolutionary shifts to and from the parasitoid lifeway in the Hymenoptera. The thickness of the arrrow is directly proportional to the number of described parasitoid species in the families which are derived from the ancestor making the shift. It does not indicate the number of times the shift has occured. Key: Ag, Agaonidae; Ap, Apidae; Be, Bethylidae; Ch, Chrysididae; Cy, Cynipidae; Eul, Eulophidae; Eum, Eumenidae; Eup, Eupelmidae; Eur, Eurytomidae; Ev, Evaniidae; Fo, Formicidae; Ga, Gasteruptiidae; Ic, Ichneumonidae; Ma, Masaridae; Po, Pompilidae; Pt, Pteromalidae; Sa, Sapygidae; Sp, Sphecidae; Ta, Tanaostigmatidae; To, Torymidae; Ve, Vespidae.

5. PATHWAYS TO THE PARASITOID LIFEWAY

(*a*) *From mycophagy*

This pathway is found in the Coleoptera and Hymenoptera. One plausibility narrative has been proposed to explain its occurrence (in the Coleoptera) and we propose a second (for the Hymenoptera) which is a modified version of the first.

(i) *Coleoptera*

In some Coleoptera (such as the Rhipiphoridae, Bothrideridae, Passandridae and Stylopoidea and perhaps the Colydiidae) Crowson (1981) has proposed an evolutionary sequence (by plausibility) as follows:

1. A mycophagous ancestor feeding in dead wood and competing for the fungi farmed by ambrosia beetles.
2. A mycophagous beetle killing the ambrosia beetle (often by ejecting it from its tunnel), and feeding on the fungi (essentially a cleptoparasitoid or cleptopredator association). This occurs in some Brentidae, Curculionidae and Colydiidae.
3. A carnivorous form feeding upon the host beetle, either as a predator or as a parasitoid. From this association the parasitoid then passes to other insect groups within the wood. Nearly all stages of the above transition are seen in the Bothrideridae (but with no chronicle to support the narrative).

(ii) *Hymenoptera*

In the Hymenoptera the shift from mycophage to parasitoid appears to have occurred only once. Using the chronicle of Gibson (1986), and Rasnitsyn (1988) we propose the following narrative.

The outgroups of the clade Apocrita plus Orussidae are the Siricoidea *sensu lato*. The bulk of the Siricoidea have symbiotic fungi which are introduced into dead wood by a piercing needle-shaped ovipositor during oviposition (Gauld & Bolton 1988). The larvae then feed on the fungi which develop in their burrows. The similarity of this lifeway to the ancestral groups of coleopteran parasitoids above is striking. Therefore, a modified version of Crowson's (1981) narrative may be applicable here:

1. Competition between siricoids leading to the appearance of forms which feed off the fungi provided by other species. Such cleptoparasitic forms have been described which have no symbiotic fungi of their own and appear to oviposit only into wood already infested by other siricids (e.g. *Xeris spectrum*, Gauld & Bolton 1988).
2. The appearance of cleptoparasitoid forms which kill the host and then feed off the host's fungus supply. Although no clear cases of cleptoparasitoidism occur at the base of the hymenopteran parasitoid lineages, it has been suggested that some first-instar larval orussids may feed on fungus in the host's burrows (Cooper 1953). If proven this would indicate that they are cleptoparasitoids.
3. A shift from feeding on the provision to feeding on the host. The least derived Parasitica (for instance, the Stephanidae and Megalyridae) are indeed associated with dead wood, and many more derived groups have primitive representatives that are associated with dead wood hosts (e.g. the Evanoidea, the Ichneumonoidea, the Cynipoidea).

Other theories explaining the development of the parasitoid lifeway in the Hymenoptera (especially that of Malyshev 1968) are not supported by the chronicle accepted here.

(*b*) *From saprophagy*

This pathway occurs in the Diptera and Coleoptera. We propose two narratives by plausibility:

(i) *Change in the timing of attack*

In groups which are primitively sarcophagous (feeding on dead animals) the shift to the parasitoid lifeway may represent a change in the timing of attack on a host individual, i.e. attacking stressed or dying individuals rather than dead ones.

The Sarcophagidae (Diptera) contain many primarily sarcophagous species (on dead invertebrates) which are also facultative parasitoids. *Apocephalus paraponerae* (Diptera: Phoridae) only attacks adult ants that are injured and dying, thus blurring the distinction between parasitoidism and saprophagy (Brown & Feener 1991). These groups may represent intermediate stages in the above shift. A similar change may have occurred among sarcophages feeding on dead vertebrates. Among the Calliphoridae (Diptera) certain species can be placed in the following (plausibility) sequence: vertebrate sarcophage; feeder on vertebrate wounds; obligate causer of wounds on vertebrates (= ectoparasites) (Zumpt 1965). A species in the final group (*Lucilia bufonivora*) attacks relatively small vertebrates and habitually kills them (i.e. is a parasitoid). In groups where host-finding is by the adult female, such a shift may also result in a change of habitat, for example if the dead organisms were originally consumed in the soil but the normal host habitat is on foliage. This may be relevant to several dipteran families which appear to have evolved from saprophagous ancestors but which are parasitoids of host taxa on plants (Pipunculidae, Cryptochaetidae, most Tachinidae).

(ii) *Change of host*

The shift from the saprophagous to the parasitoid lifeway may involve a change of host within the same environment. One such environment is the soil (and leaf litter) where dead organisms accumulate. The parasitoid taxa which have evolved from saprophages in this microhabitat commonly attack taxa which are predominantly saprophages themselves, i.e. snails (some Calliphoridae and Sarcophagidae (Diptera)), millipedes (eginiine Muscidae (Diptera)), woodlice (Rhinophoridae (Diptera)), earthworms (polleniine Calliphoridae (Diptera)), and Diptera puparia (aleocharine Staphylinidae (Coleoptera)): host taxa which are predominantly saprophages themselves. Parasitoid Chloropidae (Diptera) may also have followed a similar sequence, although this time via saprophagy within plant tissue.

(c) *From predation*

This pathway is found in both Coleoptera and Diptera. Only two plausibility narratives have been suggested for the shift from predator to parasitoid. They share similar features and we outline them below.

(i) *The Carabidae (Erwin & Erwin 1976)*

See table 1 for the biology of carabid parasitoids.

1. The ancestral species was a polyphagous predator with active larvae during all instars. Eggs were laid within the host habitat but away from the hosts themselves. Many prey items were eaten and pupation occurred away from the host.
2. The spatial clumping of prey items of a particular species led to monophagy and the reduction in mobility of later instars, although an active host searching first instar larva was retained. Pupation occurred in the host environment. The energetic saving from losing the modifications associated with high mobility meant that fewer prey items were needed.
3. A shift by the hosts to become more dispersed (or by the predator onto more dispersed hosts) placed selective pressure on the attacking species to become smaller in size (if transit times became uneconomical), and to become associated with one host only during its development. The later larval instars became totally immobile, pupating in the burrows (cells) of the host.

Erwin & Erwin (1976) proposed this as a general explanation for parasitoid evolution among the carabids, although they did not make clear whether they believed this to be a repeated pattern with several acquisitions (i.e. they were presenting an hypothesis of general applicability), or a unique feature of a single clade (i.e. a narrative explanation).

(ii) *The Sciomyzidae (Diptera)*

Berg *et al.* (1959) proposed that the family arose from a general scavenger in moist situations. There was then a specialization as a predator of stranded aquatic snails. Two lifeways then developed from this: (i) aquatic predators of snails; (ii) terrestrial predators and later terrestrial parasitoids of snails. Berg (1964) proposed a more detailed narrative for the shift from terrestrial predation to parasitoidism. His reasoning was that the (proposed) more recent stages are only found in association with the (proposed) older ones. The following sequence of changes were suggested:

1. Young larvae enter the prey shell, initially inflicting relatively little damage on the prey which increases as the sciomyzid larva grows older. The host therefore survives for longer following the attack.
2. The taxonomic range of prey is reduced, at least to family level.
3. Pupation occurs within the shell of the final prey individual.
4. The adult female attaches the egg to the prey shell rather than the prey being contacted by the first instar larva.
5. There is a reduction in the number of prey individuals consumed to one (i.e. the sciomyzid becomes a parasitoid).

The main effect of the above sequence would be to reduce the proportion of the life history the larva spends outside a snail shell. Berg & Knutson (1978) have suggested that such a (putative) shift from predation to parasitoidism, may have been driven by competition within the family, involving the transfer of the burden of host searching from the larva to the adult (which is more mobile and less vulnerable to desiccation). Parasitoidism allowed the colonisation of dry habitats and the exploitation of terrestrial and aestivating snails.

In the Drilidae (Coleoptera) a lifeway close to parasitoidism is found in all studied species. The drilid predator feeds inside the shell of the prey (terrestrial gastropods), and this is a slow process – one or two snails are eaten each year – and development may take several years (Paulian 1988).

Among the Coleoptera, Erwin & Erwin (1976) recognized certain lebiine Carabidae as intermediate between predator and parasitoid lifeways. Similar possible intermediate stages exist in the Lampyridae (Coleoptera), Sciomyzidae and Asilidae (Diptera), Berothidae and Nemopteridae (Neuroptera). In many Asilidae (Diptera) a situation exists similar to that in many sciomyzids. The early larval instars often feed on a single prey individual while the older larvae are more active and attack several prey individuals.

There are certain predictions of both the above narratives that it would be interesting to test: (i) that predator-derived parasitoids should be monophagous; (ii) that they should attack hosts that are dispersed in space; and, (iii) that they should be smaller than their predatory ancestors, if both ancestor and descendant species attack the same (or a similar sized) host.

(d) *Other pathways*

There are no definite examples of evolutionary shifts from parasitism to parasitoidism. However, *Sthenauge*, (Lepidoptera: Pyralidae) is in a subfamily (Chrysauginae) with parasitic forms. Other genera within the group are parasitic or phoretic in the fur of mammals, especially sloths (Waage 1980); and one or other of the habits (insect parasitoid or mammal parasite) may be ancestral with respect to the other. The earlier quoted example of Calliphoridae (Diptera) which cause myiasis in vertebrates may be another example of this pathway.

6. PATHWAYS FROM THE PARASITOID LIFEWAY

(a) *To predation*

Within the Hymenoptera a number of species have become predators. This is either via a provisioning parasitoid pathway (in aculeates) or directly from the parasitoid lifeway (see table 2, figure 4).

(i) *Via a provisioning parasitoid pathway*

For aculeates the evolution of a female strategy of host paralysis and transport of the host to a nesting site to provide provision for the offspring seems to have led to continuous provisioning, where many host individuals are brought to the nest (Gauld & Bolton 1988) for the developing offspring. It is likely that the Apidae (provisioning phytophages) may have arisen from such provisioning predators.

(ii) *Directly from the parasitoid lifeway*

Several chalcidoid and ichneumonoid groups have become predacious without provisioning. In some cases the habit may have arisen from feeding within highly localized discrete microhabitats such as galls, leaf mines or egg masses. Here a basically immobile hymenopteran larvae can feed on number of other organisms in a way functionally similar to a normal parasitoid (cf. the section on specialized egg predators).

(*b*) *To phytophagy*

The only insect species which have moved from the parasitoid lifeway to phytophagy are in the Hymenoptera. The pathway has occurred in several families (see table 1, figure 4). Phytophagy usually occurs in species that feed within discrete highly nutritious microhabitats (e.g. plant galls, leaf mines, etc.). Some groups appear to have shifted from being parasitoids in such a microhabitat to being phytophages in the same microhabitat (especially true of some chalcidoid groups, see Bouček (1988)). The evolution of the most species-rich group of hymenopteran phytophages which seem to have evolved along this pathway, the Cynipidae, is discussed by Fergusson (1990).

(*c*) *Other pathways*

The only shifts from parasitoid to parasite appear to have been in the Stylopoidea (Coleoptera) and the Sarcophagidae (Diptera). In a few other Diptera the host may occasionally survive (see the definitions section). Factors that may contribute to the absence of obligate parasitoid-derived parasites among the insects are: (i) The similarity in size between insect parasitoids and their hosts (in comparison with platyhelminth–vertebrate parasite associations), making successful development of the attacker without fatal damage to the host unlikely; (ii) the necessity of a later developmental stage of the parasitoid to leave the host to disperse and mate, inevitably leading (in the case of species feeding internally) to a massive rupture of the host integument; (iii) the predominance of adult female host finding within insect parasitoids. It is difficult to imagine a situation where a female (for example in a gregarious species) would fail to exploit each host to the full by laying fewer eggs than are necessary to ensure that her offspring would completely consume the host. A 'parasite' gene occurring in this context would clearly be at a selective disadvantage as it would cause the female to produce fewer offspring than her parasitoid conspecifics.

The only insect group to have shifted from parasitoid to parasitic castrator is found within the Stylopoidea (Coleoptera). The persistence of the adult female in the host, with the onus of dispersal being placed on the larval stages, means that (ii) and (iii) above do not apply. In many ways the stylopoid lifeway is very similar to that found in parasitic castrator crustaceans, such as certain Cirripedia and Copepoda (Kuris 1974).

7. THE CLEPTOPARASITOID LIFEWAY

Cleptoparasitoids are found in all three of the main parasitoid orders and in a number of provisioned sites: aculeate nests, scarabaeid dung hoards, plant galls and ambrosia beetle tunnels. Galls are exploited predominantly by Hymenoptera whereas ambrosia beetle tunnels and dung hoards are exploited mainly by Coleoptera. The ubiquity of this habit is probably due to these provisioned sites providing a rich source of protected concentrated food. We propose three routes to cleptoparasitoidism, one via a primitive association with the host (defined here as host-directed cleptoparasitoidism, broadly equivalent to the secondary cleptoparasites of Gauld & Bolton (1988)); and two via the ancestral association with the provisioning (defined here as provision-directed cleptoparasitoidism).

(i) *Host directed cleptoparasitoidism*

Several groups have moved directly from parasitoidism to cleptoparasitoidism (some Chrysididae, the Sapygidae, the Gasteruptiidae (Hymenoptera) and probably the Bombyliidae (Diptera)). This has probably been selected for due to the energetic advantage of utilizing the provision before it is ingested by the host.

(ii) *Provision-directed cleptoparasitoidism (route 1)*

This group consists of cleptoparasitoids that have a primitive association with the provision-type (rather the than specific provision on which they are now feeding). The subsequent association with a particular provision (and host) is not due to a similarity in ecology established by common descent. There are various cases:

1. The Sarcophagidae (Diptera) appear primitively to have entered aculeate (especially Sphecidae) nests to feed saprophagously on the arthropods provisioned by the wasps. Competition for the provision would then have led to the killing of the host and to a cleptoparasitoid lifeway.
2. Some Brentidae and Curculionidae (Coleoptera) are either cleptopredators or cleptoparasitoids of Scolytidae and Platypodidae (Coleoptera). Primitively they may have been competitors for provisions within dead wood (see narrative above for the evolution of coleopteran parasitoids in dead wood).
3. The Meloidae (Coleoptera), which feed on pollen in apid nests (table 1), seem to have evolved from mycophagous ancestors in dead wood but by a rather different evolutionary sequence from paragraph 2

above. If they were ancestrally fungal spore feeders then it is possible, given the close functional similarity of spores and pollen (some beetle groups have species in the same genus feeding off either one or the other: e.g. the Lathridiidae) that a switch from mycophagy to pollen feeding could have occurred without leaving the ancestral habitat, dead wood.

(iii) *Provision-directed cleptoparasitoidism (route 2)*

Many cleptoparasitoids are phylogenetically closely related to their hosts. This includes most hymenopteran cleptoparasitoids in galls and other plant tissue, apid cleptoparasitoids of other bees, scarabaeid cleptoparasitoids of dung, and curculionid cleptoparasitoids of galls. These species were all themselves ancestrally provisioners using the same resource (this is broadly equivalent to the primary cleptoparasites of Gauld & Bolton (1988)). The similarity of ecology between such confamilial (or even congeneric) species may have led, first to competition for the same provision (an individual needs to expend no energy provisioning if instead it can usurp another's provision), and later to a cleptoparasitoid association.

All pathways from the cleptoparasitoid lifeway are either to the cleptopredator or specialized egg predator lifeways. Specialized egg predators are discussed below. The shift to the cleptopredator lifeway appears to involve merely the consumption of more than one host individual in situations where the hosts occur close together. In the case of aculeate hosts this may simply be semi-social or social species where individuals nest very near each other or are found in the same nest. The attacking individual is able to devour the contents of a number of contiguous host cells with little or no requirement for an increase in mobility.

8. SPECIALIZED EGG PREDATORS

In many clades which contain parasitoids or cleptoparasitoids of soil-nesting aculeates there are subclades which are specialized egg predators (within the Mantispidae (Neuroptera), Evanoidea (Hymenoptera), Carabidae, Cleridae, Meloidae (Coleoptera), and Bombyliidae (Diptera)). However, in most cases the polarity of the shift is unknown, and we have used plausibility to infer that the specialized egg predator lifeway is derived.

The evolutionary connection between these two lifeways may be due to the functional similarity between an egg pod buried beneath the ground and a subterranean aculeate nest. Both consist of a discrete concentrated food source hidden from predators and presumably relatively commonly encountered by an active soil-dwelling first instar larva. Orthoptera egg pods are the most common type to be attacked, but cockroach oothecae and spider egg sacs are also exploited. However, not all spider egg sac predators are derived from aculeate-attacking ancestors (e.g. some Eulophidae (LaSalle 1990), and some Ichneumonidae which have evolved from ancestors attacking cocooned hosts (Gauld 1988)).

In some cases the pathway between cleptoparasitoids and specialized egg predators appears to be extremely plastic, for example in the Bombyliidae (Diptera) there must have been multiple acquisitions of the habit and reversals (Hull 1973). In the Cleridae (Coleoptera) both habits occur in the same genus (*Trichodes*, Foster 1976).

Only two parasitoid habits are found within the Anthomyiidae (Diptera): attacking adult Orthoptera or immature aculeates. The recurring association discussed above might suggest how such an otherwise strange taxonomic and ecological conjunction may have arisen.

9. CONCLUSIONS

Although non-hymenopteran parasitoids have been poorly studied they show many features essential to an understanding of the parasitoid lifeway and its evolution. This makes them highly worthy of further investigation. Even within the Hymenoptera certain taxa are poorly known (especially those that generally attack hosts of little economic importance, such as the Proctotrupoidea and Evanioidea). We have almost certainly not identified all insect parasitoid groups, especially those in dead wood and in the soil where observations are difficult to make. Much more basic observational natural history work is needed to clarify aspects of parasitoid biology. Host range information is still scanty, (even for the Hymenoptera) and the data collected so far are often unreliable (Askew & Shaw 1986). In addition, the physiological interactions of host and parasitoid are almost unknown outside the Hymenoptera.

In this paper we have had to present many evolutionary narratives unsupported by phylogenetic reconstructions. Only through estimations of phylogeny using additional data (both morphological and biological) can such narratives be corroborated or rejected (Coddington 1988). Detailed cladistic studies are vital for an understanding of the evolution of biological systems.

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We are still collecting and collating data on parasitoids, especially non-hymenopteran ones, and we would be grateful for any additional literature references or data.

APPENDIX 1. BIBLIOGRAPHY FOR TABLE 1

In addition to the general texts (Clausen 1940; Askew 1971), the following papers have been used.

Diptera

General: McAlpine *et al.* (1981, 1987).

Mycetophilidae: Hickman (1965); Matile (1981).

Cecidomyidae: Records in Barnes (1954), except for *Endaphis gregaria* (Mackauer & Footit 1979) and *Occuloxenium compitale* (Mamaev 1973*a*).

Chironomidae: *Tendipes varus* (van Jutting 1938); unidentified species in *Lymnaea limnosa* L. (Mathias & Boulle 1933).

Nemestrinidae: Records from grasshopper hosts: Greathead (1963).

Acroceridae: See general texts.

Bombyliidae: Hull (1973).

Asilidae: Knutson (1972).

Empidae: Knutson & Flint (1971 & 1979); Vinikour & Anderson (1981).

Phoridae: Ferrar (1987). Many primary sources for rearings of *Megaselia* cited in Robinson (1971). Records from earthworms and snail hosts (R. H. L. Disney, personal communication); from adult Lampyridae in Lloyd (1973); from adult ants in Brown & Feener (1991).

Pipunculidae: see general texts.

Conopidae: host groups reviewed in Smith (1966). Record from *Stylogaster* in Smith & Cunnigham-van Someren (1985).

Sciomyzidae: Berg & Knutson (1978), Ferrar (1987); but also see Bailey (1989) and Vala *et al.* (1990). Recent additional records in Barnes (1990) and (for *Sciomyza testacea*) Knutson (1988).

Phaeomyiidae: Bailey (1989) and Vala *et al.* (1990).

Chloropidae: Ferrar (1987). Evolution of lifeways within family discussed in Narchuk (1972).

Anthomyiidae: Ferrar (1987).

Muscidae: *Syngamoptera flavipes* in Ferrar (1987). *Neohelina* sp. in Bailey (1989), *Eginia ocypterata* in Bailey 1989, genus and species unknown in Ferrar (1987).

Calliphoridae: Ferrar (1987), Rognes (1986, 1992), Ibrahim (1984) (several other references to *Pollenia*).

Rhinophoridae: Ferrar (1987), Bedding (1965).

Sarcophagidae: Ferrar (1987). *Notochaeta bufonivora* in De Souza Lopes (1981), De Souza Lopes & Vogelsang (1953). Caged life expectancy of bees containing larvae of *Senotainia tricuspis* was 32 days compared with 45 days in healthy individuals (Alekseenko & Mazhar 1961), see also Simintziz (1958). Records of *Sarcophaga sarracenioides*, *Boettcharia litorosa* and *Helicobia morionella* as parasitoids or parasites of *Bombus* (Apidae: Hymneoptera) in Ryckman (1953). For records of *Sarcophaga sarracenioides* and *Gymnoprosopa argentifrons* as parasitoids or parasites of adult Scarabaeidae see Rogers (1974).

Tachinidae: Ferrar (1987). Estimations of species in the various host-finding groups (table 2) are extrapolations from the British fauna (Belshaw 1992). Records from scorpions in Williams *et al.* (1990).

Coleoptera

General: Crowson (1981), Lawrence (1982); information on relationships came from Crowson (1967, 1981).

Carabidae: General: Erwin & Erwin (1976); Erwin (1976). *Brachinus*: Erwin (1967). *Pelecium*: Salt (1928). *Lebia*: Silvestri (1902); Chabossou (1939); Lindroth (1954); *Pheropsophus* (the egg pod predator): Habu & Sadanga (1964).

Staphylinidae: *Aleochara*: Klimaszewski (1984) and references therein.

Scarabaeidae: *Onthophagus* and *Aphodius*: Hammond (1976) and references therein.

Rhipiceridae: *Sandalus*: Elzinga (1977)

Cleridae: *Trichodes*: Foster (1976) and references therein. *Isohydnocera*: Clausen (1940).

Rhipiphoridae: Selander (1957). Pelectominae: Hudson (1934), Argaman & Mendel (1988). Rhipidinae: Riek (1955). Rhipiphoridinae: Linsley *et al.* (1952). Hamilton (1978) discuss the probable wood-inhabiting ancestory of the group.

Meloidae: Phylogenies inferred from the classification in Selander (1964) and the cladogram in Kaszab (1959). They present very different schemes but neither contradicts the conclusions here. Biological data: McSwain (1956), Pinto & Selander (1970), and scattered data in papers by Selander and Pinto. Details of meloid egg pod predators in Selander (1982). Additional information on outgroup biology from Mamaev (1973*b*).

Passandridae: see Clausen (1940).

Bothrideridae: Dajoz (1977); Roberts (1980); Stephan (1989); for outgroup biology see Pal & Lawrence (1986).

Stylopoidea: Kathrithamby (1989) and references therein.

Neuroptera

Mantispidae: Lambkin (1986) and New (1989) and references therein.

Hymenoptera

Orussidae: Gauld & Bolton (1988) and references therein.

Apocrita: Boucek (1988), Brown (1982), Gauld (1984); Gauld & Bolton (1988) and references therein.

Lepidoptera

Pyralidae: Jordan (1926).

Epipyropidae: Kirkpatrick (1947).

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