

EVOLUTION AND BEHAVIORAL ECOLOGY OF HETERONOMOUS APHELINID PARASITOIDS

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■ **Abstract** In almost all species of parasitic wasps in the Coccophaginae, a subfamily of Aphelinidae, males have host relationships different from females. In these “heteronomous” species, females are generally endoparasitoids of sternorrhynchous Hemiptera, such as scale insects, mealybugs, and whiteflies. In contrast, males may be hyperparasitoids, developing in or on conspecific females or other primary parasitoids. In other species, females are endoparasitoids of whiteflies, and males are primary endoparasitoids of eggs of Lepidoptera. Males and females may both be primary parasitoids on the same species of scale insect hosts, but females develop as endoparasitoids, whereas males are ectoparasitoids. Here we review these life histories, focusing on examples of sexually dimorphic host relationships, development, and morphology. Coccophagine species may be sexual or parthenogenetic; we discuss reproductive modes and the interaction of sex ratio distorters with sex-specific host relationships. Sex allocation in the species in which males are hyperparasitoids involves choices of not what sex egg to lay, but whether to accept or reject a host of a given type; study in this area is reviewed as well as research in kin discrimination and ovicide. Last, we present the current understanding of phylogenetic relationships within this lineage and discuss hypotheses for the evolutionary origin of heteronomy in the Aphelinidae.

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INTRODUCTION

Insects are well known among free-living terrestrial animals for their often complex life histories (109, 194). Complete metamorphosis in holometabolous insects allows a sequential specialization of form and function and often the use of dissimilar resources by the larval and adult stage. Other insects exhibit generational polymorphism; aphids and gall wasps are known to produce different forms with different reproductive modes at different times of the year. Morphologically differentiated castes of social insects allow functional specialization of relatives within a colony. An often overlooked and less common type of polymorphism occurs in the sexually dimorphic "heteronomous" insects (182) in which male and female immature stages are specialized on different resources, may have morphologically differentiated larval forms, and are likely to be different sizes as adults.

Heteronomous life histories are apparently restricted to two parasitic lineages of insects. In the strepsipteran family Myrmecolacidae, male larvae develop as parasitoids of ants, whereas female larvae have been found to be parasitic on Tettigoniidae (long-horned grasshoppers), Gryllidae (crickets), and Mantodea (mantids) (93, 94). We focus here on the second, better known example, the subfamily Coccophaginae in the hymenopteran family Aphelinidae. In all but exceptional cases, female coccophagines are endoparasitoids of sternorrhynchous Hemiptera, such as scale insects, mealybugs, and whiteflies. Males of all but a very few species, however, develop in a manner different from females. In most cases, males are hyperparasitoids, developing in or on primary parasitoids, sometimes on conspecific females. Males of heteronomous species are not always hyperparasitic, however, and may develop on other hosts or as ectoparasitoids of the same host as females. In a few of the 642 valid species in the subfamily (114), both sexes develop as primary endoparasitoids. We argue that the latter probably represent rare instances of a reversal to a simpler life history.

What is the evolutionary basis for heteronomy and in particular for the life history in which males are hyperparasitoids? Sexual dimorphism in animals often

has its basis in sexual selection; for example, males may be bigger than females in species in which males engage in contests for mates. Sexual dimorphism may also be explained by natural selection, for example, when the sexes are specialized to consume different diets (135, 138). More relevant to this discussion, natural selection may also favor females larger than males when the fecundity of females is strongly dependent on body size, the fitness of males is less influenced by size, and resources are limited (17, 18). In hymenopteran parasitoids, females may preferentially lay female eggs in large hosts that will yield a larger adult parasitoid (17, 18). This precision in sex allocation is possible because hymenopterans are haplodiploid (females are diploid and males are haploid), and females are able to control the sex of their offspring by selectively fertilizing eggs as they pass through the oviduct. Whereas most of the observed cases of sex allocation on the basis of host size involve females choosing among variable hosts of the same species, facultative hyperparasitoids (that may lay eggs of either sex on either the herbivorous host or an immature parasitoid) have also been observed to lay more male eggs when parasitizing parasitoids, the smaller host resource (97).

Sex allocation theory may provide a context for understanding the evolution of these wasps with hyperparasitic males, but it is clearly not sufficient. While female eggs develop in the larger host and male eggs develop in the smaller host, heteronomous aphelinids exhibit little flexibility in oviposition behavior. Females place eggs of one sex almost exclusively on the "correct" host, and when infrequently, a male egg is laid on the "incorrect" host, it does not develop (60, 62, 82, 85, 197). Although several hypotheses have been proposed for the evolution of this life history (see "Evolutionary History" below), some are based on group-selection arguments, and all are necessarily speculative. Impeding a convincing explanation is our ignorance of the life history of the ancestor to this group. Furthermore, the taxonomic distribution of heteronomous species suggests that sex-specific host relationships arose once in an ancestral species and then diversified as the lineage diversified, so that we may be trying to explain one lucky (or unlucky) accident. Even so, the rarity of examples in which heteronomy has clearly been lost suggests that there are powerful selective forces involved in its maintenance, or little genetic variance for alternative modes of development.

Whatever the evolutionary origins of coccophagine aphelinids, these animals have been and will continue to be important in developing and challenging our fundamental understanding of parasitoid physiology, behavior, and evolution. Heteronomous species may offer systems to study the development of different mechanisms in males and females to acquire nutrients and overcome the immune responses of hosts. For example, in some mealybug hosts, female eggs and larvae of *Coccophagus gurneyi* Compere are encapsulated, but male eggs are not (13, 43, 181). Moreover, in some species female embryos are surrounded by an extraembryonic membrane, but males are not (16, 44, 89). In behavioral ecology, highly variable sex ratios of heteronomous parasitoids may sometimes be simply explained by theory developed for the ubiquitous 1:1 sex ratio, Fisher's (35) principle of equal parental investment in both sexes. Heteronomous species with male

hyperparasitoids are also potential model systems for the study of kin discrimination. In these species, searching females may be at risk of parasitizing larval or pupal sisters or daughters, or at least in a couple of species, killing their own egg in the attempt to eliminate competitors from a host (4, 112, 202). Lastly, the mechanism that maintains the sex-specific relationships of most species of coccophagine parasitoids provides an enduring puzzle, especially because one might predict circumstances in which a “mutant” conventional primary parasitoid would be at a tremendous selective advantage. An understanding of this mechanism may illuminate larger issues such as the evolution of host range or sex determination in the Chalcidoidea.

Various aspects of the biology of this group have been reviewed by Flanders (52), Viggiani (171, 172), Walter (181, 182, 184, 185), and most recently by Williams & Polaszek (203). The goal of this review is to introduce the natural history of heteronomous aphelinids to new readers, to review recent research on their sex-specific host relationships, their behavioral ecology, and their evolutionary history, and to re-examine hypotheses for the evolutionary origin of heteronomy. Throughout we attempt to identify some of the many unanswered questions about this diverse group of animals.

HOST RELATIONSHIPS

Apart from a few exceptions, most coccophagine Aphelinidae exhibit one of a few kinds of heteronomous biologies. The host relationships of females are conserved in this lineage; in almost all species, females develop as solitary endoparasitoids of coccoid (mealybug or scale insect) or aleyrodid (whitefly) hemipteran hosts. Male host relationships are more variable.

Terminology

Walter (182) made a tremendous contribution to the study of heteronomous biologies in aphelinids by reviewing the complex, scattered, and in some cases anecdotal literature and finding that all known examples could be placed into just three different categories. Prior to Walter's work (182), the terminology describing the different forms of heteronomy had become quite complex. Walter's (182) use of “heteronomy” (i.e. “subject to different laws or modes of growth”) is especially useful in setting these animals apart. Among heteronomous aphelinids, Walter called the most common life history, in which females develop as primary parasitoids and males as hyperparasitoids, “heteronomous hyperparasitoids” (182). This new term replaced “adelphoparasitoids” (“adelpho” = brother) (209) as a general category. Within heteronomous hyperparasitoids, Walter designated three terms to differentiate species on the basis of the male host relationships. “Facultative autoparasitoids” designated those species in which males develop in both conspecific and heterospecific hosts. “Obligate autoparasitoids” referred to species in which males develop only on conspecifics. Lastly “alloparasitoids” described

those species in which male eggs are always laid in heterospecific wasp hosts. The usefulness of these subcategories was later questioned because in many cases these relationships are not immutable traits of species, but are dependent on the community in which a species is found, and may vary geographically and over time with changes in community structure (203). The first two subcategories pertaining to different types of autoparasitoids may be problematic. For example, a given heteronomous species might be termed an "obligate autoparasitoid" when found sharing a host with a competitor that is invulnerable to its attack, but be termed a "facultative autoparasitoid" when the competing species is susceptible. We propose that these two subcategories be collapsed to one, "autoparasitoids," a scheme that would prevent the indelible labeling of species with traits that are likely to be ecologically labile.

Williams & Polaszek (203) suggested that obligate alloparasitism is best considered at one extreme of a spectrum of possible heteronomous hyperparasitic host relationships, the other extreme of which would be obligate autoparasitism. However, there are some species that do not appear to produce males on conspecifics in any circumstances. For example, in *Coccophagus malthusi* Girault, males and females are almost always reared from different scale insects on different host plants (1, 2, 42). For this reason, we think the term "alloparasitoid" should be retained, with the less specific "heteronomous hyperparasitoid" used as a general term and for instances in which the secondary host range of males cannot be clearly determined.

Within the heteronomous hyperparasitoids, species vary in where the male egg is laid and where the male larva develops. Males may develop as secondary endoparasitoids or secondary ectoparasitoids. Also, the male egg may be laid directly in or on the parasitoid host; species that produce males this way are called "direct" heteronomous hyperparasitoids (182). In "indirect" species, male eggs are laid in the hemipteran host, either at the same time as a female egg, or in anticipation of another parasitoid egg being laid (13, 181). The male egg does not hatch, however, until the primary parasitoid has consumed the entire hemipteran host and the dry environment induces hatching. This phenomenon has been called "inhibited hatching" because, in the absence of a primary parasitoid, the male egg may remain in a quiescent period for some time [a period of 85 days was recorded by Cendaña (16)!]. The male larva then consumes the primary parasitoid.

In addition to autoparasitism, two other less common heteronomous life histories are well documented. Males and females of "diphagous" parasitoids are both primary parasitoids of scale insects, but females develop as endoparasitoids, and males develop as ectoparasitoids (182, 185). Also, males and females of "heterotrophic" aphelinids are both primary endoparasitoids, but females develop in whiteflies and male eggs develop in eggs of Lepidoptera.

Finally, we have adopted the terms "primary" and "secondary" hosts to refer to the hemipterans and immature wasps, to avoid the potential confusion of the terms "unparasitized" and "parasitized" hosts (7, 80). The latter terms do not readily allow a distinction to be made between a female laying a female egg into a recently

parasitized host (superparasitism) and a female laying a male egg into or onto a wasp larva or pupa within the mummified hemipteran remains (hyperparasitism). In the first situation, female larvae compete for hemipteran host resources, whereas in the second, the male larva develops directly on the immature wasp.

Taxonomy of Heteronomous Aphelinidae

The literature on heteronomous biologies in Aphelinidae contains a plethora of genus, tribe, and subfamily names, not all of which are now considered valid. In part, these complications arose because of the instability of suprageneric classifications in Aphelinidae. Hayat (73) summarizes at least 10 different classification systems that have been used, with from 2 to 7 subfamilies and various tribal systems within subfamilies. We follow the classifications of Hayat (73, 74), who uses a reduced number of subfamilies compared with some authors (134, 205, 206). Hayat's concept of Coccophaginae includes all of the genera contained in Physcinae, Prospaltellinae, and Pteroptricinae by earlier workers (31, 33, 71, 96, 134). The following genera in Coccophaginae are considered valid, followed in parentheses by their more common synonyms, by which they are likely to be encountered in the literature: *Coccophagus* (*Aneristus*), *Euxanthellus* [taken out of synonymy with *Coccophagus* by Heraty et al (78)], *Encarsia* (*Prospaltella*, *Aspidiotiphagus*, and *Aleurodiphilus*), *Coccophagoides*, *Coccobius* (*Physcus*), *Lounsburyia*, *Timberlakia*, *Pteroptrix* (*Archenomus*, *Bardylis*, *Casca*), and *Encarsiella*. The following genera are also included in Coccophaginae, but there is no information on male development: *Oenrobia*, *Prophyscus*, *Dirphys*, and *Verekia*. Of the genera included in Coccophaginae, heteronomous biologies are known in *Coccophagus*, *Coccophagoides*, *Lounsburyia*, *Coccobius*, *Pteroptrix*, *Encarsiella*, and *Encarsia* or in taxa now considered to be their synonyms.

Despite several references in the literature to *Ablerus* species (*Azotus*) as "autoparasitic" (168, 169, 171, 182, 203), we can find no evidence that these species have a heteronomous biology. *Ablerus* species are commonly hyperparasitoids in armored scale insects and other hosts (30, 95, 171). Reports of autoparasitic biology seem to refer to Zinna's (210) finding that males of *Ablerus matritensis* (Mercet) occasionally develop as tertiary parasitoids on larvae of their own species. [Viggiani (168) suggested that *A. matritensis* could be a synonym of *Ablerus celsus* (Walker)]. Whereas it is interesting that only male larvae seem to do this (172), this is probably because only male larvae can develop on such a small host. Although it may be correct to refer to this biology as "autoparasitic," it is quite a different biology from that found in heteronomous hyperparasitoids, in which hyperparasitic male development is obligate, and we suggest that the term be reserved for those species with heteronomous life histories. Although *Ablerus* has at times been classified with other coccophagine Aphelinidae, it is now usually placed in a separate subfamily, Azotinae (73).

It is interesting that all of the taxa known to have heteronomous biologies are members of Coccophaginae and that, with few exceptions, all taxa of

Coccophaginae for which both males and biologies are known are heteronomous. Evidence for monophyly of this lineage is provided by a unique and distinctive conformation of the mesofurcal arms, an internal skeletal structure to which several major muscle groups are attached (77, 78). The modification of the mesofurca involves displacement and modification of several muscle groups and is unlikely to have occurred more than once in Aphelinidae. Additional evidence for monophyly of Coccophaginae [see Hayat (73)] is provided by an apomorphic configuration of the metasoma in which the syntergum and outer plates of the ovipositor are not continuous as in most other Chalcidoidea, but are separated by membrane (JB Woolley & M Hayat, unpublished data). It seems clear that heteronomous biologies arose once in the common ancestor to Coccophaginae and are now present virtually throughout this radiation.

Heteronomous Hyperparasitism: Autoparasitoids

Heteronomous hyperparasitism is the most common heteronomous life history, and as we have mentioned, there is considerable variation among species as to where the male egg is laid and how it develops. Most commonly, male eggs are laid directly into or on the secondary host within the remains of the hemipteran. This type of biology is documented in numerous species of *Coccophagus* (including *Euxanthellus*), *Coccobius*, *Coccophagoides*, and *Encarsia* (182). In addition, at least one species of *Encarsiella* is known to develop as an autoparasitoid with ectophagous males (100). Walter provides an extensive list of references and tabulates the cases in which male development is endoparasitic, ectoparasitic, or both. Most genera for which multiple cases of heteronomy are well documented (e.g. *Encarsia*, *Coccophagus*, *Coccobius*, or *Coccophagoides*) contain species with males that develop internally as well as species whose males develop externally (182). Therefore, the location of male development appears to be quite labile evolutionarily, although it generally appears to be constant within particular species. As illustrated by Flanders (42), first instar male larvae of different species of *Coccophagus* may have strikingly different morphologies, presumably adaptations to internal or external development in different host environments. Males in some species of *Encarsia* (178) and *Coccobius* (52, 155) begin development as endoparasitoids and finish as ectoparasitoids. Males of *C. gurneyi* are reported to develop internally when oviposition is direct and externally when oviposition is indirect (13, 50, 140). Further study is needed to determine whether both male forms are really contained within one species or represent two cryptic species (182).

Indirect autoparasitoids lay male eggs in the primary host and hatch when either conspecific or heterospecific parasitoids finish consumption of the hemipteran host. Indirect autoparasitism is well documented in *Coccophagus basalis* Compere (49, 56), *Coccophagus pseudococci* Compere (49, 53), *Lounsburyia trifasciata* (Compere) (39, 42, 49, 53), *C. gurneyi* (39, 40, 42, 47, 49, 52), and *Pteroptrix orientalis* (Silvestri) (57, 58, 176).

There are some reports of indirect autoparasitism that are likely to be incorrect. *Encarsia formosa* Gahan, the San Jose scale race of *Encarsia perniciosi* Tower, and *Encarsia smithi* (Silvestri) have been reported to have indirect oviposition of male eggs (52, 182). *E. formosa* is normally thelytokous (i.e. females may produce daughters without mating; see "Reproductive Modes" below). In this species, the rare male larvae, when they occur, develop as primary parasitoids of the whitefly host (167, 208). Flanders (52) reported that *E. formosa* was an indirect autoparasitoid, perhaps because an early (incorrect) report that males were hyperparasitoids was combined with the observation that oviposition in secondary hosts does not regularly occur (59). A similar situation is likely for *E. smithi*. Smith wrote to Flanders (49) that unmated females of *E. smithi* laid eggs in whiteflies. Flanders appeared to conclude from this that the species laid male eggs indirectly (52). In a later publication, Smith [see Flanders (54)] reported a population of *E. smithi* that was thelytokous; thus, the eggs laid by unmated females were likely to be female. Flanders (52) also based his categorization of *E. perniciosi* as an indirect autoparasitoid on Tower's (157) early observations on this species. Tower (157) observed eggs and larvae of different stages of *E. perniciosi* within a single host and also observed a "second larva within the body of the first." He stated that the second larva enters the body of the first, but "does not greatly injure the first larva" in this process. It seems most likely that this last statement was conjecture; Chumakova & Goryunova (19) reported that *E. perniciosi* females deposit male eggs directly inside first instar female parasitoid larvae, and there have been no subsequent reports of indirect endoparasitic male autoparasitism in this species. Thus, we are not convinced that indirect heteronomous biologies occur in *Encarsia* spp., which has few examples of males developing as ectoparasitoids at all (172). Indirect oviposition of hyperparasitic male eggs seems to occur in scattered, generally unrelated species attacking several different host families and may relate more to characteristics of particular hosts than to the evolution of some particular variation of heteronomous biology.

Heteronomous Hyperparasitism: Allopasitoids

In all but a few recorded species, conspecific females are either the only hosts for males or are one of two or more secondary host species; thus, most heteronomous hyperparasitoids are also autoparasitoids. As mentioned earlier, however, there are a few species that appear to be true allopasitoids, in which males never develop on conspecific females (182). Well-documented cases of allopasitism fall into two groups. The first group consists of indirect heteronomous hyperparasitoid species in which conspecific female larvae do not create a suitable environment for male eggs to hatch. Both male and female eggs of *C. basalis* are deposited into the subesophageal ganglion of *Coccis hesperidum* L or species of *Saissetia*. Male eggs hatch only when another parasitoid larva, such as *Metaphycus stanleyi*, has completely consumed the fluid body contents of the primary host (56). Male larvae of *C. basalis* then feed externally on the primary parasitoid larva. During

the period in which the male egg is quiescent, and apparently following oviposition by another primary parasitoid species, a black jacket forms around the male egg that may protect it from attack by the larva of the primary parasitoid (56). A similar mechanism prevents parasitism of conspecific female larvae in *L. trifasciata*, another indirect heteronomous species in which both male and female eggs are deposited internally into *Saissetia oleae* (Olivier). Female larvae of *L. trifasciata* pupate within a "respiratory sheath" that is surrounded by the fluid body contents of the primary host (16, 42); thus, they do not create a suitable environment for hatching of male eggs. Workers found that males of *L. trifasciata* were never produced in pure cultures (39), but were produced on *Coccophagus* spp. (42); thus, the allopasitoidic habit appears to be obligate in this species on this primary host. This work was conducted in lab cultures as part of the biological control effort against *S. oleae* in California, and it might be argued that *L. trifasciata* might not be allopasitoidic on other primary hosts in its original habitat. However, *L. trifasciata* is a common parasitoid of *S. oleae* in South Africa (23), from which it was originally collected (22), and we have been able to find only one record of it attacking another primary host species, a *Lecanium* sp. (156). Further, the respiratory sheath formed by the female larva suggests that females of this species may be adapted to develop on large hosts (16, 42).

The second group of allopasitoids contains species in which males are laid directly in or on the secondary host. The best documented of these species is *Coccophagus malthusi* Girault, which Flanders (42) lists as the equivalent of a direct heteronomous hyperparasitoid with ectoparasitic male larvae, based on rearing records in the literature (which, unfortunately are not provided). Flanders (42) noted that females of this species are always reared from species of *Ceroplastes* but that males are always reared from soft scale insects such as *Saissetia*. This pattern was reinforced by the comprehensive revisionary studies of Annecke (1) and Annecke & Insley (2), which provide numerous rearing records for this species from South Africa. None of the series of *C. malthusi* examined contained mixed broods. Females were reared only from *Ceroplastes*, *Waxiella*, and *Gascardia*, and males from parasitoids of *C. hesperidum*, *Coccus proteae* Brain, *Saissetia* spp., and *Parasaissetia* spp., almost always on different host plants from the hosts of females. It is interesting that, if oviposition of male eggs is indeed direct in this species (42), inhibited hatching of the male egg is presumably not involved; thus, the basis for the obligate allopasitoidic habit in *C. malthusi* must be something different than in *L. trifasciata* and *C. basalis*. A host that is too large for females to consume entirely could also prevent oviposition of male eggs by species that do not lay eggs of ectoparasitic males until there is an air-filled cavity within the hemipteran cuticle (61, 87). Whatever the mechanism, it seems possible that transitions between autoparasitism and allopasitism could occur as a result of host shifts (184).

Allopasitism is likely to be underreported because of the difficulties in ascertaining the precise host relationships of males, especially when the herbivorous hosts are different. Some life histories are unresolved but suggest allopasitism. In one example, a large and concerted effort was made to rear and import *Pteroptrix*

chinensis Howard for biological control of California red scale (48). Daughters were readily produced from exposure of red scale to field-collected females, but exposure of unmated females to various stages of primary hosts and conspecific and heterospecific secondary hosts of various species failed to yield male offspring, although unmated females readily oviposited. Males were clearly necessary for reproduction but were only collected in sweep samples in areas where adult females were emerging (48).

Diphagous Species

In diphagous species, males and females are both primary parasitoids, but males are ectoparasitic. In these species, females exhibit different oviposition behaviors for the deposition of eggs of each sex, drilling through the scale cover into the scale insect for oviposition of a female egg and inserting the ovipositor along the substrate below the scale for oviposition of a male egg (46, 49, 52, 55, 209). Although the nature of sex allocation in diphagous species is unknown, Walter (185) found that superparasitizing females of *Coccophagus bartletti* Annecke & Insley (2) were more likely to lay a second egg of the same sex as the first egg, suggesting some association of certain host qualities with eggs of one sex. Diphagous development is known from *C. bartletti* (183, 185), as mentioned, as well as from *Coccophagus hemera* (Walker) (209), *Coccophagus longifasciatus* Howard, *Coccophagus ochraceus* Howard (49), and *Coccophagus matsuyamensis* Ishihara (170). Based on a personal communication from Rössler, Walter (182) listed *Coccophagus saissetiae* (Annecke & Mynhardt) as a diphagous species. This was confirmed for *C. saissetiae* and *Coccophagus varius* (Silvestri) by Mazzone & Viggiani (106), who also found that male and female larvae have different forms in these species. Silvestri (137) distinguished *Encarsia ectophaga* (Silvestri) from other species partly based on his observation that both sexes of larvae develop as external parasitoids, but Flanders (49) suspected that this may actually be a case of diphagous development. Ferrière (33) listed *Encarsia coniugata* (Masi) and *Encarsia partenopea* Masi in a biological category equivalent to diphagous development; however, he provided no further evidence for either species. Both species are parasitoids of whiteflies, and both are now considered synonyms: *E. partenopea* is a synonym of *Encarsia inaron* (Walker), a species in which both sexes develop as primary internal parasitoids of whitefly (discussed below), and *E. coniugata* is a synonym of *Encarsia tricolor* Förster, an autoparasitoid. Thus, diphagous biologies appear to occur only in *Coccophagus*, and there is currently no convincing evidence for diphagous development in *Encarsia*, although the interesting case of *E. ectophaga* deserves further study.

Heterotrophic Species

This rather extreme form of heteronomous biology, in which females develop as endoparasitoids of whiteflies and males develop as primary endoparasitoids of eggs of Lepidoptera, was first noted by Flanders (36–38), who reared males of an

unidentified *Encarsia* sp. from codling moth eggs in California. Beingolea (9, 10) reared an unidentified *Encarsia* from *Anomis texana* Riley (Noctuidae), and Stoner & Butler (144) reared *Encarsia* males from *Helicoverpa zea* (Boddie) and *Trichoplusia ni* (Hübner) (both Noctuidae). Rojas (130) found that unmated females of *Encarsia porteri* (Mercet) reared from whiteflies would oviposit in eggs of several families of Lepidoptera (Noctuidae, Yponomeutidae, Gelechiidae, and Pyralidae) and that male *E. porteri* developed successfully in these hosts. In these studies, males were reared from Lepidoptera eggs and females from whiteflies, but Polaszek (121) questioned whether the host relationships of these species are obligate and therefore justify special terminology. His misgivings were based in part on the Stoner & Butler (144) determination of the parasitoid reared from noctuid eggs to be *Encarsia lutea* (Masi), a species known to be an autoparasitoid. The matter was settled in part by a study of the voucher specimens, which showed that the species was actually an undescribed species near *E. porteri* (125). Further, experimental studies with *E. porteri* indicated that males are unable to develop as either primary or hyperparasitoids of whiteflies, but are indeed restricted to eggs of Lepidoptera (89). To date, the heterotrophic biology is known only from two closely related species of *Encarsia*. Egg parasitism is also known in an undescribed species related to *E. inaron* (in which both sexes are primary parasitoids of the whitefly), but this species is not heterotrophic because both sexes appear to be capable of developing in Lepidoptera eggs (203). Otherwise, egg parasitism is not known in Coccophaginae.

Exceptional and Nonheteronomous Species

With very few exceptions, arrhenotokous coccophagine Aphelinidae with known biologies are heteronomous. In some instances, sex ratios are implicated in populations that produce males as primary parasitoids [see "Sex Ratio distorters" below; 85, 88]. Otherwise, cases of male Coccophaginae developing as primary parasitoids are quite limited. In *Encarsia*, most of the ~40 species for which information on biology is available are heteronomous hyperparasitoids or are thelytokous (204), but both males and females of *E. inaron* and *Encarsia longicornis* Mercet are primary endoparasitoids of whiteflies (67, 175).

In *Pteroptrix*, two species are known in which both males and females are primary parasitoids of armored scales. Bar & Gerling (8) demonstrated that both male and female larvae of *Pteroptrix smithi* (Compere) develop as primary parasitoids of *Chrysomphalus aonidum* (L.), and Viggiani (173, 176) showed that both males and females of *Pteroptrix longiclava* (Girault) are primary parasitoids of *Quadraspidotus ostreaeformis* Curtis.

Coccobius fulvus (Compere & Annecke) represents the third instance in which males, as well as females, are primary parasitoids. Both sexes of *C. fulvus* develop on armored scale insects (117, 154). All other *Coccobius* species whose biologies are known (five species) are autoparasitoids (26, 118, 126, 172, 177, 197, 198), and all species of *Coccophagus* or *Coccophagoides* that are currently known are either heteronomous or thelytokous.

Two other taxa are noteworthy because females develop on unusual hosts. All four members of the *flavoscutellum* species group of *Encarsia* are known to attack aphids in the family Hormaphididae (32). *Encarsiella boswelli* (Girault) is known to be an egg parasitoid of species of Plataspidae (Heteroptera) (123). It is not yet known whether these species are heteronomous.

SEX-SPECIFIC DEVELOPMENT

Reproductive Modes

All Hymenoptera are haplodiploid and technically parthenogenetic because haploid eggs develop without fertilization (193). Most sexually reproducing species are arrhenotokous; males develop from unfertilized eggs, and mating must occur for the production of diploid females. In thelytokous species, some mechanism restores diploidy of unfertilized eggs, leading to the production of a diploid female (145). A term that has declined in use and general usefulness is deuterotoky [or amphitoky; see Walter (182)], in which unfertilized eggs may give rise to males or females. Because thelytokous species commonly produce a few males, DeBach (25) proposed that species in which <5% of the offspring are males should still be termed thelytokous. Because parthenogenesis in some species is caused by the vertically transmitted bacteria *Wolbachia* (148), it is reasonable to assume that many of the thelytokous species that produce a few males, as well as some species that have been termed deuterotokous, are infected with parthenogenesis-inducing (PI) *Wolbachia* with less than perfect vertical transmission (102; for recent reviews of PI *Wolbachia*, see 84, 145, 189). Thus, unfertilized eggs that are infected develop as females, and eggs that are uninfected develop as males. There may be, however, at least one genuine instance of deuterotoky in a heteronomous species. Unmated females of *P. orientalis* regularly lay both male and female eggs within the scale body of the white peach scale (57). Males then undergo delayed development and develop as indirect hyperparasitoids. Both mated and unmated females produce similar numbers of males, but the offspring sex ratios of mated females are more female-biased as their fecundity is greater. How this extraordinary reproductive biology is accomplished is still not known, but females appear to have differentiated ovarioles (57).

Thelytokous Parthenogenesis Thelytokous parthenogenesis, in which females develop from unfertilized eggs, appears to be relatively common in parasitoids in the Chalcidoidea relative to the Ichneumonoidea (102). An estimation of the proportion of thelytokous species across the coccophagine lineages is not available, but within the single genus *Encarsia*, 9 of the 40 species for which reliable information is available have at least some thelytokous populations (204). The origin of thelytoky in all but one coccophagine species is unknown. Three parthenogenetic populations of *Encarsia* have been treated with antibiotics, and

in two cases, *E. formosa* and *Encarsia hispida* De Santis, males were produced, suggesting microbe involvement (85, 208). *Encarsia formosa* was subsequently shown to be infected with *Wolbachia* by PCR amplification of *Wolbachia*-specific DNA sequences (146, 165). In the third case, a population of *Encarsia pergandiella* Howard from Brazil did not produce males after antibiotic treatment, and PCR reactions with the *Wolbachia*-specific primers were negative (DD Shoemaker, unpublished data). Three lines of indirect evidence suggest that *Wolbachia* may be involved in many, but not all, of the instances of thelytoky in coccophagine aphelinids. First, *Wolbachia* is widespread. A survey of a large collection of insects in Panama showed that ~16% of all of the insects were infected (190), although the reproductive phenotypes were not determined and would have included phenotypes such as cytoplasmic incompatibility-inducing *Wolbachia*. Second, theory predicts that PI *Wolbachia* should not be able to invade species with complementary sex determination, such as the Ichneumonoidea, in which heterozygosity at one or more sex alleles causes diploid eggs to develop as females. The mechanism of diploid restoration in PI-infected wasps causes complete homozygosity, a condition that would result in diploid males in groups with complementary sex determination (147). Given this, one might expect that the higher frequency of thelytoky in the Chalcidoidea (in which complementary sex determination has not been recorded) might be caused by infection from PI *Wolbachia*. Last, surveys of thelytokous species or populations in the Trichogrammatidae (148) and *Aphytis* (207) suggest that most if not all are infected with PI *Wolbachia*. It would be especially interesting to know whether the incidences of infection with PI *Wolbachia* are similar among heteronomous aphelinids, in which the unusual host relationships may provide some obstacles to invasion by these microorganisms and the fixation of an infection may lead to novel oviposition behavior.

Sex Ratio Distorters

Infection with PI Wolbachia and Heteronomous Host Relationships The host relationships of thelytokous populations of coccophagine aphelinids have long been thought to be simply truncated versions of those of their heteronomous hyperparasitoid ancestors (52). Thelytokous and autoparasitic arrhenotokous species are intermixed within lineages and include closely related species pairs, such as the autoparasitic *Encarsia luteola* Howard and the thelytokous *E. formosa* (122). Thus, there is support for the idea that many thelytokous populations arose from autoparasitoids, but the apparent similarity in female host relationships masks a difference in female oviposition behavior. Whereas sexual females lay only fertilized eggs in the primary host and only unfertilized eggs in secondary hosts, thelytokous females lay unfertilized eggs in primary hosts. These eggs then double their chromosome complement and develop as females. That the rare males produced in the thelytokous *E. formosa* are produced on the whitefly host (85, 167, 208), not as hyperparasitoids as was originally reported (59), reflects the difference in oviposition behavior of thelytokous females.

In one study, the oviposition behavior and developmental requirements of males in two microbe-induced parthenogens, *E. formosa* and *E. hispidula*, were examined and compared with those characteristics of a sexual autoparasitoid population of *E. pergandiella* (85). Unmated, antibiotic-treated *E. pergandiella* showed typical autoparasitoid host relationships; very few eggs were laid in whiteflies, the primary host, and males were produced only as hyperparasitoids. *Encarsia formosa*, a species in which only thelytokous populations have been known since the 1920s, showed the opposite pattern; few eggs were laid in the secondary hosts, and males were produced only as primary parasitoids. *Encarsia hispidula* was somewhat intermediate between the other two species; eggs were laid in both primary and secondary hosts at similar rates, but males developed almost exclusively in primary hosts (85). These results suggest that fixation of an infection of PI *Wolbachia* in a population of an autoparasitoid leads to relaxed selection for oviposition and successful development of males in the secondary host, as well as increased selection for oviposition of unfertilized eggs in the primary host. It is not at all clear, however, why males successfully develop in the whitefly host following antibiotic treatment of their thelytokous mothers. There should be no selection on male function in thelytokous populations, and in sexual populations, males do not ordinarily develop in the primary host, even when virgin females lay haploid eggs there (see "Sex-Specific Development" below) (60, 82, 85, 197).

Paternally Inherited Sex Ratio Distorter in *E. pergandiella* Another sex ratio distorter, this one paternally inherited, is responsible for the only other exception to the rule of hyperparasitic male development in an autoparasitoid. In a population of *E. pergandiella* from Ithaca, NY, males were observed to develop both as hyperparasitoids and as primary parasitoids of whiteflies. The cause of primary male development was a factor that induced fertilized eggs laid in whiteflies to lose the paternal set of chromosomes and develop as males (88). The factor was found to act in a similar manner as the paternal sex chromosome (PSR) supernumerary chromosome discovered in the pteromalid parasitoid *Nasonia vitripennis* (Walker) (115, 188). In *N. vitripennis*, fertilization of an egg by sperm from a PSR male results in the loss of all paternal chromosomes except the PSR chromosome. The PSR chromosome then joins the maternal set, thus producing another PSR-bearing male. The factor causing genome loss in fertilized eggs in *E. pergandiella* is not yet known; a supernumerary chromosome was not found (88). Like PSR, the factor in *E. pergandiella* is predicted to be able to invade a population if the fertilization rate is greater than $1/(1 + \text{the transmission rate})$ (187). The transmission rate of the factor in *E. pergandiella* was found to be relatively low; ~28% of eggs fertilized by primary *E. pergandiella* males developed as primary males. However, invasion was still predicted to occur because of the very high rate of fertilization. Relatively low rates of parasitism throughout the season meant most hosts encountered by *E. pergandiella* females were whiteflies, hosts in which only fertilized eggs could be laid (83). One might predict autoparasitoids to be particularly susceptible to invasion by paternally inherited sex ratio distorters in cases like this one, when

extremely female-biased sex ratios are common. However, known examples of PSR-like elements are few and include only the two described here and one recently discovered in a species of *Trichogramma* (R Stouthamer & R Luck, unpublished data). It seems that these elements may thus be limited as much by the frequency with which they arise in populations as by opportunities to invade.

Sex-Differentiated Embryogenesis and Larval Development

In this section we focus on dimorphism in heteronomous aphelinid development. Male and female immature heteronomous aphelinids are by definition dimorphic in the sense that eggs of the two sexes are laid in different hosts or in different environments on the same host and are likely to have concomitant developmental requirements specific to those host types. In addition they may be, but are not invariably, morphologically distinct in the course of development (42). First, morphological differentiation may occur in the egg stage as a result of different treatment of the eggs of the two sexes by the adult female (181). Second, male and female embryogenesis may differ by the presence or absence of an extraembryonic cellular membrane (89, 181). Third, male and female larval morphology may differ particularly in the number of functional spiracles in particular instars (181).

Sex-Specific Development In heteronomous hyperparasitoids, the restriction against male development in primary hosts is fairly easily tested by placing unmated females on primary hosts. Observations suggest that unmated females oviposit reluctantly if at all on these hosts, and any eggs laid do not develop (60, 62, 82, 85, 197). In *Coccophagus rusti* Compere, embryonic development is complete, but first instar larvae die shortly after hatching (53). The restriction against female development in secondary hosts is supported by careful observation of many species reared for the purposes of biological control but is not easily tested. Flanders dissected dead first instar female larvae from a secondary host in a species with dimorphic larvae, *C. rusti* (53). Thus, at least in this example, females may not be perfectly accurate in their sex allocation on secondary hosts, and there appears to be a developmental restriction against production of females in these hosts. Hyperparasitic female development was observed in a thelytokous population of *E. hispidus* (85; M Giorgini & G Viggiani, unpublished data). Females laid unfertilized eggs in the secondary host that then developed as females. This example suggests that in sexual heteronomous hyperparasitoids, accurate sex-specific oviposition behavior may also be involved in the lack of observations of hyperparasitic female development. However, because of the involvement of a microorganism with *E. hispidus*, one cannot assume that hyperparasitic female development could occur in related sexual autoparasitoids if the ovipositional restraint were absent. The development of females as ectoparasitic hyperparasitoids was also reported in *E. smithi* (113), but here normal males develop as secondary endoparasitoids, and simple larval competition in the whitefly host might explain this report.

Solitary vs Gregarious Development and Sex-Specific Host Relationships All but a few heteronomous species are solitary, although gregariousness occurs sporadically within the Coccophaginae. *Coccophagus basalis* and *Coccophagus semicircularis* (Förster) are gregarious or semi-gregarious (12, 16, 47, 56, 90). [Note that for many years *C. semicircularis* was misidentified as *Coccophagus scutellaris* (Dalman) (128) and that much of the literature on the latter species actually refers to the former]. In *C. semicircularis*, a direct autoparasitoid, females lay only female eggs in the primary host. Female larvae in this species may be parasitized early in development, so subsequent females arriving on the host may lay both a female egg in the coccid and a male egg in the conspecific larva (90, 172). In *C. basalis*, males are indirect allopasitoids, and females were observed to occasionally lay both female and male eggs in the same insertion of the ovipositor. This is curious because males cannot develop on conspecific females (56). Gregariousness is also found in some members of *Pteroptrix* (51), as well as in *Dirphys* (124) and in *Eriaphytis*, the putative outgroup of the Coccophaginae (71, 78). In *Pteroptrix wanshiensis* (Compere), males and females are produced within the same host; males emerge at the same time or ≤ 2 days after females (48, 51). Flanders (51) concluded that males were unlikely to be hyperparasitoids because of the small difference between male and female emergence times. However, in the solitary *P. orientalis*, a female may lay a male egg and a female egg in the same host (57), but the development of the male is delayed until the female larva finishes consuming the host, whereupon the male develops at her expense. Because of the accelerated development of the male, males emerge only shortly after females of the same cohort (176). In light of this evidence from a congener, as well as Flanders' (48) observation that males of *P. wanshiensis* cannot be produced by unmated females unless a mated female is also present, it seems likely that *P. wanshiensis* is also an indirect autoparasitoid.

Differential Treatment of the Egg by the Adult Female Because male and female ovarian eggs are necessarily identical (with the possible exception of *P. orientalis* discussed in "Reproductive Modes" above), any dimorphism in eggs must occur after oviposition by the adult female. Most commonly, the externally deposited eggs of males have a stalk or pedicel at the anterior end that may be twisted or crimped (e.g. 49). In the many examples reviewed by Walter (181), all of the male eggs that received this treatment were direct ectoparasitoids. Endophagous male eggs are identical to female eggs in shape. It seems most likely that the pedicel is associated with the ectoparasitic lifestyle and it may serve to attach the egg to the host (181) or to prevent water loss. In *Euxanthellus philippiae* Silvestri, male eggs have a pedicel on the side used in attachment to the secondary host; because of its location, it is likely to be of glandular origin rather than a simple deformation or twisting of the egg chorion (140, 181).

There is also indirect evidence that females may use glandular secretions to differentially coat the surfaces of male and female eggs. Different surface treatment of eggs is suggested by the observation that the indirect secondary male eggs of

C. gurneyi are not encapsulated in a mealybug host that regularly encapsulates female eggs (13, 181). This report is especially intriguing because here eggs of both sexes are generally laid into the same fluid environment; one might also expect that females may treat the surfaces of male and female eggs differently when male eggs are to be laid in a dry environment.

Lastly, heteronomous females may deposit male and female eggs in the same or a different location in their respective hosts. Heteronomous aphelinids may lay male and female eggs in the same location even though they eventually develop on different hosts. In the indirect allopasitoid, *C. basalis*, male and female eggs are invariably laid in the subesophageal ganglion (56). In other cases, both female and male eggs of direct autoparasitoids may be laid within the hemocoel of their primary and secondary hosts (60). In still other species, eggs of each sex may be laid in different precise locations within the two host types. In *Coccophagus semicircularis*, female eggs are generally laid in the midgut of the coccid host, whereas male eggs are laid in parasitoid larvae as young as first instars (90, 172). In *E. smithi*, female eggs are laid in the Malpighian tubules of their whitefly host, whereas male eggs are laid within the mature larvae or pupae of parasitoids (54, 113).

Embryogenesis As in many animals, egg load (number of mature eggs at one time) and egg size tend to be inversely correlated in heteronomous aphelinids. For example, *E. tricolor* produces relatively few [7.3 per day (200)], large [0.169 mm long (136)] eggs, whereas the egg load of newly emerged *E. perniciosi* may range from 46 to 102, and the egg is 0.085 mm in length (157). In general, small eggs tend to be hydropic (i.e. relatively yolk free), and large eggs tend to be anhydropic (well provisioned with yolk), and within the genus *Encarsia*, both types may be found (MS Hunter, unpublished data). However, there is yet little information about how the two types of eggs are distributed in different coccophagine genera or even whether the yolkeness of eggs is a continuous (rather than a bimodal) trait. Hydropic eggs of parasitoids are laid only inside hosts (129), so we would expect that hydropic eggs constrain some lineages of heteronomous hyperparasitoids to endoparasitic development of both males and females.

Embryogenesis has been studied in a handful of heteronomous aphelinid species. It appears that all species studied to date have superficial cleavage (88, 136), unlike some other species of endoparasitic Hymenoptera with hydropic eggs and complete cleavage (68, 136). Early embryogenesis of three *Encarsia* species, *E. inaron* (as *E. partenopea*), *E. tricolor* (as *E. coniugata*), and *Encarsia berlesei* (Howard), was described by Silvestri (136). With the exception of parthenogenetic development of *E. berlesei*, embryogenesis of the females of these three species is very similar. In all cases, the polar bodies remain detectable for several divisions, but eventually deteriorate and do not form an extraembryonic cellular membrane (136). In *E. pergandiella*, however, the polar bodies do not degenerate and are a possible source of a polyploid layer that surrounds the embryo (82). An extraembryonic layer formed from the polar bodies is called a trophamnion (129, 159), is more

often associated with hydropic eggs (69), and is thought to have a role in nutrient acquisition as well as possibly host immune suppression (69, 129, 158, 159).

It appears that in some cases a trophamnion may be associated with female but not male development. In the heterotrophic *E. porteri*, a cellular layer of unknown origin covers the developing female embryo, but not the male (89). Flanders (44) asserts that a "trophic membrane" surrounds the female embryo of *Coccophagus capensis* Compere, but not that of the male. Later he mentions that the female larva encloses "...itself in a cellular trophamnion, the male not doing so" (49). The evidence for this appears only in Cendaña (16), who describes and illustrates a cellular capsule surrounding a larva "already hatched" and who does not mention the sex of the larvae observed. Whether this capsule is truly a trophamnion that persists after hatching, what the source of the capsule is, and whether it is restricted to females all deserve additional attention.

Larval Morphology The most consistent difference in larval morphology of heteronomous aphelinids concerns the presence or absence of functional spiracles in the first two instars. Male ectoparasitoids have open spiracles in the first and second instar, but females are apneustic (lack spiracles) (see 181 for a thorough review of the different examples of this). This difference has been documented in several species of heteronomous hyperparasitoids with ectophagous males. Conversely, larvae of heteronomous hyperparasitoids with endophagous males are often similar in appearance and are both apneustic in early instars. Less easily explained are differences in the spiracle number of the last instar male and female larvae of some *Encarsia* species. Males of *E. aleuroilicis* Viggiani, *E. tricolor*, and *E. lutea*, all have nine pairs of spiracles, compared with eight in females (99, 119, 174), whereas in *E. dichroa* (Mercet) males have six pairs and the females have five pairs (99).

In some cases, males and females may be quite different in form. In *C. capensis*, males are secondary endoparasitoids, so both males and females develop within hosts, but female larvae are caudate, whereas males are teleaform and are well covered with spines on the abdomen (42, 181). In *E. porteri*, males are primary endoparasitoids of Lepidoptera eggs and are heavily armored with hornlike processes on the head and long spines on the venter, whereas the female larvae developing within whitefly nymphs are hymenopteriform throughout larval development (89). The reason for the sexual dimorphism in larval form is unknown, but the fact that in both cases males appear to be better defended by spines is similar to the pattern observed in sexually dimorphic mymarid larvae (161), in which both sexes develop as primary endoparasitoids of eggs.

In *C. gurneyi*, two types of males were described by Compere & Smith (24) and Flanders (50), the indirect ectoparasitic form and the direct endoparasitic form. These forms are distinguishable by subtle differences in development. The first instar is a planidial form, and the indirect ectoparasitic male hatches from the egg when the primary parasitoid has created a dry environment. The planidial form presumably allows the first instar male to navigate the surface of the primary parasitoid and establish a feeding site (181). The direct endoparasitic males do

not hatch from the chorion until the beginning of the second instar. The second instar of both forms bears two pairs of spiracles, but in the endoparasitic form, the spiracles are not functional (50). If these two types of males are indeed contained within one species, this observation indicates considerable phenotypic plasticity in male development.

BEHAVIORAL ECOLOGY

Sex Allocation and Kin Selection

The process by which the male and female eggs of heteronomous aphelinids are correctly allocated to host type was misunderstood for many years (e.g. 52 and the history of the discussion, reviewed in 181). It was assumed that all males were produced by virgin females and that mated females produced only female offspring. Walter (181) ended the controversy by providing numerous examples in which selective fertilization by mated females was shown. Although a couple of records of inflexible sex allocation behavior in heteronomous species remain in the literature (see 181), these species should be reexamined in light of more recent understanding.

Sex allocation in heteronomous aphelinids has been recently reviewed (116) and is more briefly summarized here. Heteronomous parasitoids have long been known to exhibit "extraordinary sex ratios" (e.g. 45, 98, 198), but not for the reasons that Hamilton (70) proposed. Hamilton (70) suggested that female-biased sex ratios may occur when mating occurs in small groups and males compete with their brothers for mates ("local mate competition"). Local mate competition is unlikely to occur in autoparasitoid populations in which host populations are often large and highly aggregated, the emergence site of males and females may be spatially separated (27, 28), and males have been observed to move frequently within patches to mate (92).

A theory developed for heteronomous aphelinid sex ratios is a variant of Fisher's (35) sex ratio theory (65). Fisher predicted that parents should invest equally in male and female offspring. When the cost of males and females is equivalent, a 1:1 sex ratio should result. In heteronomous aphelinids, the sex allocation strategy should vary depending on whether the reproductive success of females is limited by their egg load and rate of egg maturation (egg limited) or by their encounter rate with hosts (host limited). When eggs are limiting, females should seek to lay equal numbers of males and females, and the sex ratio should approach equality. When hosts are scarce and females are host limited, females should accept all hosts they encounter, and the sex ratio (proportion of males) should then reflect the proportion of all hosts encountered that are secondary. In the host-limited case, when primary and secondary hosts are in distinct habitats, search time is the limiting resource, and females should thus search for equal amounts of time in both habitats. When primary and secondary hosts are intermixed in the same habitat, females search for both primary and secondary hosts simultaneously. This latter situation is interesting

and perhaps unique in that it violates a key assumption of Fisher's (35) theory—that there is a tradeoff between the production of male and female offspring (64, 86). There is no tradeoff as long as eggs are not limiting and handling time is negligible, because only one sex can be laid on a host of a given type.

There is some experimental support for the theory. In an experiment with *E. tricolor*, the total host densities were varied in an effort to vary the limiting resource from hosts (at relatively low densities) to eggs (at high densities). As predicted, sex ratios were closest to the proportion of secondary hosts (either 25% or 75%) at low host densities and moved towards equality at high densities (86). Another experiment (MS Hunter & SE Kelly, unpublished data) that manipulated experience and measured egg load directly failed to show an effect of egg load on sex allocation in *Encarsia sophia* (Girault) [= *Encarsia transvena* (Timberlake) (75)]. Here the proportion of secondary hosts was the only important influence on sex ratios. Field investigations too have generally shown a good correspondence between the proportion of secondary hosts and sex ratios (28, 83). This may be because these wasps are chronically host limited. In fact, confidence in the theory has led to the use of sex ratios as a means of assessing the degree of host or egg limitation of autoparasitoids in the field (191). However, field studies have yet to illustrate a shift towards equal production of males and females in high-density host patches (28, 83). These results are difficult to interpret. Field sex ratios may simply be too variable to discern subtle changes at particular spatial scales (83). Second, acceptance of all suitable hosts could be interpreted as evidence of a fixed strategy that has evolved in wasps that are commonly host limited (83). Third, the field results could be interpreted as evidence of a nonadaptive sex allocation strategy (28, 186). These conflicting hypotheses are difficult to distinguish. An independent assessment of the degree of host or egg limitation in autoparasitoid populations would help to test the idea that egg limitation is sufficiently rare that natural selection has not selected for flexibility in sex allocation behavior.

Other factors may influence autoparasitoid sex ratios. The substitution of one species of secondary host for another, preferred species has been shown to increase the relative production of males (7, 199). Host feeding, which is generally restricted to the primary host, may also have this effect because primary hosts used for host feeding are not used for oviposition of female eggs (7, 86). In one experiment, the spatial arrangement of hosts was found to influence sex ratios in *E. tricolor* through host feeding. When primary and secondary hosts were on separate leaves, females host fed less (and produced a higher proportion of females) than when both host types were on the same leaves (86).

The effect of host feeding could be incorporated into predictions about autoparasitoid sex ratios under conditions of host and egg limitation. Strictly egg-limited females should feed more than host-limited females, but in this case feeding should not have an effect on sex ratios because search time is not limiting. Sex ratios in strictly host-limited wasps, however, should reflect the encounter rate of primary and secondary hosts. Less host feeding is expected because these females are not limited by eggs, but an increase in the sex ratio is expected in accordance with the

number of primary hosts used for feeding rather than oviposition. This prediction is untested, and the exact effect on sex ratios will depend on the host-feeding dynamics of host-limited wasps at different rates of host encounter.

Colgan & Taylor (21) predicted female-biased autoparasitoid sex ratios when parasitism of relatives was common. The fitness return of producing a male is reduced by the probability that the secondary host used to produce the male is a daughter or a sister. There has been no testing of this theory. The theory does not consider variation in the relative abundance of primary and secondary hosts, and so its predictions are unlikely to be very accurate, but it could be incorporated into the more general Godfray & Waage (65) model, if evidence of parasitism of relatives was found.

In general, the large and aggregated population structure of many hemipteran hosts and time delays owing to autoparasitoid development may make encounters between adults and their immature offspring uncommon (202). In some autoparasitoid species, females are not vulnerable to parasitism until the late-larval-early-pupal stages (81, 195). The longevity of any autoparasitoids in the field is unknown, yet even if females lived long enough, it would seem unlikely that females would remain on the same patch and re-encounter their own immature daughters at a stage at which they might be used as a host. In other species, immature wasps only 2–3 days old may be vulnerable (19, 90, 200), but even this amount of time may be longer than adult females normally spend on a patch. Another possibility is that immature females may be parasitized by their sisters if there is sufficient variation in development time that some adult females on a patch emerge in proximity to vulnerable immature sisters on the same patch. Variable development times of females have been recorded in heteronomous aphelinids, both the expected variation of koinobionts that attack more than one host stage, and in some species, variation despite constant host age and environmental variables (reviewed in 181). Kajita (91) observed emerging autoparasitoid females in the field ovipositing in secondary hosts on the same leaf, suggesting that there might be some risk of encountering relatives if sufficient variation in development time occurs.

In the only experiment that addressed whether autoparasitoid females discriminate between related and unrelated conspecific immature females, Williams (202) found that *E. tricolor* did not discriminate between pupal daughters and nonrelatives. It would be valuable to conduct similar experiments with other species and using relatives that females are more likely to encounter: young larval daughters or pupal sisters. *E. tricolor* females did prefer to parasitize heterospecific secondary hosts more than conspecifics (7, 199). Williams (199) suggested that this preference may have evolved in response to kin selection and may reduce the probability of females parasitizing kin when they are not able to distinguish related from unrelated conspecifics. In other *Encarsia*, no preference has been found between suitable stages of conspecific or heterospecific hosts (15, 87, 120), but there are not yet enough observations on this subject to draw any general conclusions.

Ovicide

Egg killing, or ovicide, has been documented in several hymenopteran ectoparasitoids (reviewed in 105) and in two closely related coccophagine endoparasitoids, *E. formosa* and *E. luteola* (5, 112; M McElveen & M Hunter, unpublished data). The lack of observations of ovicide in endoparasitoids may be because of observer bias, because it is generally difficult or impossible to observe the action of ovipositors within hosts. Furthermore, dead eggs may be found readily upon dissection and confused with live eggs (112). Alternatively, ovicide may be genuinely rare among endoparasitoids owing to the difficulty of endoparasitoids finding eggs within hosts (105). If this is the case, heteronomous hyperparasitism may be preadaptive for ovicide (112). Heteronomous hyperparasitoids with endoparasitic males must find immature wasps within the hemipteran host. Whereas in some species, the secondary hosts may be mature larvae or pupae (62, 81, 87), in others the larvae may be only a few days old and free within the host hemolymph. Females then must use their ovipositor to locate a small larva in a relatively large volume of host (19, 90, 200). Because of the convergence in behaviors in these species between oviposition of a male egg and ovicide, one might predict that ovicide is likely to be more widely spread than in the two species of *Encarsia* in which it has been observed to date.

Strand & Godfray (150) proposed that ovicide may evolve when the competitive advantage of the first egg or clutch of eggs is great and is more likely to occur under host-limited conditions, when encounters with parasitized hosts are common and the travel times between hosts are long. In this situation, the probability of ovicide occurring is then dependent on the time cost of egg killing. In *E. formosa* no time cost was found; females took no more time to kill an egg before oviposition than they did to superparasitize the host (112). In this system, with an unassailable competitive advantage accruing to the female that kills the first egg and no time cost to ovicide, it remains to be explained why females are still more likely to reject parasitized hosts than unparasitized hosts.

Other costs may be more important in this system and include the potential cost of killing one's own eggs if kin discrimination does not occur (141). *E. formosa* females appear more likely to perform an "antennal rejection" of hosts that they have parasitized over hosts parasitized by conspecifics (166), but observations of ovicide of daughter eggs have also been made (112). Last, ovicide may not always be favored if the quality of a parasitized host is lower than an unparasitized host, even when the probability of winning the contest with the previous occupant is 100%. Host quality may decay as the interval since the first parasitism increases, because changes in the host occur that make it less suitable for initiation of development (179). Host quality may also decline because of physical damage to the host by the wasp ovipositors. A greater understanding of the quality of parasitized hosts and the probability of a female killing her own egg would shed light on ovidical behavior in *E. formosa*.

Several questions about ovicide in heteronomous aphelinids remain to be addressed. Is ovicide restricted to two of *Encarsia*, and if not, how is ovicide

distributed across the Coccophaginae? In one study, *E. tricolor* females were confined on whiteflies for 24 h, and then hosts were dissected at different time intervals (6). The dissections showed that most, but not all, supernumerary offspring die in the egg stage before embryological development occurs. The authors suggest that egg death is caused by physiological suppression, but ovicide is another possible explanation for these results. Constraints may play a role in the distribution of ovidical behavior. For example, ovicide may not occur when the hemipteran host stage attacked is large in volume relative to the egg size. Even the volume of a greenhouse whitefly nymph may be too large for parasitoids with small hydrotic eggs to search. One might also wonder whether ovicide of hyperparasitic male eggs also occurs. In many primary and secondary hosts of heteronomous species, direct observation of ovicide may not be possible, and careful experiments to determine the viability of dissected eggs will be necessary. One might favor ovicide over physiological suppression as an explanation for egg death when a set interval between ovipositions results in a variable outcome; in some cases one egg is dead, and in others, both eggs hatch. Knowing whether ovicide occurs is important if one wants to understand the oviposition behavior of a given species. Ovicide may increase the likelihood of superparasitism and change the outcome of competition on the primary host.

EVOLUTIONARY HISTORY

Evolution of Heteronomous Biologies: Phylogenetic Hypotheses

To consider properly the evolution of heteronomous biologies in coccophagine aphelinids, one would require a robust model for the phylogenetic relationships among included taxa. Although we still do not have such a model, recent work provides clues to phylogenetic relationships within the group. Eriaphytinae (containing only the genus *Eriaphytis*) is the apparent sister group to Coccophaginae (76). The evidence for this relationship is the shared presence of a small peg on the mandible, used by emerging adults to orient the mandible when chewing through the host cuticle. Unlike most aphelinids, *Eriaphytis* has a plesiomorphic configuration of the mesofurca, which bears a dorsal arch to which the muscles to the profurca are broadly attached (78). This is the conformation of the mesofurca in most Chalcidoidea, which suggests that *Eriaphytis* is basal in Aphelinidae. This enigmatic genus contains only two species, one of which is a gregarious parasitoid of *Cerococcus* species (Cercococcidae) (71); the other is a parasitoid (Coccidae) of *Vinsonia stellifera* (Westwood) (Coccidae) (72, 74). Little is known of the biology of the genus *Eriaphytis*, but as yet there are no reports of heteronomous biologies in this genus.

The genus *Euxanthellus* may contain the basal members of Coccophaginae (78). As noted above, *Euxanthellus* has recently been considered a synonym of *Coccophagus* (73), but Heraty et al (78) found that *Euxanthellus* spp. have a

plesiomorphic form of the mesofurca with a complete dorsal arch. *Euxanthellus philippiae* is a direct heteronomous hyperparasitoid. Females of this species were observed to oviposit stalked male eggs externally on the cuticle of larvae of *Coccophagus* sp. (probably *lunatus* Howard) inside brown soft scale (3, 140). Males of this species have also been reared as hyperparasitoids of the citrus psylla *Trioza erythrae* (Del Guercio) (14, 107, 128) and as parasitoids of larvae of conspecific females and *Metaphycus maculipennis* (Guerrieri & Noyes) (= *M. timberlakei*), as well as an unidentified eunotine pteromalid and an unidentified primary parasitoid in a whitefly pupa (160).

Evolution of Heteronomous Biologies: Hypotheses Based on Life History

Speculation by previous authors on the evolution of heteronomous hyperparasitism has included adaptive arguments for the benefits of this life history at the population or individual level and/or have connected sequences of life histories in a proposed pathway, but few have integrated both, perhaps in part because of the uncertainty surrounding the ancestral biology of this group. The various scenarios for the evolution of heteronomous biologies in aphelinids have been thoroughly summarized by Walter (182 and especially 184) and will be more briefly discussed here.

Flanders (52) suggested that indirect heteronomous hyperparasitoids evolved first from conventional primary parasitoids. Indirect heteronomous hyperparasitism then gave way to direct heteronomous hyperparasitoids via an intermediate condition in which species oviposit haploid eggs both directly and indirectly. Under this scenario both diphagous and heterotrophic biologies would be derived from heteronomous biologies. Walter (184) considered the initial step of this model to be unlikely because it is unclear why selection would favor the evolution of male eggs that must wait for the arrival of a primary parasitoid species to hatch when they might otherwise develop directly on unparasitized hosts. Note that the Flanders (52) pathway might be more convincingly applied to a gregarious ancestor if, as we suggest below, males may gain a competitive advantage over their sisters by delayed hatching (131).

Other proposals suggest an adaptive explanation without a clear pathway. Some early schemes involved group selection arguments that autoparasitism arose as a means of population regulation (171, 210) or to bias sex ratios toward female production (49). These arguments cannot explain the selective advantage of this life history to individuals (196).

Williams (198) and Viggiani (172) suggested that the apparent competitive superiority of autoparasitoids over primary parasitoid species could explain the evolution of this biology. Whereas it seems likely indeed that autoparasitism arose in an environment in which the level of host exploitation was high, no ancestral biology or evolutionary pathway was proposed by these authors. Walter (181, 184) also initially invoked selection on competitive ability as the force driving the

series of transitions proposed originally by Zinna (209, 210). Zinna's pathway was endorsed by Walter (181, 184) because of the stepwise increase in complexity of host-searching behaviors. In this model, conventional parasitoids give rise to diphagous species (in which males are primary ectoparasitoids, generally but not always of the same hosts as females). Ectoparasitic development of males could be adaptive if it enabled males to prevail over competitors in superparasitism. From diphagy, heteronomous hyperparasitism arises, a step that requires the adoption of different host acceptance criteria for oviposition of male and female eggs. Finally, heterotrophic species arise from heteronomous hyperparasitoids (184); in this group the evolution of different host searching behaviors may be required for oviposition of male and female eggs.

Walter (184, 185) hypothesized that if diphagy arose as a competitive strategy, diphagous males should be competitively superior to females under conditions of superparasitism. In the one experimental test of a model for the evolution of this group, male *C. bartletti* did not prevail over females in instances of superparasitism (185). Concluding that selection on competitive ability is thus unlikely to have been important in the evolution of this group, Walter (184) suggested an alternative origin that explicitly has no adaptive explanation. He proposed that initially a small sex-specific difference in oviposition behavior occurs. Such a difference has been observed in some ectoparasitic *Aphytis* spp. (Aphelinidae:Aphelininae) that are known to deposit male and female eggs in different locations on the host (101). From here, the evolution of male and female larval development was uncoupled and could proceed independently as each sex adapted to new circumstances or new hosts, to result in diphagy, heteronomous hyperparasitism, and then heterotrophic development.

A limitation with the pathway of Zinna & Walter is the absence of evidence that diphagy occurs in probable basal Coccophaginae such as *Euxanthellus* or in putative out-group taxa such as *Eriaphytis*. An alternative view of diphagy is not as an ancestral state, but as a result of the reversal of ectoparasitic heteronomous hyperparasitism to primary parasitism, with males retaining ectoparasitic development. If diphagy is not ancestral, then, too, the lack of competitive advantage for male ectoparasitoids in *C. atratus* does not invalidate the "competition" model for consideration. We suggest that competition is likely to be an important selective force in the evolution of heteronomous hyperparasitism, but that the likely pathway is from primary parasitism of both sexes through a transitional stage of facultative hyperparasitism to heteronomous hyperparasitism.

We propose some mechanisms for the evolution of heteronomous hyperparasitism from a conventional primary endoparasitoid. As a starting point, we agree with Walter (184) that, given that female endoparasitism is conserved throughout the group, endoparasitism is a likely ancestral state. Behaviors and competitive mechanisms known in other parasitic Hymenoptera can be combined in more than one way to construct a scenario leading to heteronomous hyperparasitism. In addition to the model presented below, we explored the possibility that heteronomous hyperparasitism arose from a gregarious ancestor. The gregarious origin scheme

supposes that males may gain a competitive advantage over sisters from hatching later and eventually develop as indirect secondary ectoparasitoids. Because gregarious Coccophaginae are uncommon, we regard this model as less likely than one based on a solitary origin. However, our intention is not to defend a specific sequence of events per se, but to underscore that within-host competition is a plausible selective force to have initiated the evolution of heteronomy.

The model for a solitary primary parasitoid ancestor assumes host-limitation of females, widely assumed to be the most common condition for parasitoids in the field (63). Females thus may superparasitize hosts, and we assume that, when they do so, they are more likely to lay male eggs. A male bias in the sex ratio of a superparasitizing female is well known in gregarious parasitoids, but recent evidence suggests that it occurs in some solitary parasitoids as well (34, 163). There are two possible adaptive explanations for this, one or both of which may apply. First, male fitness may be less strongly correlated with body size than female fitness (17, 18), and regardless of which wasp wins the competition in the host, a superparasitized host may be of lower quality than an unparasitized host and yield smaller wasps (29, 127, 162). Second, in some species, male eggs hatch earlier and thus may stand a better chance of winning a competitive bout with a female egg laid at the same time (11, 34).

There is then likely to be selection on adult females to accept or reject parasitized hosts based on the probability that a male egg could develop there. In general in hymenopteran parasitoids, the outcome of intraspecific competition within a host is dependent on the interval between the first and the second oviposition. Among the examples of interval-dependent outcomes, both younger and older parasitoids may win (103, 104, 149, 180), but in most of the examples in which the younger larva wins, it is because first instars are equipped with enlarged fighting mandibles with which they overcome older larvae that have smaller mandibles and are less mobile (103). First instars of Coccophaginae do not have the enlarged mandibles that would lead one to predict their victory over older conspecifics. We might then expect ancestral coccophagine females to accept recently parasitized hosts, where stochastic variation in hatching time, as well as possibly a more rapid embryonic development, may increase the odds that the second-laid male egg may prevail. However, we must also assume that hosts occupied by a late larval or pupal wasp may also be acceptable, and males may then develop as hyperparasitoids. Facultative hyperparasitism of this sort was reported by Strand (149) and by Strand & Vinson (151), who found that a *Trichogramma pretiosum* (Riley) female, when presented with a host egg containing a mature third instar *Telenomus heliothidis* Ashmead, may lay an egg directly within the gut of the *Telenomus*. Her progeny then develops as a secondary endoparasitoid. Similarly, facultative hyperparasitism of conspecifics was observed in a mymarid egg parasitoid, *Anaphes victus* Huber, where encounters with mature larvae resulted in uncharacteristic oviposition behavior involving stinging the wasp larvae followed by oviposition and development of a secondary endoparasitoid (162). These behaviors are especially interesting in Trichogrammatidae and Mymaridae, groups in which hyperparasitism

is otherwise very rare or absent (66, 152), and these observations suggest facultative hyperparasitism may sometimes be cryptic.

Once males of the ancestral coccophagines began to develop as hyperparasitoids, one can assume a tradeoff between males developing as primary parasitoids and hyperparasitoids, such that adaptations for one developmental pathway are disadvantageous for the other. Given a high level of host exploitation, one might imagine that selection would favor lineages that specialized in hyperparasitic male development and that male hyperparasitism would eventually become obligate.

This model was considered but dismissed by Walter (184). He considered that facultative hyperparasitism could lead to heteronomous hyperparasitism if one assumes tradeoffs between the ability of males to develop as primary or secondary parasitoids. In 1987, Walter (184) concluded that facultative hyperparasitism was an unlikely starting point, given that it is relatively rare in the Aphelinidae, and that the majority of facultative hyperparasitoids are ectoparasitic (63, 184). However, the more recent findings of cryptic facultative hyperparasitism in endoparasitoids discussed above (149, 151, 162) provide more support for facultative hyperparasitism as a potential original state.

This model will be difficult to test. The pathway we suggest is solitary endoparasitism, then facultative secondary endoparasitism of males, then obligate secondary endoparasitic male development. As we learn more about the biology of basal groups in the Coccophaginae, support for this pathway may be gained by evidence of a preponderance of species with males that develop as secondary endoparasitoids, although, as we have seen, the site of male development appears very labile throughout the subfamily and even within genera (see "Host Relationships" above). Perhaps more importantly, the identification of primary parasitoids that are in sister groups to the Coccophaginae could enable experiments to determine whether there is evidence for any of the competitive mechanisms proposed here. We would be particularly interested in knowing (a) whether there is a sex ratio bias towards males in superparasitizing females, (b) the intervals between the first and second oviposition in which younger larvae may prevail over older ones, and (c) whether facultative secondary endoparasitism occurs.

Evolutionary Transitions from Heteronomous Hyperparasitism Heteronomous hyperparasitism may have arisen once, but it is clear that changes in male host relationships have occurred many times in this group. One could imagine two means by which new male host relationships might arise, both of which may have occurred. In one, the hosts for females remain the same, but a new host for males is adopted. Although there appears to be little evidence of males of heteronomous hyperparasitoids occasionally developing in the primary host (see "Evolutionary Maintenance" below), there are examples of other extraordinary hosts for males. For example, in *E. sophia*, an autoparasitoid of whiteflies, males have been reared as hyperparasitoids of aphids through aphidiine braconids [as *E. transvena* (142; K Hoelmer & M Hunter, unpublished data)]. The oviposition behavior of unmated

females (which only lay male eggs) may be more variable than that of mated females (e.g. 197). Variability in oviposition behavior may result because virginity is generally a relatively ephemeral or uncommon condition and is less likely to be the target of stabilizing selection and canalization than oviposition behavior of mated females (143). One might then expect that ovipositional "mistakes" might be more common with male eggs than with female and that some of these may eventually lead to the adoption of a new host type or mode of development for males of a species. Viggiani (171, 172) suggested that the adoption of hosts for males that are very distant taxonomically from the original host, such as Lepidoptera eggs, might be explained by the morphological similarity of these hosts or "morphotypical" specialization (171). This hypothesis has not been tested, but support for this idea might be gained by finding that the identification of hosts by wasps in this lineage is more dependent on shape, size, and structural characteristics of the host (e.g. a soft-bodied ovoid sedentary insect) than by surface chemistry.

Host shifts in the primary host, likely to be accompanied by speciation events, may also be an important source of interspecific variation in male-host relationships (184). As an example, one might imagine that a shift to a larger primary host might lead to female larvae not consuming enough of the host to stimulate oviposition of ectoparasitic male eggs or hatching of male eggs in indirect species. If another host for males is adopted, such a species would then become an alloparasitoid.

Evolutionary Maintenance: Active Selection or Lack of Genetic Variation?

The fact that heteronomous biologies are characteristic of a single, monophyletic group of aphelinids suggests that they had a single evolutionary origin. What is so striking in the literature on coccophagine aphelinids is the relatively small number of cases in which heteronomous biologies appear to have been lost (summarized above in "Exceptional and Non-Heteronomous Host Relationships"). Apart from thelytokous and diphagous species, the known cases of primary male development in Coccophaginae can be explained minimally by three reversals to a non-heteronomous biology (one in *Encarsia*, one in *Pteroptrix*, and one in *Coccobius*). Coccophaginae presently contains >640 valid species (114), the vast majority of which are apparently heteronomous. Whatever led to the origin of heteronomy, the factors that maintain it must be extremely strong.

The maintenance of heteronomous life histories could be because of active selection against development of individuals in the "wrong" host. Apparent support for this idea is provided by the development of the rare male *Encarsia formosa* in the primary host (see "Infection with PI *Wolbachia*..." above). If, in sexual populations, there is selection acting against males that develop in the primary host, then one might expect this result from relaxation of selection on males in *Wolbachia*-infected thelytokous populations such as *E. formosa*. Nevertheless, it is difficult to understand how active selection alone can maintain heteronomous life histories. At least in temperate populations, scarcity of secondary hosts early in the season or in newly colonized host patches may produce highly

female-biased sex ratios (12, 28, 83). In such a situation, a mutant female able to produce males on the primary host would be strongly favored by natural selection. Further, whereas one might speculate that trade-offs could be important, for example between production of males as primary parasitoids and male fitness, none have yet been identified.

It appears more likely that lack of genetic variation, at least for the ability of males to develop in the primary host, maintains heteronomy. Although heteronomous species have been the subject of careful scrutiny for >60 years, we are unaware of any records of males of a heteronomous hyperparasitoid species developing in the primary host (with the exception of the examples involving sex ratio distorters, as discussed). An understanding of both the developmental mechanism that restricts the development of males and females to their correct host type and its genetic basis would likely shed light on the maintenance of heteronomy in the vast majority of Coccophaginae and its loss in select taxa.

CONCLUSIONS

We have restricted our current review to aspects of heteronomous aphelinid life history, behavior, and evolution, yet their importance in population regulation of homopterous pests is responsible for much of the wealth of knowledge of their life histories. The obligate nature of the sex-specific host relationships of these species was first elucidated by Flanders (40, 41) as a result of working with these species in importation biological control programs. Heteronomous hyperparasitoids, as well as thelytokous Coccophaginae, have been used on multiple occasions for biological control and have been responsible for moderate to spectacular successes (20, 30, 79, 110, 111, 132, 139, 164), in spite of some ongoing concern about the possible disruptive effects of hyperparasitism on population suppression of the hemipteran host (108, 133, 153). The population and community ecology of heteronomous hyperparasitoids is clearly complex and has been the subject of recent study (87, 108, 201). Heteronomous hyperparasitoids that directly parasitize their competitors may offer the acid test of the ongoing debate among biological control workers about whether interference competition between natural enemies may in some circumstances disrupt the control of the pest provided by a single effective natural enemy.

In aspects of behavior and evolution, as well as in ecology, the complexity of heteronomous life histories forces us to rethink well-worn ideas or apply them in a new context. Whereas heteronomous life histories are inherently fascinating, they may seem too exceptional to yield general insights into principles of evolution and behavior. Yet these unusual biologies provide opportunities to explore the evolution of parasitoid life history at a finer scale than is otherwise possible. For example, workers have speculated on the frequency of transitions between ecto- and endoparasitism in the parasitic Hymenoptera and the mechanisms that are involved (e.g. 192). The Coccophaginae offer examples in which these transitions have occurred between closely related species, where, within a species, males and females may develop differently, and even the example of males of

C. gurneyi developing as both ecto- and endo- secondary parasitoids (50). From this we may understand the minimal changes needed to make this transition. Similarly, the “dichotomous hypothesis” of parasitoid life history suggests that large, anhydropic eggs and small, hydropic eggs tend to be associated with a number of other divergent characters (63), but in heteronomous aphelinids, there are congeneric species that have different egg types, yet attack the same host. This allows one to study the tradeoff between egg size and number. Large eggs are presumably costly, and many endoparasitoids have lost them; in the heteronomous species in which both sexes are endoparasitic and large eggs have been retained, do they have any benefits?

Lastly, insight into much of the life history diversity in the Coccophaginae would undoubtedly be gained by more knowledge of the phylogeny of the group. There is little question that this group, like many chalcidoid lineages, has undergone the type of rapid radiation that makes phylogeny reconstruction a challenge. Yet we remain optimistic that morphological and molecular analyses (78, 124; Babcock, Heraty, DeBarro, Driver, & Schmidt, unpublished data) will eventually result in robust phylogenies. These phylogenies will provide an analytical context to further explore the wonderfully convoluted life histories of this group.

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