Essay on the evolution of adult-parasitism in the subfamily Euphorinae (Hymenoptera: Braconidae)

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Об эволюции паразитизма на взрослых хозяевах у браконид подсемейства Euphorinae (Hymenoptera: Braconidae)

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Abstract. The phenomenon of adult-parasitism by the euphorine Braconidae is characterized and discussed. Hypotheses regarding the evolution of adult-parasitism are outlined. It is suggested that adult-parasitism arose from ancestors that were koinobiont larval-larval parasitoids, but never from idiobiosis directly, because koinobionts evolved rapid oviposition behavior necessary as a pre-adaptation for attacking mobile adult insects. Adult parasitoids are shown to have a unique combination of koinobiont and idiobiont characteristics. The new terms, imagobiosis and imagophagy, are proposed for characterization of those koinobionts that have specialized for attacking adult insects. The implications of the imagobiont strategy relative to diversity patterns in the tropics are discussed.

Key words. Hymenoptera, Braconidae, Euphorinae, adult-parasitism, koinobionts, evolution, imagobiont.

Резюме. Обсуждается явление паразитирования на имаго хозяев у браконид подсем. Euphorinae. Рассмотрены гипотезы об эволюции имагинального паразитизма. Предложено, что паразитизм на имаго возник от предков, которые были койнобионтными личиночно-личиночными паразитоидами. Невозможно его возникновение непосредственно из идиобиозиса, так как койнобионты обладают быстрой откладкой яиц в хозяина — поведением, являющимся преадаптацией к заражению подвижных взрослых насекомых. Показано, что паразитоиды на взрослых хозяевах обладают уникальной комбинацией койнобионтных и идиобионтных характеристик. Предложены новые термины для тех койнобионтов, которые специализируются на заражении взрослых насекомых-хозяев — имагобиозис и имагофагия. Обсуждается роль имагобионтной стратегии в биоразнообразии в тропиках.

Ключевые слова. Hymenoptera, Braconidae, Euphorinae, имагинальный паразитизм, койнобионты, эволюция, имагобионт.

Introduction

The order Hymenoptera includes numerous species that are parasitoids of other insect species, but the vast majority of these attack immature stages of their hosts (eggs, larvae, or pupae). The utilization of the adult (imago) stage of insects as hosts is comparatively rare within the Hymenoptera, however the

braconid subfamily Euphorinae provides the best known example of a lineage where adult-parasitism has not only evolved but has been highly successful (S. Shaw, 1985, 1988a). Upon first consideration, parasitism of adult stages seems rather difficult and rather unlikely to succeed. Adult insects are highly mobile and very able to evade parasitoids by flying or running. They are able to defend themselves against parasitoids by biting, kicking, and sometimes by use of chemical defenses. Adults are more densely sclerotized than immature stages, therefore are harder to oviposit into (literally). Finally, as compared with immature stages of the same host species, they are simply far less numerous, therefore provide a more difficult target for parasitoids in time and space (Fig. 1). However, once these obstacles were overcome, parasitism of adult insects provided a pathway to great diversification in the Euphorinae (S. Shaw, 1988a). Therefore, the euphorine Braconidae provides a special case for understanding the diverse pathways of the evolution of parasitic strategies in the order Hymenoptera. The purpose of this paper is to outline the evolutionary pathways by which adult-parasitism evolved within the Euphorinae, and to outline the remarkable aspects of this mode of parasitism.

It is a great honor and pleasure to write this paper on the occasion of the 75th birthday of Professor Vladimir I. Tobias. His studies on the evolution of Euphorinae (Tobias, 1965, 1966, 1967) provided a stimulus and a starting point for my own studies of this fascinating subfamily. Thank you, Professor Tobias, for these pioneering efforts toward understanding the evolution of this remarkable lineage of Braconidae. This paper is dedicated to you, on the happy event of your birthday, with gratitude for setting my feet on this fascinating pathway of study.

The phenomenon of adult-parasitism in the Braconidae

The braconid subfamily Euphorinae is a cosmopolitan lineage of small parasitoid wasps that utilize the adult stage of various insects as their hosts. The most commonly used hosts are adult Coleoptera, especially the families Chrysomelidae and Curculionidae, but across the Euphorinae many other kinds of adult insects are used, including Hymenoptera, Neuroptera, Hemiptera, Psocoptera, and some Orthoptera (S. Shaw, 1985, 1988a). When the host is an insect with gradual metamorphosis, then middle to late instar nymphs may be used as hosts, in addition to adults (S. Shaw et al., 2001). But in these cases the maturing nymphal host is very similar to the adult insect host in terms of feeding behavior, habitat preference, degree of mobility, appearance, and behavior.

Adult-parasitism is comparatively unusual within the family Braconidae, and indeed within the entire order Hymenoptera (Quicke, 1997). The vast majority of parasitoid Hymenoptera species attack immature stages of their hosts, larval-larval parasitoids being especially common (Whitfield, 1998). Within the Braconidae, most subfamilies are larval-larval parasitoids (M. Shaw, Huddleston, 1991). Other braconids are egg-larval parasitoids (Cheloninae, Ichneutinae), or larval-pupal parasitoids (Opiinae, Alysiinae), but virtually none are strict pupal-parasitoids.

Other than Euphorinae, only the Aphidiinae and neoneurine braconids attack adult host stages. The Aphidiinae are a moderately diversified lineage entirely restricted to parasitism of aphids (M. Shaw, Huddleson, 1991). These were formerly classified as a distinct family group (Mackauer, 1968) but recent studies place them clearly as a lineage within the Braconidae (Achterberg, 1984; Quicke, Achterberg, 1990; Wharton et al., 1992). Technically, the aphidiines must be sometimes regarded as true adult-parasitoids because some oviposit directly into reproductive adult aphids, or emerge from the adult stage of the aphid. But for most aphidiines the second and third nymphal instars are the preferred hosts, and first and fourth instar nymphal aphids are also sometimes used as hosts (Mackauer, 1973). In fact, some aphidiines have even been recorded ovipositing directly into embryos (Mackauer, Kambhampati, 1988). Thus, aphidiine braconids utilize hosts from the widest possible range of host age classes, ranging from embryo to adult stage. Although some aphidiines are adult-parasitoids, they are not restricted to parasitism of the adult stage (as most euphorine braconids), and most show a preference for other stages. Even when adult aphids are attacked, the situation is qualitatively very different from the condition encountered by most euphorine parasitoids of adult insects. Aphids are very numerous, highly clumped, relatively soft-bodied, and comparatively defenseless, as compared to hosts such as adult beetles used by many euphorine braconids. Hence, although the case of the Aphidiinae is worth mentioning, the aphidi-

ines are not so highly specialized for attacking only adult hosts, and their case is less relevant towards understanding the evolutionary origins of adult-parasitism.

On the other hand, the neoneurine braconids are true adult-parasitoids, attacking and developing in the abdomens of adult formicine ants (S. Shaw, 1993; Poinar, 2004). For many years the neoneurines were treated as a separate lineage (subfamily Neoneurinae), but Tobias (1966) proposed classifying the neoneurines within the Euphorinae because they attack adult insects. However, aside from their habit of attacking adult insects, there is no clear evidence for classifying neoneurines within the Euphorinae (S. Shaw, 1985). Some recent studies place the Neoneurinae as a separate subfamily independent from the Euphorinae (Wharton et al., 1992; S. Shaw, 1995). More recent molecular analyses place the neoneurines within the helconoid lineage of Braconidae, near the base of the Euphorinae, if not within them (Whitfield, 2002). The precise phylogenetic placement of the neoneurine lineage remains an interesting and controversial question, worthy of continued research. Whether the neoneurines are placed in the Euphorinae (common evolution of adult-parasitism) or classified as a separate subfamily (convergent evolution of adult-parasitism), it is clear that the study of neoneurines can provide useful insights into the origins and evolution of adult-parasitism. The recent discovery of a neoneurine larva emerging from an adult ant embedded in Baltic amber demonstrates that parasitism of adult insects existed at least 40 million years ago (Poinar, Miller, 2002). This observation is consistent with molecular-based estimates indicating that the polydnavirus-bearing lineage of Braconidae emerged about 74 million years ago (Whitfield, 2002).

The origin of adult-parasitism in the Euphorinae

Studies of Baltic amber also suggest that adult-parasitoid Euphorinae existed at least 40 million years ago (Brues, 1933). The Baltic amber species *Microctonus nanus* Brues and *Parasyrrhizus ludens* Brues clearly establish the presence of Euphorinae in that time-frame. Further, the presence of both tribes Microctonini and Centistini in the Baltic amber fauna indicates that the subfamily Euphorinae was already moderately well-diversified (see: S. Shaw, 1985), therefore adult-parasitism probably originated at an earlier time, maybe 50–60 million years ago.

Initial studies of Euphorinae phylogeny by Tobias (1966) placed the meteorine braconids basally with the majority of euphorines emerging from that lineage. Several subsequent studies corroborate the hypothesis that the meteorine braconids comprise the sister-group to the adult-parasitoid Euphorinae (Achterberg, 1984; S. Shaw, 1985, 1988a; Maeto, 1990; Quicke, Achterberg, 1990; Wharton et al., 1992; Zitani, 2003). There remains some debate about the classification of meteorine braconids. Some authors, including myself, treat the meteorine lineage as a distinct subfamily Meteorinae, emphasizing the habit of larval-larval parasitism, and restricting the Euphorinae (largely) to the lineages of adult-parasitoids (S. Shaw, 1985, 1988a; Maeto, 1990; M. Shaw, Huddleston, 1991; Hanson, Gauld, 1995; Wharton et al., 1997; Zitani et al., 1997, 1998; Zitani, 2003). Other authors continue to place the Meteorini as a tribe in the subfamily Euphorinae, emphasizing perhaps the smooth morphological transition between these groups (Achterberg, 1984; Belokobylskij, 2000b). This classification issue is a classic case of whether to split or whether to combine (lump) groups, and there may not be a clear and unambiguous solution. The key point is that the classification issue really does not matter here, because there is a general agreement about the phylogeny of the lineages involved. Classification issues aside, clearly studies of the meteorines can provide important insights regarding potential preadaptations for adult-parasitism.

Tobias (1966) also proposed the hypothesis that adult-parasitism in the Euphorinae originated by parasitism of the beetle family Chrysomelidae. The "chrysomelid-hypothesis" is based on the observation that in certain cases euphorine females will oviposit into larvae in addition to adults, and in those cases the host is usually a leaf beetle (Tobias, 1966). Because adult and larval leaf beetles live and feed on the same plants, it is hypothesized that the host-shift from larval-parasitism to adult-parasitism was facilitated by ecological coincidence in time and space. It has also been suggested that adult chrysomelids may sequester lower levels of plant toxins than larvae of the same species, thus adult chrysomelids may be more suitable hosts than their larvae (Poinar, pers. comm.).

If the chrysomelid-hypothesis is valid, then one would predict that leaf beetle parasitoids should be phylogenetically basal within the subfamily Euphorinae. This is precisely the pattern that phylogenetic studies have demonstrated (S. Shaw, 1985, 1988a). Four euphorine tribes (Perilitini, Townesilitini, Mi-

croctonini, and Centistini) that parasitize Chrysomelidae occupy basal or intermediate positions on the euphorine phylogenetic tree. On the other hand, the relatively more apical tribes (Dinocampini, Euphorini, Myiocephalini, Cosmophorini, and Syntretini) all conspicuously lack leaf beetle parasitoids. The chysomelid-hypothesis provides a plausible working model for the origin of adult-parasitism from larval-parasitism. Tobias' chrysomelid-hypothesis has been corroborated by phylogenetic studies, and no alternative hypotheses have been suggested in the 38 years since it was proposed.

Across the family Braconidae, parasitism of leaf beetles is rather rare and almost entirely restricted to the Euphorinae lineage. The meteorine braconids (presumed sister-group of the adult-parasitoid Euphorinae) parasitize the larvae of many Lepidoptera and Coleoptera, but usually not Chrysomelidae (West, Miller, 1989; M. Shaw, Huddleston, 1991; Zitani, 2003; Zitani, S. Shaw, 2002; Zitani et al., 1997, 1998). One rare exception is a single species of *Meteorus* that parasitizes larval Chrysomelidae (M. Shaw, 1988). There is no particular evidence that adult-parasitizing euphorines evolved from this particular meteorine lineage. However, even if this instance of host use is a convergence, it still demonstrates that chrysomelids are within the potential host range of meteorines. The idea that the common ancestor of the Euphorinae was meteorine-like, and that adult-parasitism evolved in conjunction with chrysomelid-parasitism, is a very plausible scenario.

Some other meteorine lineages, such as the *M. albizonalis, M. corax*, and *M. hirsutipes* species-groups, are known to attack other coleopteran hosts, such as beetle larvae in wood or mushrooms (Maeto, 1990). Traditionally these have been regarded as basal and primitive lineages within the Meteorini, and Maeto (1990) hypothesized that lepidopteran parasitism in meteorines evolved from these groups of beetle parasitoids. However, recent studies of meteorine phylogeny by Zitani (2003) indicate that the beetle-parasitizing meteorines comprise a derived lineage within the group, and that the most basal meteorines were parasitoids of exposed-feeding Lepidoptera. This has important implications regarding the evolution of adult-parasitism because it implies that the basal Euphorinae evolved from ancestors that attacked mobile hosts (such as caterpillars) rather than from ancestors using comparatively immobile hosts in substrates.

Preadaptations for adult-parasitism

More than 20 years ago, I was asked to answer a seemingly simple (but perhaps rather complicated) question by a friend and colleague, ecologist Paul Gross. "What is it about euphorines that preadapted them for attacking adult insects?" My initial answers to that question were very much influenced by my background as a morphologist. It is very tempting, at first, to look at the various and fascinating morphological mechanisms the Euphorinae have evolved for coping with adult insect hosts. They are visually attracted to moving hosts (Bryden, Bishop, 1945; Walker, 1961), so many euphorines have large eyes that converge on the front of the face. They have sharp, blade-like, and very flexible ovipositors for placing eggs between thick host sclerites, into softer membranous tissues of the mouth, neck, coxal cavities, between abdominal sclerites, anus or gonopore (Belokobylskij, 1996c). It is interesting to note that the aphidiine braconids show behavioral modifications for coping with moving hosts, such as grasping the host aphid with their front legs (Völkl, Mackauer, 2000). Likewise, many euphorines have quite remarkable adaptations for grasping hosts that may be highly mobile (Belokoblyskij, 1996b, 1996c). *Cosmophorus* has huge mandibles and a large oral space used to grasp host beetles during oviposition. The highly modified mandibles of *Proclithrophorus* (Vikberg, Koponen, 2001) are probably used for the same purpose (Belokobylskij 1996c). The Neotropical genus *Plynops* has species with strangely modified mandibles and deeply excavated faces, so that the head morphology of each species seems to form a unique "beetle clamp" (S. Shaw, 1996). Some euphorines of the tribe Centistini have dense pads of setae on the venter of the mesosoma, metasomal sternites, or hypopygium (Achterberg, 1992; Belokobylskij, 1996c). Other Centistini possess hooks on the venter of the mesosoma (S. Shaw, 1985), or even "clasper-like" structures at the tip of the female metasoma (S. Shaw, unpublished data) that appear to be adaptations for host manipulation. Finally, members of the genera *Streblocera* and *Marshiella* have curiously modified antennal flagellums that are raptorial in appearance (Belokobylskij, Ku, 1998a; S. Shaw, 2000). Presumably these wasps use their antennae for grasping the host during oviposition (Belokobylskij, 1996c). However, all of these useful adaptations are found only in relatively more advanced lineages of Euphorinae

(S. Shaw, 1985, 1988a). Therefore none of these features can be regarded as a pre-adaptation for adult-parasitism.

When comparing the meteorine braconids with rather basal genera of Euphorinae, such as *Perilitus* or *Microctonus* (sometimes regarded as a subgenus of *Perilitus*), one is struck by the apparent lack of dramatic morphological changes accompanying the transition to adult parasitism. Aside from some rather minor changes in wing venation, the basal adult-parasitizing euphorines are very similar to meteorine braconids in outward appearance. The main morphological feature that seems to provide a pre-adaptation for adult-parasitism is the constriction of the first metasomal segment into a narrow, elongate petiole. This allows the female wasp to flex the metasoma forwards, to extend the ovipositor forward under the meso-soma, and out in front of the head. It is an obvious morphological and behavioral difference separating the meteorines and euphorines from most other parasitic Hymenoptera. While most parasitic Hymenoptera drill downwards into a substrate, or sting downwards into a host while standing on it, the meteorines and euphorines mostly extend the ovipositor tip in front of the face and run directly at a host. In the case of the meteorines, which attack caterpillars, the host caterpillars may be capable of crawling rapidly, thrashing with defensive motions, or dropping away on a silk thread. A forward mode of attack is clearly a valuable adaptation for dealing with moving caterpillars. Certainly this is also a useful pre-adaptation for attacking adult insects, because adult insects are likely to be very mobile. Also, a forward method of attack allows the euphorine female to more precisely place eggs into the softer parts of an adult insects body armor. Some euphorines accomplish this frontal attack by having a moderately long ovipositor in addition to flexibility of the petiolar first metasomal segment. Others, such as *Wesmaelia* and *Chrysopopthorus* have a much shorter ovipositor, but a much longer and exceedingly slender petiole (S. Shaw 1997). Either way, the frontal attack is accomplished. Aphidiines accomplish the frontal attack in a different fashion, by extending and telescoping the metasomal segments (Völkl, Mackauer, 2000). Neoneurines have retractable ovipositors that can be extended some distance from the body during oviposition (S. Shaw, 1993). While neoneurines do also use a frontal approach for attacking ants, they do not bring the ovipositor in front of the head while attacking. Neoneurines approach an ant from behind, land momentarily on the ant's abdomen while grasping the ant with modified legs, rapidly inject an egg in the posterior end of the ant, then quickly fly away (S. Shaw, 1993; Poinar, 2004). In this respect the neoneurines are different from most euphorines, but perhaps most similar to the Centistini, which attack adult beetles using similar postures and may grasp the host beetle with their legs during oviposition (Belokoblyskij, 1996b).

Consideration of these morphological features of the ovipositional stance leads to consideration of related behavioral characteristics, which may provide a more important pre-adaptation for adult-parasitism. Meteorines and euphorines, as well as aphidiines and neoneurines, are all very rapid in their oviposition behavior. They are very fast. In fact, they are extremely fast, as compared to many Hymenoptera. Observations of meteorines indicate that they take only a second, or several seconds, to oviposit (DeLeon, 1933; Simmonds, 1947; Fuester et al., 1993; Zitani, 2003). Probably this speed is an adaptation to effectively attacking hosts that move quickly, can thrash in defense, or will drop or move away quickly when disturbed. Euphorine wasps also attack their hosts very rapidly, taking only a fraction of a second, to a few seconds, to insert an egg (S. Shaw et al., 2001). Likewise, the neoneurines (S. Shaw, 1993, 1995; Poinar, 2004) and the aphidiines (Völkl, Mackauer, 2000) are also very rapid, again taking only a fraction of a second, or up to a few seconds, to oviposit. Given the lack of compelling morphological similarities between euphorines, aphidiines, and neoneurines, it appears that the most significant pre-adaptation for adult-parasitism may not be any single morphological feature. The behavioral feature of rapid oviposition sequence seems far more significant, because it adapts these organisms for attacking highly mobile, and fast-moving, adult hosts.

Idiobiosis and koinobiosis

In recent years, new terminology has emerged for categorizing parasitoids by their method of interacting with the host at the time of oviposition (Haeselbarth, 1979; Gauld, 1988). This terminology provides a useful conceptual viewpoint for examining the evolution of adult-parasitism. Parasitoids that inject the host with a paralyzing venom, from which the host does not recover, are termed i d i o b i o n t s.

Idiobiosis is exhibited by parasitoids that induce an arrested state of development where the host does not develop further, and those where the parasitoid larva consumes the host essentially as it was at the time of egg deposition (without allowing the host to grow further). Parasitoids that do not inject the host with a paralyzing venom, or those which use a temporary venom from which the host recovers, are termed k o i - n o b i o n t s . The key feature of koinobiosis, therefore, is that the host continues to remain active and grow following parasitism (M. Shaw, Huddleston, 1991; Quicke, 1997). According to this terminology, the euphorine adult-parasitoids would be characterized as koinobiont endorparasitoids because the hosts are not permanently paralyzed and remain active after oviposition.

Modern studies of parasitic Hymenoptera evolution have concluded that idiobiosis is the ancestral condition for parasitic wasps (Gauld, 1988; Whitfield, 1998). All of the most basal lineages of parasitic Hymenoptera, such as Orussidae, Stephanidae, and Megalyridae, are idiobiont ectoparasitoids of wood-boring insect larvae (Quicke, 1997; Whitfield, 1998). Many of the more basal lineages within the Ich-neumonidae and the Braconidae also preserve this primitive, but effective, strategy (Gauld, 1988; M. Shaw, Huddleston, 1991). Figure 1 provides a useful diagrammatic hypothetical context for viewing these modes of parasitism. Depicted are two lines representing changes in a hypothetical host population over time. In the case of idiobiont larval parasitoids, imagine that the lines represent a local population of wood-boring beetles that are suitable as hosts. Line N depicts the number of individual hosts present in the local habitat and available for potential parasitism. This may be considered as any example of a type II or type III insect survivorship curve, as depicted, for example, by Price (1980, 1984, 1994). As Price (1994) noted, "for all insects there is an inevitable attrition of a cohort through the life cycle from egg to adult, generating some kind of negative slope in a survivorship curve." Eggs are the most numerous host stages. From there the population of hosts declines over time, as individual hosts die for various reasons. Of course the line would not be straight, and it would fluctuate differently for different host species, but over time host populations would decrease in numbers towards the adult stage. Line B depicts another aspect of the same host population: the total available host biomass. Imagine that all the host individuals could be weighed at any given point in time. The sum of their individual biomasses would be the total host biomass available for parasitism at any given point in time. This curve would also fluctuate over time. It would start low because eggs, although numerous, have relatively little biomass. Line B would
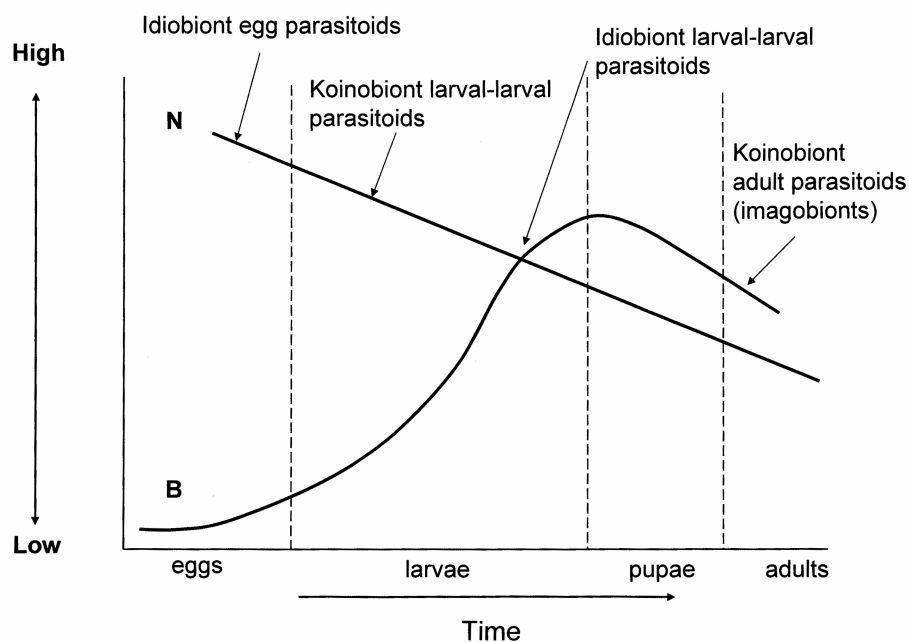
Fig. 1. Relationship of parasitoid strategies to total host biomass (B) and total available hosts (N) over time.

increase dramatically over the larval stages of the host as the host insects feed and develop greater biomass. But since pupae do not feed, and are subject to mortality, the curve for line B would fall in the host pupal stage. Although adults feed and may add some biomass, there would be increasing mortality as the individual adult hosts age, so the line B would continue to fall over time, until eggs are laid and the cycle repeats.

Viewed in these terms, it may come as no surprise that the evolution of the parasitoid habit in Hymenoptera, that is to say, the origin of idiobiont larval parasitism, corresponds to the point in time where these two lines N and B meet (Fig. 1). Simply stated, idiobionts tend to attack large larvae because they provide the largest amount of biomass for consumption. Since idiobionts induce a permanent paralysis of the host, the host does not grow further or increase in biomass after parasitism, so there is little apparent advantage for idiobionts to attack smaller hosts. There is considerable evidence that idiobiont parasitoids spend significant time assessing host size and host quality, and may preferentially place female offspring or larger clutch sizes into larger and more suitable hosts (Charnov, 1982; Charnov, Skinner, 1984; Godfray, 1994). Following the late instar larval stage, total available host biomass would fall, so pupal and adult hosts would be both less numerous and provide less available biomass for parasitism. Thus, idiobiont larval parasitism seems to optimize these two factors, available host numbers (N) and available host biomass (B). Late larval hosts are also easier for parasitoids to find because they are still actively feeding and thus releasing various signals that can be used by wasps for host location (chewing sounds, heat, kairomonal chemicals released from feeding, frass). Once the hosts pupate, these cues are lost.

Idiobionts spend a long time laying relatively fewer eggs (as compared with koinobionts) so they tend to be K-selected species. Because they attack hosts that are usually inside plant tissues, and because they take the time to inject venom and wait for ensuing paralysis, idiobionts tend to take a very long time for their oviposition sequence. The female idiobiont must drill through a substrate, probe the host, inject a venom, wait for paralysis, probe and assess host quality, deposit an egg, and finally withdraw the ovipositor from the substrate (Quicke, 1997). Consider, for example, the tropical species *Ecphylus costaricensis* Matthews, an idiobiont ectoparasitoid of bark beetle larvae. A female of *Ecphylus costaricensis* spends 25 to 42 minutes drilling through wood to reach a host, and another 11 to 19 minutes to lay an egg and withdraw the ovipositor (Matthews, 1969). Thus, an entire oviposition sequence for an idiobiont species may require up to an hour or more to complete. When compared to the rapid oviposition behavior of euphorine adult-parasitioids, the contrast is quite amazing. A euphorine female that deposits an egg in one second is acting 3660 times faster than the idiobiont species in this example. It is worth mentioning that in all known cases, adult-parasitoids have evolved from koinobiont ancestors (e.g. the case of meteorines and euphorines) rather than from idiobiont ancestors. In fact, it seems unlikely that adult-parasitism could ever evolve directly from idiobiosis. Idiobionts are far too slow, and adult-parasitism requires a faster oviposition speed, such as seems to be associated with the evolution of koinobiosis.

The paradox of koinobiosis

As depicted in Fig. 1, the phenomenon of koinobiosis evolved within the context of wasps using smaller (but more numerous) larval hosts (Gauld, 1988; Whitfield, 1998). The vast majority of known koinobionts are endoparasitoids of young larval insects (M. Shaw, Huddleston, 1991; Quicke, 1997). An egg is injected into the young larval host, but it is not paralyzed, and it continues to grow. Price (1973a) suggests that parasitoids that are "early colonizers" have high fecundity and low competitive ability, thus are "r strategists". Koinobiont larval-larval parasitoids usually do produce lots of small (metabolically inexpensive) eggs and are r-selected species (as compared with most idiobionts). In most cases, the host larva molts one or more times and increases very substantially in biomass before the parasitoid larva completes its feeding and kills the host. The evolution of koinobiosis seems to present a paradox: if idiobionts prefer to attack larger hosts, and if such hosts provide a better quality resource for development, then why would koinobiosis develop from idiobiont ancestry?

By moving in the direction of utilizing smaller hosts, koinobionts are optimizing host availability (N) at the expense of available biomass (B). One solution to this problem is simply the evolution of smaller adult body size. On the average, koinobiont larval parasitoids (such as microgastrines) are much

smaller than idiobiont larval parasitoids (such as Orussidae). Those Hymenoptera with the smallest body sizes (Chalcidoidea) evolved to parasitize the smallest available hosts (eggs). Those egg parasitoids that have paralyze or kill the embryo have evolved idiobiosis again, but have optimized the use of available hosts (N). In many cases, however, small body size does not provide the complete solution to this paradox. Many koinobiont larval parasitoids (perhaps most) place their eggs into individual hosts that, at the time of oviposition, are too small to provide sufficient nutrients for the parasitoid larva to develop to maturity. Only by allowing the host to continue to grow and develop biomass can the parasitoid possibly develop and survive. This feature, allowing the host to continue growing, is the key element of koinobiosis. But when viewed from the perspective of what the female wasp is doing, placing an egg in a host too small to provide sufficient food for her offspring, it seems to present another paradox. It would seem to be maladaptive, perhaps almost ridiculous, and certainly very risky, for a female wasp to lay eggs in hosts that are too small to provide (at that time) sufficient nutrients for her offspring to survive.

"Baldufian" parasitism

The key to understanding this puzzle lies in the behavior of the parasitoid larva. Many koinobiont larval-larval parasitoids have first instar larvae that develop slowly, or diapause, allowing the host larva to feed and develop considerably greater biomass before it is killed. This parasitic strategy (delayed larval development) was outlined in detail by Balduf (1963) in his classic (but often overlooked) paper, "A distinct type of host-parasite relationship among insects." In that paper Balduf described a type of parasitism characterized by delayed larval development usually with a diapause of the first larval instar, followed by breaking of diapause, rapid larval feeding, and rapid larval development prior to pupation of the host. Balduf notes that this mode of parasitism is common in many ichneumonoid, chalcidoid, proctotrupoid, and cynipoid parasitic Hymenoptera. He did not invent a name for this mode of parasitism, so for discussion we can call it "Baldufian" parasitism. It is perhaps regretable that Balduf did not propose a term of his own for this mode of parasitism, as it corresponds closely to what we now call koinobionts. He was perhaps the first author to coherently outline an important aspect of koinobiont behavior.

It is clear in retrospect that all "Baldufian" parasitoids are also what we now call koinobionts. However, not all koinobionts are "Baldufian" parasitoids (adult-parasitoids are not "Baldufian" parasitoids). "Baldufian" parasitoids are never idiobionts. Clearly there would be no adapative advantage for an idiobiont to delay its larval feeding, when the food is already paralyzed and ready to consume. The development of "Baldufian" parasitism adds a further element of mystery to the paradox of koinobiosis, but also provides the key to the puzzle. Why would larval diapause evolve? Not feeding seems like a poor strategy for any immature organism. If they don't eat they can't grow, and the longer they delay development the longer they are exposed to potential mortality factors. But this double-paradox of koinobiosis reveals a remarkable situation. Either the koionobiont adult behavior or the koinobiont larval behavior viewed separately seems to be maladaptive. If an adult wasp places an egg in a host that it too small and the larva develops immediately, the parasitoid larva would probably die. However, when the two behaviors are evolved together the result is highly adaptive. By attacking small hosts at an earlier stage, adult koinobionts are optimizing the number of available hosts (N) and also getting their offspring into the host an earlier time and so avoid competition. By delaying feeding and development the "Baldufian" koinobiont larva re-gains the advantage of idiobiosis, by allowing the host to build sufficient biomass for the parasitoid's development.

Viewed in these terms, it appears that larval-larval koinobiosis might now be divided into two types: "Baldufian" koinobiosis and "non-Baldufian" koinobiosis. Presumably "non-Baldufian" larval-larval parasitoids might also enjoy the benefits of attacking young hosts (high N, competitive advantage of getting in the host early) but could only survive if they evolve small body sizes that require less biomass for development, or if their larvae simply feed very slowly, developing gradually. What is the ratio of "Baldufian" to "non-Baldufian" species among larval-larval koinobionts? Truthfully, we do not know. It is much easier to determine koinobiosis by observing adult behavior. The host is stung, it recovers, and you know you are dealing with a koinobiont. Determining "Baldufian" vs. "non-Baldufian" parasitism is much more difficult, requiring dissections and repeated observations of larval behavior. But such studies will be an important area for future parasitoid research.

As compared with idiobionts, koinobiont species tend to attack hosts more directly, and much more rapidly. For example, the egg-larval koinobiont parasitoid *Chelonus curvimaculatus* completes its oviposition sequence in 17–21 seconds (Leluk, Jones, 1989). The koinobiont microgastrine, *Glyptapanteles thompsoni*, injects 20 to 25 eggs in a single thrust requiring only a few seconds (Vance, 1931). So the oviposition behavior of koinobiont larval-larval parasitoids is very rapid in comparison to their idiobiont ancestors, but not quite as rapid as that displayed by koinobiont adult-parasitoids. The quick oviposition behavior of koinobionts probably evolved in response to several factors. Koinobionts tend to attack exposed hosts, so much time is saved by not drilling through substrates. By attacking exposed hosts, they are more likely to be attacking hosts that can move or possibly escape parasitism. Therefore fast oviposition would provide a real advantage. Koinobionts do not permanently paralyze the host, so there is no need to wait for venoms to induce paralysis. Finally, if koinobiont larval-larval parasitoids are attacking small hosts (that at the time of oviposition are too small for the parasitoid larva to develop to maturity) it would be difficult, or impossible, for the adult female wasp to fully assess host quality at time of egg-laying. Therefore, koinobionts may reduce oviposition time by reducing (or eliminating) behavior relating to assessing host quality. This has profound implications for understanding the evolution of adult-parasitism. Adult-parasitoids must have evolved from koinobiont larval-parasitoid ancestors, because idiobionts are too slow, and only the koinobionts evolved the necessary oviposition speed to cope with attacking mobile adult insects. But it is also important that koinobionts show a reduction in host quality assessment behaviors. This behavioral change allows koinobionts to make more potential "oviposition mistakes", to sometimes place eggs in novel hosts, and allow for more diversification of host-ranges over time (S. Shaw, 1988a). Koinobiont adult-parasitism could probably only evolve from a state of koinobiont larval-larval parasitism, for both of these reasons.

The paradox of adult-parasitism

The adult-parasitoids (e.g. Euphorinae) can be technically defined as koinobionts because the host is not permanently paralyzed. But in many respects, the adult-parasitoids are quite different from other koinobionts. While the larval-parasitoid koinobionts have evolved to optimize host availability (N), the adult-parasitoids have reversed that trend and evolved in the direction of using the host stage with both low available host numbers (N) and low available total host biomass (B) (see Fig. 1). That would seem to present yet another paradox: why did evolution reverse the koinobiont trend of searching for numerous, small hosts, and why would wasps evolve to seek adult stages that seem sub-optimal in terms of both N and B?

The solution to this paradox has already been suggested. The usual koinobiont trend was reversed through the evolution of the use of Chrysomelidae as hosts (S. Shaw, 1988a). This allowed for the host-switch from larval leaf beetles to adult leaf beetles directly, because larvae and adults of such insects co-exist in the same micro-habitats, eat the same plants, and presumably release similar signals that might attract the parasitoid. But why specialize on the adult stage when it is less numerous, harder to catch, harder to penetrate, and has not substantially more biomass? The most likely answer is that adult beetles presented a totally novel and unoccupied "adaptive zone". Once inside adult beetle hosts the euphorine braconids enjoyed an "enemy free space" that was devoid of competing parasitoid species. There may have been other advantages as well, such as rich nutrients available by consumption of the adult female beetle's ovaries and ova, lower sequestered plant toxins, or there may have been less resistance by the adult host's immune system response.

Whatever the reasons, adult-parasitoids have become specialized in various ways that distinguish them from koinobiont larval-larval parasitoids. Unlike larval hosts, the adult host does not go through additional molts. Since the adult host is approaching the end of its life, there is no advantage for the larval euphorine to delay its development. There is no larval diapause by the euphorine larva unless the adult (or nymphal) host is diapausing as well. The euphorine larva does not diapause to allow host biomass accumulation, nor does it cue into metamorphic hormonal changes. Therefore, euphorines are not "Baldufian" parasitoids. Since the euphorine larva feeds and develops immediately, without larval diapause, the larval behavior is more characteristic of an idiobiont parasitoid larva. Also, since euphorines attack the least numerous host stage (lowest N), they tend to be relatively more K-selected rather than r-selected. This is

consistent with observations that "as host abundance declines during a generation, the ovarioles per ovary are less abundant in parasitoid species attacking successively less abundant stages of the host" (Price, 1973b). So in being K-selected adult-parasitoids are more like idiobionts than koinobiont larval-larval parasitoids. Finally, although they retain the koinobiont habit of fast oviposition behavior, they have carried it to an even greater extreme. They are the fastest of the parasitic Hymenoptera in their egg-laying habits.

Since the adult-parasitoids are so distinctive in several ways, it may prove useful to have some special terminology to discuss this mode of parasitism. Because they specialize in utilizing the adult (imago) stage of insects, I'm proposing the terms i m a g o b i o n t and i m a g o b i o s i s to describe the lifeways of these insects. They might also be called i m a g o p h a g e s, to describe their unique feeding habit, i m a g o p h a g y. The term imagobiont can be used for any of the parasitoids that utilize adult insects as their hosts. Imagobionts are also koinobionts but they represent an advanced stage of koinobiont evolution. Imagobionts differ from koinobiont larval-larval parasitoids by being relatively more K-selected, by having rapid larval development, and more rapid oviposition behavior.

Another aspect of imagobiosis that deserves to be investigated further is the number of larval instars. As with "Baldufian" behavior, this aspect of larval development is difficult to observe. As pointed out by M. Shaw and Huddleston (1991) there are few observations and some of the observations reported in the literature may not be correct. The primitive condition for idiobiont braconids appears to be 5 larval instars, while koinobiont braconids seem to vary between 3–5 larval instars (Wharton et al., 1992). It is interesting that 3 larval instars have been reported in some meteorine braconids, as this might be interpreted as another pre-adaptation for imagobiosis (shorter larval duration would allow exiting from an adult host more quickly). Even so, a range of variation from 5 larval instars (Loan, 1967), to 4 larval instars (Balduf, 1926), to 3 larval instars (S. Shaw et al., 2001) has been reported among different euphorine species. The imagobiont neoneurine *Elasmosoma* is reported to have 3 larval instars (Poinar, 2004). So while some imagobionts express the fewest larval instars (3) seen in hymenopteran development, this does not seem to be a requirement of imagobiosis. This is probably because their larval development is rapid, in any event, and also because adult life spans vary among different potential adult insect hosts.

Finally, another aspect of imagobiosis is that several species have been reported to exhibit thelyotokous development (Balduf, 1926; Jackson, 1928; S. Shaw, 1988b, 2002; S. Shaw et al., 2001). This behavior would be a useful adaptation for adult wasp populations existing at very low population densities.

Host shifts and diversification within the Euphorinae

The pattern of host-shifting and diversification in the Euphorinae was discussed in my previous essay (S. Shaw, 1988a). The idea that imagobiosis allowed the colonization of a new "adaptive zone" (adult insects) is corroborated by the observation that the Euphorinae s. str. is roughly twice as diverse as its sister-group, the meteorine braconids. Adaptive radiation on adult hosts has occurred in the Coleoptera, Hemiptera, and probably also in adult Hymenoptera (by the tribe Syntretini). Many novel host-shifts are indicated with the Euphorinae, including shifts from Coleoptera to Orthoptera; Coleoptera to Hymenoptera; Coleoptera to Hemiptera; Hemiptera to Neuroptera, Psocoptera, and back to Coleoptera (bark beetles). It appears that the rapid oviposition behavior of imagobionts allows for more frequent oviposition mistakes, but occasionally to use of entirely novel hosts, which present new opportunities for adaptive radiation. Imagobiont host-shifts appear to involve hosts in the same microhabitat and having similar feeding habits. This is consistent with a model of host-location by visual cues and host-produced kairomones. It appears that minor host-shifts, between related hosts, are more frequent than major host-shifts (across insect orders). But imagobionts express behaviors that do allow major host-shifts from time to time, and these events have provided important opportunities for diversification over evolutionary time.

Implications regarding diversity patterns in the Euphorinae

Recent studies of tropical insects have concluded that the diversity of life on this planet is substantially higher than previously imagined, with most of the world's species being insects of the tropical rain

forest canopies (Wilson, 1992). Erwin (1982, 1988) has estimated that insects alone may account for as many as 30 million species. Estimates as high as 50 to 80 million world species have been suggested, but conservative estimates are much lower, around 7 to 10 million species (Hanson, Gauld, 1997). The implications for imagobiont research are very important. Even by the most conservative estimates, there must be several *millions* of Coleoptera species in the tropical forest canopies of the world. A large portion of these are species of the hyperdiverse families Curculionidae, Chrysomelidae, and Carabidae, the very host groups that are targeted by Euphorinae. We know that imagobiont Euphorinae have existed for at least 40 million years. If they have been exploiting and radiating on these beetle hosts for that period of time, how diverse are the euphorine Braconidae really? In the 1980s, I estimated that the number of known world species of Euphorinae was around 750 species (S. Shaw, 1988a). Many new euphorine species have been discovered in recent years (Achterberg, S. Shaw, 2000; S. Shaw, 2000; Belokobylskij, 2000b, 2000c, 2000d, 2000e, 2000f, 2000g, 2001; Belokobylskij, Ku ,1998; Chen et al., 2001; Papp, S. Shaw, 2000) and even several new genera (Achterberg, S. Shaw, 2001; S. Shaw, 1987, 1988b, 1996; Belokobylskij 1998, 2000a), bringing the world total of named species to near 1,000. My studies of Malaise trap samples from Costa Rica for over 15 years demonstate that Euphorinae are exceptionally diverse, both in generic richness and species richness, even from that small country. The tribes Microctonini, Centistini, and Syntretini are hyperdiverse in Costa Rica, with large numbers (probably hundreds) of new species awaiting description (S. Shaw, unpublished data). But how many imagobiont euphorine species remain to be discovered in the tropical forests of the entire world? Hundreds, certainly. Thousands, possibly. Millions? It is not beyond possibility, assuming that the above insect species estimates are correct. There certainly are enough adult insect hosts available. So the number of imagobiont species in the world remains one very uncertain factor that might affect world species estimates.

If imagobionts are really hyperdiverse in the tropics, why haven't we discovered this before now? Well, truthfully I think we are discovering it, but rather slowly. Our existing knowledge of Euphorinae is based more on temperate zone species, and on particular species that may be of benefit to agriculture (Varis, Achterberg, 2001; S. Shaw et al., 2001; Williams et al., 2003). By comparison, our knowledge of tropical species is rather pathetic. Euphorines are comparatively rarely collected by traditional sampling methods, but our knowledge of imagobiont biology provides a clear explanation for this. Imagobionts are K-selected species that exist in low population numbers. This is why they are usually characterized as "rare" (Belokobylskij, 1996a; Belokobylskij, Ku, 1998b). They are specialized for attacking adult insects, so spend most of their life history either as immature stages inside the adult insect host or outside the host (high in the canopy?) as a cocooned-pupa. The adults have a short life span, and spend that time chasing other adult insects, probably those active high in the rain forest canopy. It's a wonder that we have discovered as many as we have. Still, many more imagobionts must remain, awaiting discovery. Most ecologists and biological control workers studying insects focus their studies on the immature stages (such as leaf-feeding caterpillars). Very few people actually collect adult insects (such as leaf beetles or weevils) with the intent of keeping them alive for extended study, or seeing what parasites emerge. Even more challenging is the prospect of discovering the hosts of Syntretini species, if they are utilizing active hosts such as abdomens of adult bees and ichneumonid wasps. Our methods of study will need to change in the future, for unless we gain detailed knowledge of the nature and extent of imagobiosis in the tropics, we will never have a complete knowledge of biodiversity on this planet.

Acknowledgments

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