1. Origin and occurrence of predation among Hymenoptera: A phylogenetic perspective

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Abstract. Predation in its narrowest sense—where the predator attacks and consumes its own prey—is proportionally less important in Hymenoptera, being restricted to adult feeding behaviors such as host feeding with lethal consequences in a few ichneumonids and dryinids, and direct predation by adult tenthredinids hunting other insects for self nutrition. Predation in Hymenoptera occurs mostly for larval feeding and is carried out by adult wasps acting as provisioning predators. Provisioning predation has undoubtedly evolved from the parasitoid mode of life and one of the key features in this transition involves the relocation of the host. Host relocation—a term used here to characterize a series of behaviors associated with movement of the host (or prey), commonly to a concealed site, from the place where it was originally found and subdued—is found only among the aculeate Hymenoptera. Here, the evolutionary pathways that probably led some hymenopterans to adopt a predatory way of life are briefly summarized and the number of times in which prey relocation and provisioning behavior evolved within the order is investigated. Not taking into consideration the pompilid wasps, prey relocation might have originated from one to three times independently, the different
scenarios dependent on the phylogenetic hypothesis and mode of character optimization. A separate analysis, at genus level, carried out for the Pompilidae postulates two separate origins for prey relocation involving two main clades, one within the Pepsinae and the other within the Pompilinae. It is concluded that further advances in understanding should come with more robust phylogenies. Additional phylogenetic reconstructions at genus, or species level, within polymorphic clades such as the Pompilidae and Scoliidae, are also necessary for more precise groundplan estimations. More stable and unambiguous reconstructions at family level within the Aculeata, however, will require data from clades for which we currently lack any biological information. Knowledge on the biology of some key groups, such as the Bradynobaenidae, remains elusive and will not be obtained without concentrated effort.

**Introduction**

In ecology, predation has been defined as a competitive biological interaction where a consumer (predator) feeds on another organism (prey) which is always alive at the time the predator first attacks it and this interaction usually results in the death of the prey [1]. Predation represents one of the major evolutionary forces [2] and has evolved many times at different taxonomic levels, including within insects where several groups have independently evolved to be predators. Most predatory insects feed on other arthropods and, in this way, are involved in regulating their communities by reducing the prey’s population to a lower level than would occur in the predator’s absence [3].

In its classical sense, a predator kills its prey more or less immediately after attacking it, and during its lifetime, the predator will kill several prey individuals, often consuming them entirely. In a broader sense, predation can also result from interactions like grazing and parasitism, and includes more subtle interaction processes like parasitoidism [1]. Grazers attack several prey during their lifetime, but only take a portion of each one, usually affecting them in a limited way and rarely being lethal in the short term [2]. Mosquitoes are an example of grazers amongst insects and some kinds of host feeding in parasitoid Hymenoptera [4] can be accounted as such too.

A parasite is a symbiotic organism that feeds on a single prey (host)—rarely a few more under special circumstances—being harmful in the long term but rarely causing death in the short term. The parasite benefits at the expense of the host, reducing its fitness in several ways: it reduces the host’s capability of reproducing, may induce different degrees of pathology and also modify the behavior of the affected organism [1].

Parasitoidism involves the traits described for parasites, but the interaction between the parasitoid and its hosts unavoidably results in the
death of the latter or—less frequently—in the loss of its reproductive viability [5]. In some sense, parasitoidism may be considered a somewhat intermediate mode of life between classical parasitism and predation [6, 7]. Similarly to predators, parasitoids will directly impact their host populations by reducing their numbers.

Among insects, the parasitoid lifeway has arisen most commonly in the Diptera, where it has evolved independently in 21 families (probably over 100 times). It has arisen in 11 coleopteran families but probably only once in the Hymenoptera [8]. In most cases host searching is by the adult female parasitoid but in a significant minority of cases host-searching is by the first instar larva of the parasitoid, or (more rarely) by the host ingesting the parasitoid egg [8].

Predation in its narrowest sense—where the predator attacks and consumes its own prey—is proportionally less important in Hymenoptera, being restricted to adult feeding behaviors such as host feeding with lethal consequences [9, 10] and direct predation by adult tenthredinids hunting other insects for self nutrition [11; see below]. In Hymenoptera, predation is carried out not only for self nutrition, and its peculiarities make its definition and distinction from parasitoidism a matter of controversy [12].

The peculiarities of predation in Hymenoptera are directly inherited from a series of evolutionary steps dating back from the origins of the order as such. The groundplan life-style of Hymenoptera is phytophagy, probably endophytic into highly nutritious tissue [12] as exhibited by xyeline Xyelidae, this family being recognized as the sister lineage to the remainder of the Hymenoptera [13, 14]. Although several basically exophytic phytophagous lineages (Tenthredinoidea, Pamphiloidea and Cephoidea) appeared afterwards as sideshoots within the order, an important behavioral consequence of endophytic nutrition is direct oviposition within the food source, a feature that will be maintained throughout the order [5] with just some minor modifications and losses (notably in Perilampidae, Eucharitidae and Trigonalidae, which just lay their eggs in the substrate that will potentially be transited or consumed by a host).

At some point, the main lineage of Hymenoptera—in the grade containing the superfamilies Siricoidea and Xiphydrioidea—adopted an important shift in larval feeding habits as endophytic symbiotic mycoxylophages [15, 16, 17]. It is in the clade containing Orussidae and the Apocrita that entomophagy appears as idiobiont parasitoidism a single time in the evolutionary history of the Hymenoptera.

Theoretical pathways to parasitoidism have been suggested from classical predation, saprophagy and mycophagy [8]. This last pathway seems to have happened in Hymenoptera, starting in the endoxylophagous scenario
characteristic of the ancestral lineage of Orussidae plus Apocrita [8]. Orussids and some rather basal families of Apocrita are parasitoids of wood-burrowing insects (mostly Coleoptera, but also larvae of Siricidae and Xiphydriidae) [12, 18]. Some authors have clearly demonstrated that species of Orussidae develop as parasitoids of the larvae of Buprestidae and Siricidae [18, 19, 20, 21, 22]. There has been some discussion whether the oviposition is in protected burrows of stems, in which the young larva searches and feeds on larvae of other arthropods, or directly on the host. Nevertheless, the idiobiont way of life seems to have evolved in the lineage that gave rise to the Orussidae plus Apocrita, with many changes along the evolution of the derived members within the order. At its origin, parasitoid entomophagic behavior in larval Hymenoptera probably evolved from facultative carnivory in a cleptoparasitic species, in which its larva fed both on the host immature (or even on a conspecific larva), as well as on plant substrate [8].

Here, the concept of predation as applied to Hymenoptera is discussed and definitions for complementary terms are introduced. We also briefly summarize the evolutionary pathways that probably led some hymenopterans to adopt a predatory way of life, compile information on the predatory lineages and investigate how many times this behavior has evolved within the order.

**Predation in the Hymenoptera**

Predation in Hymenoptera occurs mostly for larval feeding and, more rarely, as adult self nutrition. Most cases of predation for larval feeding are carried out by adult wasps acting as provisioning predators, while a few records of direct predation by larvae are known in many families of otherwise typical parasitoids [7]. Adult self nutrition derived from provisioning predation seems to be restricted to social vespids, that malaxate their prey before providing it to the larvae [23], and to some solitary eumenine and apoid wasps that bite or pierce the prey to suck up fluids, sometimes also partly consuming prey tissue [24, 25]. The few cases of adult predacious feeding, not related to larval provisioning, are known in tenthredinid sawflies and some apocritan parasitoid wasps preying directly on their hosts.

**Adult predacious feeding**

Although the basal hymenopteran lineages have phytophagous larvae, a large number of adult sawflies in the family Tenthredinidae have been observed preying on other insects [11, 26]. At least 63 species in 27 genera have been reported to hunt and feed directly on a number of holometabolous insects, including adult flies (Bibionidae, Calliphoridae, Empididae,
Fanniidae, Scatophagidae, Stratiomyidae, Syrphidae, Tachinidae, Tipulidae), adult sawflies (Tenthredinidae), adult beetles (Cantharidae, Nitidulidae), larvae and pupae of chrysomelid beetles and immature Lepidoptera [11, 26].

Another remarkable case of adult predation is known in one species of Ichneumonidae, which uses a wide range of moth larvae as hosts [9]. Adult females are not able to oviposit without first consuming some host tissue, usually hemolymph. This could be included simply as a case of host feeding [27], except that very small hosts can be entirely consumed by the females during the feeding process [9].

The Dryinidae comprises another case where adult females are known to also prey on their auchenorrhynchous hosts [10, 28]. Females of three species kept under confined conditions were reported to feed partially on their hosts, which subsequently were either discarded or parasitized [10]. They usually consumed the first host captured in the day.

These cases of adult predacious feeding are based either on anecdotal field observations or on behaviors exhibited under experimental conditions. It must be taken into account that laboratory factors might have influenced the results observed for Ichneumonidae and Dryinidae, although it seems likely that these wasps behave similarly in nature. Unfortunately the limited information available for Hymenoptera precludes an evaluation of the importance and impact of this kind of predation in the wild.

**Idiobiont parasitoidism and host relocation**

In Hymenoptera, provisioning predation has undoubtedly evolved from the parasitoid mode of life and one of the key features in this transition involves the relocation of the host, usually to a site far away from where it was subdued. Parasitoidism is a mode of life exhibited by a vast portion of hymenopteran lineages, of which the most diverse are the Ichneumonoidea and the Chalcidoidea [29]. Hymenopteran parasitoids have long been classified in a dichotomy, distinguishing where their development on the arthropod host takes place, either internally or externally, respectively endoparasitoidism or ectoparasitoidism. However, these traits are somewhat vague and must be used for particular cases only. For major tentative classifications, the terms idiobiont and koinobiont (more appropriately transliterated as ‘cenobiont’ [30]) should be adopted [5, 31].

Idiobiosis is commonly related to ectoparasitoid behavior, but by no means all idiobionts are ectoparasitoids. The term idiobiont is better related to the influence that the parasitoid exercises over its host, that is, its larva consumes the host while the latter has its development interrupted by the adult female, which paralyzes the host prior to or during oviposition [5]. Koinobiosis (or
better, ‘cenobiosis’), on the other hand, is commonly related to endoparasitoidism, but yet again this is no absolute rule. This is an apomorphic condition compared to idiobiosis, and the parasitoid larva consumes the host only after having allowed it to develop to certain stages of its lifespan [5].

Most idiobionts attack hosts living in concealed places [5, 32] and they can be divided into two basic groups depending on how the female wasps reach the hosts. In the first group, the parasitoid females reach the hosts deploying an elongate ovipositor that both injects substances that paralyze and alter the host physiology and transfers the parasitoid egg to its body surface. Under this situation, the parasitoid female does not get within close reach of the host. This is assumed to be the primitive condition among parasitoid Hymenoptera, having evolved from mycoxylophagous ancestors that inserted the eggs and their symbiotic fungi deep into the plant substrate.

Alternatively, in other groups of idiobionts, the female moves through the substrate in search of hosts and needs to enter in direct contact with them for paralysis and oviposition. Host stinging usually takes place through a short, modified ovipositor, and the female attaches its egg on the external surface of the host body. This mode of attack is characteristic of the aculeate hymenopterans that behave as idiobiont ectoparasitoids [12].

In their direct contact with the host, these parasitoid females are repeatedly confronted with the decision to leave it in the same place or to move it somewhere else. In the latter situation, females may relocate their host, usually for considerable distances, before ovipositing. Host relocation is exhibited by many aculeate wasps (see below) and this term is used here to characterize a series of behaviors associated with movement of the host (or prey), commonly to a concealed site, from the place where it was originally found and subdued.

Host relocation has probably evolved as a means to reduce host usurpation, predation, superparasitism or hyperparasitism of the developing immature [7]. In the short term, it is likely to be most effective against competition from conspecific females, which supposedly would not forage in places where the hosts are not expected to thrive. Independent of the putative advantages related to relocation of the hosts, fixation of this behavior in several aculeate lineages has undoubtedly opened up major avenues leading to complex behaviors associated to nest construction and sociality.

**Host relocation, nest building and provisioning predators**

The most widespread mode of predation within Hymenoptera is carried out by adult wasps capturing other arthropods that are taken to and stored in nests as food for their larvae. Wasps with this life history have been termed provisioning predators [7], since they will only rarely feed on the prey
themselves, and therefore do not behave as typical predators. This kind of predation, destined to larval feeding, occurs only among aculeate lineages and involves host/prey relocation in a first stage and nest building in a second stage [33].

Host/prey relocation in aculeate wasps has almost always led to evolution of behaviors associated with active construction of a nest, a place especially prepared by females to which the prey are transported and stocked. Nests are most commonly built as tunnels and chambers dug in the ground, although more elaborate and complex nests are found in all nest-building aculeate groups, such as aerial nests built with plastered material (mud, resins or plant fibers mixed or not with glandular secretions produced by the adult insects or their larvae). Most nests also have as their basic unit the brood cell, primarily a cavity built and provisioned for the development of a single immature.

Predatory wasps can be single or multiple provisioners depending on the number of prey items fed to each immature. A multiple provisioner can be either a mass or a progressive provisioner. Mass provisioning occurs when the adult stocks all of the food necessary for the development of the larva in a single process before sealing the containing cell. The egg is normally laid on the food after the stocking is complete, but in some groups it is laid prior to provisioning. Progressive provisioning occurs when the adult provides fresh food to its larva from time to time until its complete development. The cell is either permanently open or the adult opens and re-seals it each time a new load is provided.

The thin boundary between an idiobiont parasitoid and predatory Hymenoptera has traditionally been considered to reside in the behavior of the female towards its host/prey: a female wasp that does not relocate its host/prey is considered a parasitoid, while one that relocates it is considered a predator [7, 25]. There is, however, a seamless gradation among aculeate wasps from species that behave as parasitoids to those that move the paralyzed prey only for short distances and hide it in pre-existent crevices to those that prepare a nest previously to prey hunting [25]. Therefore, any attempt to label species strictly according to behavioral categories is necessarily arbitrary. For this reason, we focus here in a specific behavior—host relocation—instead of on behavioral categories.

**Occurrence of prey relocation in Hymenoptera**

All known cases of host/prey relocation in Hymenoptera are restricted to the Aculeata, a large clade in which the females have their ovipositor modified as a sting apparatus used to inject venom into their host or prey, and therefore no longer used for laying eggs. In their groundplan, the aculeates
behave as idiobiont parasitoids, attacking beetle larvae living in concealed places. From this parasitoid groundplan, host/prey relocation and predatory behavior have evolved a number of times within the Aculeata. The formicids, vespids, most apoid wasps and, to some extent, the pompilid spider wasps behave as typical provisioning predators, paralyzing their prey and transporting it to their nests for larval feeding. Nevertheless, cases of limited host relocation are known in Bethylidae, Tiphiiidae and Scoliidae, families that otherwise behave as typical parasitoids (see below).

A summary of the main biological features for the aculeate families is given in Table 1. Biological information is lacking for three key basal lineages in the Aculeata—Plumariidae (Chrysidoidea), Sierolomorphidae (Vespoidea) and Heterogynaidae (Apoidea). Based on morphological and some behavioral evidence, the first two families are likely to exhibit the groundplan biology of the aculeates, behaving as parasitoids upon beetle larvae living in the ground. As regards the Heterogynaidae, it has been suggested that their biology is probably similar to that exhibited by the Ampulicidae [34]. Also, data on the biology of Bradynobaenidae is virtually lacking, except for anecdotal information on a species of Typhoctinae [35].

**Bethylidae**

Bethylids as a whole seem to be adapted for searching hosts living in cryptic situations [39] and many species have developed host relocation and nest closure similar to that observed in other predatory aculeates. It is likely that these behavioral traits have evolved independently and possibly several times within the family, but the knowledge of the biology and phylogeny of bethylids is still by far too incomplete as to get a good picture of their evolution. Host carriage to a bembicine wasp nest burrow used by the female bethylid as a starting point for her own adventitious and poorly elaborated nest has been reported for *Epyris eriogoni* [40]. Also females of *Epyris extraneus* hide their host in a temporary shelter, dig a burrow and then re-transport it to the burrow [41]. Both species of *Epyris* subdue and transport tenebrionid larvae much larger than their own size. Host relocation has also been reported for other genera such as *Allepyris*, *Bethylus*, *Cephalonomia*, *Holepyris*, *Laelius*, *Parascleroderma* and *Trachepyris* [40, 42].

**Apoidea**

Besides the bees (Apidae *sensu* Melo [34]), Apoidea contains a varied assemblage of predatory wasps in the families Ampulicidae, Sphecidae and Crabronidae, and rare cases of parasitoidism (e.g. genus *Larra* in the
Table 1. Summary of main biological features for the families of aculeate Hymenoptera (character states are assumed to be part of the family’s groundplan). Classification according to Brothers [36], Carpenter [37] and Melo [34]. A “?” indicates lack of information, and a “—”, an inapplicable character.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Relocation of larval food</th>
<th>Larval hosts or provisions</th>
<th>Number of larvae per host batch</th>
<th>Nest building</th>
<th>Larvae reared in:</th>
<th>Number of prey items per brood cell</th>
<th>Egg laid in:</th>
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<td>individual brood cells</td>
<td>multiple</td>
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</table>

¹There are reports of limited host relocation (see text for details). ²Some species also lay a single egg per host. ³Amiseginae and Loboscelidiinae parasitize eggs of Phasmatodea. ⁴Ampulicidae does not build nests in a strict sense. ⁵Groundplan states are based in Melo [34] and an unpublished analysis. ⁶There are reports of limited host relocation (see text for details). ⁷Diamminae is an exception and uses Gryllotalpidae as hosts [38]. ⁸There is no available reconstruction for the groundplan states of Pompilidae; therefore it is considered polymorphic for characters of columns 1 and 4 (see text for details). ⁹Based only on anecdotal information for a species of Typhoctinae [35]. ¹⁰Food items in Formicidae are very diverse; here all states, except “pollen”, are attributed to the family. ¹¹Formicids do not lay their eggs directly onto the prey; however, they are likely to have originated from a species with gregarious larvae. ¹²There are reports of limited host relocation and preparation of a rudimentary chamber (see text for details).
Crabronidae) [34]. All ampulicids are known to attack only Blattaria and to behave rather uniformly: after capturing and stinging a roach, the female waits until it partially recovers from the paralysis, drags it by the antenna to a suitable natural cavity (in the soil, in wood or in hollow stems), lays an egg on it and then finally blocks the opening of the cavity with pieces of various kinds of debris [43, 44, 45, 46]. Therefore, there is no true nest construction among ampulicids, only hiding of the prey in a suitable pre-existing cavity. Sphecidae and Crabronidae, on the other hand, use as prey a large number of insect orders, as well as spiders, and most species build their nests before prey hunting [25, 47, 48]. Nesting behavior is most diverse in the Sphecidae, with nests being constructed before or after prey capture, being made underground, in wood cavities or made of plastered mud, containing single or multiple brood cells, and provisioned with single or multiple prey items.

**Pompilidae**

The pompilid wasps are well known predators of spiders [25, 26, 49, 50, 51]. Behavioral diversity in the family includes both idiobiont and cenobiont ectoparasitoids, obligatory cleptoparasites and a variety of nest-building predators, ranging from those that make simple, unicellular burrows in the ground only after prey capture to those that prepare elaborate multicellular mud nests before prey hunting. Despite this variability, all known pompilids attack only spiders and always provision a single prey item per larva.

**Tiphiiidae**

Most female tiphiiids seek for the host—usually scarabaeid grubs—underground, temporarily paralyze it by means of several stings, oviposit on it and immediately leave it alone without relocation or modification of its original place [25, 26, 52]. In some cases, as in the genera Methocha (Methochinae), Diamma (Diamminae) and Pterombrus (Myzininae), the host is stung and buried in its own burrow by the female wasp, the host burrow serving as a sort of rudimentary nest [53, 54, 55]. Nevertheless, special cases of relocation and burrow digging to hide the host when it is located above the ground have been described for some species of Methocha [55], Myzimum (Myzininae) and Tiphia (Tiphiiinae) [52]. Secondary evidence of host relocation and cell conditioning has also been recorded for females of Cosila chilensis (Anthoboscinae) as the paralyzed and oviposited larvae of its host (the scarabaeoid Pseudadelphus ciliatus) were found away from their food source and all surrounded by earth while active individuals of the same species were found near plant roots and surrounded by a mixture of earth and degraded wood [56].
Scoliidae

Although there has been very little published on the biology of scoliids, the available information indicates that these wasps attack only scarabaeoid larvae living in soil [25, 26, 41, 52]. Females searching for hosts spend most of the time underground and apparently require direct contact with host body odors and feces to locate them [57]. Relocation of the host, sometimes several feet underground, followed by preparation of a cell, where oviposition on the host takes place, has been assumed as part of their groundplan [26, 52]. Some species, however, apparently do not move their host from the place in which it is paralyzed [45].

Vespidae

All vespids are nest-building predators and one of the key features of their biology is oviposition into an empty cell built before prey capture [58]. As far as is known, the basal vespids are mass multiple provisioners, with the Euparagiinae (extant subfamily sister to the remaining Vespidae) using larvae of Coleoptera as prey [59]. Although most of the remaining lineages utilize Lepidoptera larvae as food resource for the immatures, some genera of Eumeninae also provide their offspring with Coleoptera larvae as well [23, 24]. Nevertheless, no generalization can be made for the entire subfamily, since information regarding their biology is by far the least known among vespids. The Masarinae are an exception within the family, providing their nests entirely with pollen and nectar, as bees do [60].

Formicidae

While extremely diverse in many morphological, behavioral and ecological features, ants are rather uniform when compared to other provisioning aculeate predators: all species are eusocial, rear their larvae in communal chambers and feed them progressively [61]. Nests are most commonly a series of tunnels and chambers dug in the soil or in decaying wood. Although primarily predators, ants have evolved to explore a wide range of food items, among them cultivated fungus mycelia and harvested seeds [61, this book].

Origins of predation in Hymenoptera

How many times has provisioning predation arisen among the aculeate hymenopterans? Only an approximate answer to this question is currently
Origin of predation in Hymenoptera possible and we discuss here some putative scenarios based on hypothesized changes in behavioral features—prey relocation in particular—optimized on available phylogenies for the Aculeata [34, 36, 37, 62]. The analyses focus only on the lineages showing typical provisioning predatory behavior—Apoidea, Pompilidae, Formicidae and Vespidae—and employs the information of the first three columns of Table 1. The outgroup, assumed to behave as an idiobiont ectoparasitoid on beetle larvae, had its character states based on the biology of Orussidae and other apocritan groups, such as Stephanidae and Megalyridae.

Postulated character reconstructions are shown in Figs. 1 and 2. At family level and not taking into consideration the Pompilidae (see below), prey relocation might have originated from one to three times independently, the different scenarios dependent on the phylogenetic hypothesis and mode of character optimization (either accelerated or delayed state changes). A single origin (Fig. 2A), at the ancestral lineage of Apoidea plus Vespoida, is recovered under Pilgrim’s et al. hypothesis [62] when applying accelerated optimization. Two origins (Fig. 1), one at the ancestral lineage of Apoidea and the other in the lineage leading to Formicidae and Scoliidae plus Vespidae, result from Brothers’ hypothesis [36], independent of the optimization. Three separate origins (Fig. 2B), once each at the ancestral lineages of Apoidea, Formicidae and Vespidae, is recovered under Pilgrim’s et al. hypothesis when applying delayed optimization.

No resolution can be attained for Pompilidae at family level when treating it as polymorphic for prey relocation (see Table 1). A separate optimization was carried out using an available phylogeny [63] having as terminals the genera for which there is biological information [51]. As shown in Fig. 3, current phylogenetic hypotheses favor two separate origins for prey relocation involving two main clades within Pompilidae, one within the Pepsinae and the other within the Pompilinae. This scenario, as opposed to a single origin, is favored because all basal lineages within the family behave either as cleptoparasites (Ceropalinae) or as spider parasitoids (Minagenia in Pepsinae, the Ctenoceratinae and basal Pompilinae).

Considering the low resolving power of the resulting reconstructions at family level (Figs. 1 and 2), one can hardly exert preference for a given scenario over the others. Nevertheless, it is possible to evaluate the different hypothesis against the available evidence. Among the three main scenarios, a single origin for prey relocation seems the most unlikely, since it requires two reversals, one involving a large clade of Vespoida and another for the Rhopalosomatidae. Reversal to an idiobiont behavior has occurred quite infrequently and the few known cases are restricted to Apoidea and Pompilidae, with no occurrence in Vespidae or Formicidae.
Figure 1. Ancestral state reconstruction for selected behavioral characters in Aculeata Hymenoptera. Characters 1 to 3 (see Table 1) were optimized on a combined phylogeny for Chrysoidea [37], Apoidea [34] and Vespoidea [36]: (1) Relocation of larval food, (1.0) absent/ (1.1) present; (2) Larval hosts or provisions, (2.0) orthopteroids (Embioptera, Blattaria, Mantodea, Orthoptera and Phasmatodea)/ (2.1) immature Hemiptera/ (2.2) immature Coleoptera/ (2.3) immature Lepidoptera/ (2.4) immature Hymenoptera/ (2.5) pollen/ (2.6) arachnids; (3) Number of larvae per host, (3.0) single/ (3.1) multiple (gregarious larvae). A, acctran optimization; B, deltran optimization.

It has been commonly assumed that nesting behavior, and in the present context prey relocation, has originated independently among the aculeates [e.g. 33, 64]. Perhaps the main evidence for an independent-origin scenario rests in the distinct behavioral features exhibited by the provisioning predators
Figure 2. Ancestral state reconstruction for selected behavioral characters in Aculeata Hymenoptera. Characters 1 to 3 (see Table 1 and legend of Fig. 1 for character description) were optimized on a combined phylogeny for Chrysidoidea [37], Apoidea [34] and Vespoidea [62] (see their Fig. 8B). The Chrysidoidea are not shown (see Fig. 1). A, acetrans optimization; B, deltran optimization.
Figure 3. Ancestral state reconstruction for selected behavioral characters in Pompilidae. Phylogenetic relationships and subfamilial classification from Pitts et al. [63]; biological information from Shimizu [51; see his Fig. 378]. Characters: (1) Relocation of larval food, (1.0) absent/ (1.1) present; (2) Nest building (applicable only to those taxa receiving state 1.1), (2.0) after prey capture/ (2.1) before prey capture. Reconstruction under delayed optimization.
in the Aculeata, each clade having a number of idiosyncrasies not found in the others.

A separate origin in the Apoidea has support in their somewhat isolated phylogenetic position. The lineage that gave rise to them probably behaved similarly to how the extant ampulicids do (see above), with prey relocation by foot and only a rudimentary nesting behavior. Evolution of true nesting behavior, involving construction of a nest before prey capture, occurred in the ancestral lineage of the clade formed by Sphecidae and Crabronidae plus Apidae [34]. Indeed, some of the synapomorphies from the adult morphology shared by this clade may have evolved in conjunction with changes in their nesting biology. For example, the modifications of the mid- and hind coxae, as well as adjacent areas of the mesepisternum and metepisternum, may be correlated with changes in prey transport mechanisms and/or with the evolution of nest digging behavior [65]. The enlargement of the coxal bases is probably associated with larger and stronger coxal muscles that are required for using the legs for carrying prey and for digging underground nest tunnels [65]. In Sphecidae and Crabronidae, the prey is always actively carried and not just guided to the nest site as ampulicids do. They transport their prey in flight or in case of a large prey over the ground, but always moving forward with the prey secured by the legs and/or the mandibles [6, 66].

As regards the formicids and vespids, two independent origins also seem more likely for them. The single-origin scenario for this lineage (Fig. 1) depends somewhat on the groundplan behavior of scoliids, which were here scored as polymorphic, with prey relocation both present and absent. The rudimentary prey relocation exhibited by some scoliids, however, might not have been present in their ancestral lineage. Unfortunately, biological information for the scoliids is scant and fragmentary, with less than ten species investigated [25] and no data available for the putative archaic genus *Proscolia*.

Also, the peculiar biology of formicids, as compared to vespid wasps and other nest-building aculeates, favors a scenario of parallel evolution for prey relocation and nesting behavior. Little can be said of the behavior of the ancient lineage that gave rise to formicids, but it has been often assumed that ants evolved from wasps that subdued large, soil- and wood-dwelling arthropod hosts, rearing the larvae gregariously on them [61, 67]. Host/prey relocation might not have been present in the initial stages due to the large size of the hosts. Alternatively, ancestral ants might have behaved as some basal ants of the subfamily Amblyoponinae still do [68, 69], dragging entire chilopods to their nests and then placing the larvae to feed directly on them [61].
Diversity of host/prey use within aculeate Hymenoptera

The lineage that gave rise to the aculeate Hymenoptera diversified around 160-150 mya in the late Jurassic [70, 71], with the majority of the extant lineages being already established by the early Cretaceous (~130 mya). Although these extant lineages use a wide variety of arthropod groups as host/prey for their immature (Table 1), the ancestor of the Aculeata probably behaved as an idiobiont ectoparasitoid on beetle larvae.

Aculeate wasps, however, differ from other Apocrita groups also primitively associated with beetle larvae in having evolved from a lineage that specialized in hunting for hosts in the ground [70], living in association with dead plant matter either lying over the surface or buried underground. Use of ground-living host/prey is widespread within the three aculeate superfamilies and is reflected in the behavior exhibited by those families that hunt for beetle larvae as well as those that attack other arthropods. As detailed below, all switches for host/prey living in above ground substrates occurred later in the evolutionary history of these clades and are scattered among independent aculeate lineages.

In Chrysidoidae, Plumariidae probably exhibits the groundplan condition for the aculeates, since the morphology of the females (apterous) and their collecting sites (under rocks) suggest that they search for hosts on the soil surface or underground [72]. In the remainder of the superfamily, there are four main host switches (Fig. 1): immature Lepidoptera in Bethylidae (Bethylidae), immature Hymenoptera in Chrysididae, Embioptera in Sclerogibbidae and Auchenorhyncha (Hemiptera) in Drynidae + Embolemidae. Also, a switch in host choice to phasmid eggs in the ancestor of Amiseginae + Loboscelidiinae occurred in Chrysididae, but apparently maintaining the plesiomorphic search behavior in regard to the host substrate.

A switch in prey choice, from beetle larvae to orthopteroid insects (most likely cockroaches), has occurred early in the history of Apoidea (Figs. 1 and 2), but this switch also did not involve a major change in the prey substrate. Nothing is known about the biology of Heterogynaidae, but due to the brachypterous condition of the females, it has been suggested that they might behave as idiobiont parasitoids [73]. On the other hand, despite their brachyptery, females might drag their prey in a way similar to that of Ampulicidae [34]. There are two additional main host switches within Apoidea (Fig. 1): Hemiptera in the ancestral lineage of Crabronidae + Apidae, and pollen in Apidae. The further diversifications in food choice and substrate search behavior in Apoidea have been enormous and a detailed discussion of these changes is beyond the scope of the chapter.
Seeking for host/prey living in the ground is also the basic pattern for the entire Vespoidea, with only the Vespidae diverging early to above-ground prey searching behavior. Use of Coleoptera is maintained as a groundplan feature for Tiphiidae, Scoliidae and probably also for Vespidae and Sierolomorphidae. Although the biology of sierolomorphid wasps remains unknown, specimens have been collected after emerging from decaying logs on the ground [74]. Host/prey choice is diverse in this superfamily and the main switches are: immature Hymenoptera in Sapygidae + Mutillidae, Araneae in Pompilidae, Orthoptera in Rhopalosomatidae, and immature Lepidoptera and pollen within Vespidae. Other switches involve Bradynobaenidae and Formicidae, but in these cases, there is no unambiguous state at family level. The basic condition for Bradynobaenidae is hard to define, since only anecdotal information is available for one species of Typhoctes which parasitize Solifugae (Arachnida). Formicidae seems to have gone through multiple early switches to a broader repertoire of prey, followed by later diversification in their diet, including non-animal food sources (fungi, harvested seeds, etc.). In their groundplan, however, they are clearly associated with ground-living prey, many groups being specialized in diverse arthropod groups, including chilopods, diplopods, diplurans and beetle larvae.

**Concluding remarks**

Despite the major adaptive radiations opened up in the aculeate Hymenoptera by the acquisition of a predatory way of life, our understanding of its early evolution is still precarious for many clades. Current phylogenetic hypotheses offer only limited resolution in pinpointing in which lineages prey relocation and provisioning predation first evolved.

The traditional view that provisioning predation evolved independently in the main predatory groups has only partial support from ancestral-state reconstructions. Not considering the pompilid wasps, possible scenarios involve from one to three independent origins. Nevertheless, those postulating convergent evolution seem more plausible in view of the distinct behavioral features exhibited by the different clades of predators.

Further advance should come with more robust phylogenies, derived from morphology and/or molecular data. Additional phylogenetic reconstructions at genus or species level, within polymorphic clades such as the Pompilidae and Scoliidae, are also necessary for more precise groundplan estimations. More stable and unambiguous reconstructions at family level within the Aculeata, however, will require data from clades for which we currently lack any biological information. Knowledge of the biology of some key groups, such as the Bradynobaenidae, remains elusive and will not be obtained without concentrated efforts at sites in which these wasps are most abundant.
References

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