

Characterizing basal apocritans (Hymenoptera: Apocrita)

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О характеристике базальной ветви апокрит (Hymenoptera: Apocrita)

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Abstract. A principal feature of the Apocrita is the failure of the proctodeal invagination to join the mid-gut during larval development, resulting in a closed gut. We discuss the evolution of this feature, and suggest that a primary function may be increased assimilation efficiency. We also discuss host exploitation and cocoon formation in terms of the evolution of the Apocrita from putative ancestors within the siricoid grade of the Symphyta.

Key words. Hymenoptera, Apocrita, gut closure, cocoon formation, labial silk glands, ectoparasitism, endoparasitism.

Резюме. Личинку Апокрита отличает разделение средней и задней кишки на протяжении всего периода ее развития. Обсуждается эволюция этой важной особенности и высказывается предположение, что изначальной функцией такого замкнутого кишечника может быть увеличение эффективности ассимиляции пищи. Обсуждаются использование хозяина и формирование кокона в эволюции апокрит из сирикоидной ветви Symphyta.

Ключевые слова. Нуменоптера, Апокрита, замкнутый кишечник, формирование кокона, губные шелковые железы, эктопаразитизм, эндопаразитизм.

Introduction

In most textbooks on entomology and in most other general accounts, the Hymenoptera, one of the largest orders of insects, continues to be divided into two suborders: the Symphyta and the Apocrita. This classification does not reflect the long-standing recognition that the Symphyta do not constitute a natural, or monophyletic, group (Börner, 1919; Gibson, 1985; Vilhelmsen, 1997, 2001; see: Hennig, 1981 for summary of early literature). By contrast, the Apocrita, a much larger group containing the vast majority of the species of Hymenoptera, is supported as monophyletic on the basis of the waist-like constriction between the first and second abdominal segments. The first abdominal segment in Apocrita (the propodeum) is fused to the metathorax, and the constriction between the first and second abdominal segments is

in the form of a tergal-tergal articulation. Vilhelmsen (2001) discussed some other less obvious autapomorphies.

As noted by Whitfield (1992), there has been a long-standing interest in the evolution of the Hymenoptera in general and the Apocrita in particular. Stimulated in part by the works of Malyshev (1968), Rasnitsyn (1975, 1980), and Königsman (1976, 1978), numerous investigations have been conducted over the last 20 years. Several such studies have examined individual characters across taxa or sets of related character systems such as thoracic musculature (Gibson, 1985), midcoxal articulations (Johnson, 1988), the metapostnotum (Whitfield et al., 1989), mesofurca and metapostnotum (Heraty et al., 1994), and 16S rRNA (Dowton, Austin, 1994), while others have attempted a broader synthesis (e. g. Rasnitsyn, 1988; Ronquist et al., 1999). Nevertheless, it is hard to refute the recent observation by Dowton and Austin (2001) that the development of a robust phylogeny for the parasitic wasps has proven to be a rather elusive goal.

Despite this problem, several excellent studies using morphological data sets (e. g. Gibson, 1985; Rasnitsyn, 1988; Vilhelmsen, 2001; Schulmeister, 2003) have repeatedly uncovered the following set of relationships useful to understanding the evolution of the Apocrita: (all other Symphyta + (Siricidae + (Xiphydriidae + (Orussidae + Apocrita))). The orussid-apocritan relationship, in particular, seems very firmly established as evidenced by the work of Gibson (1985) and Johnson (1988), and the number of apparent synapomorphies that Vilhelmsen (2001) summarized in a recent analysis of extant basal lineages of the Hymenoptera. In essence, this hypothesis suggests that the Apocrita share a sister-group relationship with the Orussidae, and that there was a step-wise transition through the siricoid grade leading to the Orussidae. Alternative hypotheses, such as a cepheid ancestor to the Apocrita (Malyshev, 1947, 1949, 1968; Königsman, 1976), have not found support in recent morphology-based studies. Though less firmly established, the Stephanidae are frequently treated as one of the most likely basal groups within the Apocrita (Whitfield, 1998; Vilhelmsen, 2001, 2003a), with both the mesotrochanteral muscle and prepectus providing perhaps the best support for this basal position (Gibson, 1985, 1999). Vilhelmsen (2003a) lists other characters shared by orussids and stephanids, at least some of which (coronal spines or their analogs) are found in other apocritan taxa attacking wood-boring insects. Support for basal nodes in analyses of apocritan relationships is generally weak (e. g. Sharkey, Roy, 2001), and Stephanidae consequently do not always appear as the basal group, as perhaps best exemplified by Ronquist et al. (1999) and Dowton and Austin (2001).

If the currently accepted set of siricoid-orussid-apocritan relationships is accurate, then we have to assume transition from phytophagy in the siricoid grade to the parasitoid lifestyle of the Apocrita. This transition must involve a woody habitat because at least siricoids and orussids, and possibly many of the putatively basal apocritans, feed in wood or attack hosts feeding in wood. This is not a novel concept. The ichneumonoid literature, for example, is full of references to basal lineages being parasitoids of xylophagous coleopteran larvae (Telenga, 1952; Tobias, 1967, van Achterberg, 1984), and these can be traced back at least to the early 1900s (Handlirsch, 1907). Similarly, over the last few decades, several authors (e. g. Gauld, Bolton, 1988; Eggleton, Belshaw, 1992, Whitfield, 1998) have noted that other putative basal groups such as stephanids, megalyrids, ibaliids, and aulacids attack hosts living in wood.

The above assumptions and observations lead to a series of questions about the evolution of specific biological and morphological traits within the Apocrita. Dowton and Austin (2001) have criticized prior assumptions about groundplan biologies of certain taxa within the Apocrita as “intuitive”, adding that parsimony should be allowed to arbitrate the groundplan biology. These authors make a valid point about the lack of explicit arguments supporting certain groundplan states, but all such proposals, including parsimony-based analyses, should be viewed as testable hypotheses. This is the approach taken here. Parsimony, in any case, has thus far been notably inconsistent in providing stable support for relationships among superfamilies at the base of Apocrita (e. g. Dowton, Austin, 1994, 2001; Dowton et al., 1997), which compromises its ability to arbitrate biological or other assumptions based on inferred relationships.

Three of the biological and morphological features that have been proposed in the context of groundplan states for either the Apocrita or Orussidae + Apocrita are reviewed here. The goal is to facilitate understanding of the transition from the siricoid grade to the Apocrita. This work is dedicated to Prof. V.I. Tobias, who, in addition to his extensive contributions to our understanding of the braconid fauna of Russia, has published several noteworthy papers on the evolution of character systems within Apocrita.

Why a closed gut?

One of the key features of the parasitoid lifestyle is the closure of the larval gut at the midgut/hindgut junction (or, more precisely, the failure of the proctodeal invagination to join the midgut). Gut closure usually persists until the onset of pupation, with the fecal pellet (meconium) that was stored in the closed midgut being released just before pupation or upon eclosion of the adult. Similarly, the conventional organs of excretion, the malpighian tubules, are poorly developed during larval stages of many parasitoids (Fisher, 1971). A “fouling the nest” argument has often been used to explain evolution of gut closure, as perhaps most eloquently stated by Gauld and Bolton (1988, p. 9): “By postponing defaecation until they have finished feeding, apocritan larvae avoid fouling their immediate environments and are thus able to live in very confined spaces, such as within a closed cell or in the body cavity of another insect”. As noted by Gauld and Bolton (1988), the feature pertains not just to parasitoids, but to all Apocrita, including Aculeata. Vilhelmsen (2003b) provides documentation for this condition in several apocritan superfamilies. A fouling the nest argument is perhaps most compelling for endoparasitoids, but if ectoparasitism is the groundplan for Apocrita, then the orussid-Apocritan transition is a good place to begin exploring hypotheses regarding the origin, evolution and function of a closed gut.

Symphytan larvae have a completely connected/open digestive tract with a functional hind gut and anus. In the case of “wood wasps” in the families Siricidae and Xiphydriidae, the food consists of bulky, fungal-laced woody substrate from which nutrients are extracted. Several authors have noted that mycophagy may have facilitated the transition from phytophagy to parasitism, with this association perhaps most elaborately explored by Eggleton and Belshaw (1992). Alternatively, Cooper's (1953) observations on *Orussus* could suggest that a scavenger mode of life may have been important in the transition between phytophagy/mycophagy in siricoids and ectoparasitism in stephanids. The actual biology of orussids has been the subject of some controversy (see partial review in: Vilhelmsen et al., 2001). Work in New Zealand on *Guiglia* (Rawlings, 1957) clearly indicates that the species examined is an ectoparasitoid in its early stages, with females piercing the host with her ovipositor after the ovipositor penetrates the wood. For *Orussus*, there have been suggestions that the egg may be laid some distance from the host, and that early instars may feed on microbes or fungus in frass with later instars possibly being ectoparasitoids or scavengers (Cooper, 1953). There is some disagreement in this regard, because at least some authors argue that members of this genus are exclusively parasitic (Burke, 1917). Vilhelmsen (2003b) recently examined the condition of the gut in Orussidae and found an open gut for *Orussus abietinus* (Scopoli). Key questions that remain to be answered for orussid biology are whether the food ingested by the earlier instars of *Orussus* (as suggested by the work of Cooper, 1953) is simply too bulky for a closed gut system, whether the cuticular folds in the hind gut noted by Vilhelmsen (2003b) enable larval *Orussus* to have a functionally closed gut when processing food, and whether the gut is open in all orussids, including *Guiglia* with its clearly described ectoparasitic biology. It also remains to be shown whether gut closure occurs in putatively basal apocritan taxa such as Stephanidae and Megalyridae. However, present evidence indicates the absence of a midgut/hindgut pass-through connection during larval development is not a synapomorphy of Orussidae + Apocrita, but rather is another defining trait of Apocrita. The closed gut appears to have evolved after the development of a parasitoid lifestyle in Hymenoptera, suggesting that the change from a somewhat fibrous diet to a more liquid diet was a prerequisite for gut closure. Consequently, the function of gut closure in Hymenoptera may be more closely associated with ingestion of a liquid diet than the habitat in which consumption takes place. Slansky (1986), though emphasizing the lack of data largely associated with the technical difficulties of such studies, provided useful information in this regard. Gut closure facilitates a high percent assimilation of nutrients and the rapid growth that characterizes many parasitoids. Some modification of the gut, such as gut closure during the feeding stages, is essential for high assimilation efficiencies. An “increased assimilation efficiency” hypothesis is thus offered as an alternative to the “fouling the nest” hypothesis for explaining the evolution of gut closure in Hymenoptera.

This alternative hypothesis provides a better explanation for why a closed gut is also found in larval Planipennia (Neuroptera) (Withycombe, 1925; Tauber, 1991), most of which are highly mobile predators that consequently do not have a “fouling the nest” concern. Planipennia larvae feed only on body fluids of their prey, having mouthparts specifically modified for this purpose. Further, defecation in a

confined space is a common phenomenon among subcortical insects, and this alone seems a relatively weak argument for evolution of a closed gut among ectoparasitoids. Yet ectoparasitism has long been hypothesized as the basal mode within the Apocrita. A fouling the nest argument, as noted above, is perhaps more appropriate for an endoparasitoid. The evolution of a blind midgut in ectoparasitoids, initially to enhance nutrient assimilation, may represent a “preadaptive” feature that, once evolved, facilitated transition from ectoparasitism to endoparasitism, a transition that occurs repeatedly among Apocrita.

Host exploitation by putatively basal members of the Apocrita

If orussids are truly the sister group to the Apocrita, the groundplan biology of the Apocrita is most likely ectoparasitism of wood-boring larvae. This assumes a biology for the Orussidae that fits the description provided by Rawlings (1957). Coleopteran larvae are frequently mentioned as the most likely hosts [initially as proposed by Handlirsch (1907) and most recently reiterated by Dowton and Austin (2001)], but it is sometimes overlooked that siricoid hosts are also probable for Orussidae. Eggleton and Belshaw (1992), in fact, hypothesized that evolution of parasitism in the Hymenoptera occurred through competition among siricoid larvae, and Kasparyan (1996) emphasized the role of Hymenoptera as hosts in the evolution of parasitism in this insect order. Given the known host range for stephanids and megalyrids, which are putative basal lineages, a generalist ectoparasitoid of xylophagous and/or mycophagous hosts is very possibly the groundplan biology for the Apocrita (rather than specialization on a single host group such as Coleoptera or Hymenoptera). Though recognized for some time, the overemphasis of xylophagous Coleoptera as hosts in some general reviews has until recently (Vilhelmsen et al., 2001) clouded a clear articulation of this point.

Stephanids and megalyrids are undoubtedly idiobiont ectoparasitoids of holometabolous larvae [see Gauld (1995) and S. Shaw (1990) respectively for reviews of these two groups]. Other putatively basal apocritan parasitoids of wood-boring hosts, such as aulacids and ibaliids (Dowton, Austin, 1997), oviposit in host eggs or early instars of siricoids and are koinobiont endoparasitoids at least in their early development (Chrystal, 1930; Skinner, Thompson, 1960). Female aulacids and ibaliids search for oviposition holes rather than for host larvae, which requires a different search strategy (e. g. Spradbery, 1974) than that employed by female stephanids, who drill through wood to paralyze and then oviposit onto larval hosts (Taylor, 1967). Once an oviposition hole is located, female aulacids and ibaliids oviposit through the wood into the embryos or newly hatched larvae of their hosts by sending the ovipositor down the previously drilled bore hole of the host.

Once a search strategy for location of host eggs in a concealed habitat, such as wood, and mechanisms for dealing with the host immune system are developed, then oviposition into eggs, an alternative closed environment, opens up a wealth of opportunities to leave the wood environment and diversify accordingly. An important question is whether egg parasitism represents a groundplan state leading to koinobiont larval parasitism, thus providing an alternative pathway relative to the hypotheses put forth by M. Shaw (1983) for the evolution of endoparasitism through gradual internalization of the placement of the egg on larval hosts in Rogadinae s. l. These considerations are relevant to hypotheses that have been put forth (mostly in literature dealing with physiological interactions between hosts and parasitoids) concerning selection for attacking early host instars. Obviously, there is no selection for attacking early host instars if this is a primitive condition in the lineage of interest.

Discussions of the transitions from ectoparasitism to endoparasitism and the potential for reversals have figured prominently in recent papers on the evolution of various apocritan groups (Whitfield, 1998). Dowton and Austin (2001), for example, suggest that instances of ectoparasitism in Proctotrupomorpha represent reversals from a groundplan biology of endoparasitism for the group. Examination of the biology of the putatively basal, extant apocritans noted above leads to the suggestion that the success of the Proctotrupomorpha, and its seemingly explosive radiation, may be linked to the multiplicity of approaches adopted within the group for attacking concealed hosts. This hypothesis incorporates not only behavioral traits but the variety of equipment utilized for host location. Thus, while a single origin of parasitism is usually invoked for the Apocrita, an almost immediate, rapid diversification after origin of parasitism may provide the best explanation for our difficulty in resolving relationships among basal taxa,

as noted most recently by Quicke (1997) and discussed by a number of earlier workers (e. g. Telenga, 1952). Immediate diversification also helps to explain why all basal lineages are not larval ectoparasitoids.

Apocritan cocoons

Within Symphyta, cocoon formation via silk produced from labial glands is found in Xyelidae (Blank, 2002), most Tenthredinoidea (but not Blasticotomidae: Schedl, 1991) and Cephidae (Gauld, Bolton, 1988). Perhaps as a result, cocoon formation by labial silk glands is frequently treated as a plesiomorphic trait in apocritan groups such as the Ichneumonoidea. This is difficult to justify, however, because in Symphyta cocoon formation is absent in Pamphiliidae (Schedl, 1991), Siricidae (Schedl, 1991), Xiphydriidae (Schedl, 1991), and Orussidae (Vilhelmsen, 2003b). Further, among the Apocrita it is absent from Stephanidae (Taylor, 1967) and from several other groups, or, when present (such as in Aulacidae), the silk originates from a different source (Skinner, Thompson, 1960). Because cocoon formation represents a large investment of resources it is probably easily lost. In any event, the state in the common ancestor of Apocrita, or even of Hymenoptera, cannot be decided with certainty based on present knowledge. It is possible that the common occurrence of silk production from labial glands in Ichneumonoidea and Aculeata is not symplesiomorphic but rather is synapomorphic for the two taxa.

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