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Biology and immature stages of *Panteles schnetzeanus* (Hymenoptera: Ichneumonidae), a parasitoid of *Lampronia fuscata* (Lepidoptera: Incurvariidae)

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Abstract

Panteles schnetzeanus (Roman), a parasitoid of the gall-forming incurvariid moth *Lampronia fuscata* (Tengström) and currently placed in the Stilbopinae, is shown to be a solitary koinobiont larval endoparasitoid. The large dark-pigmented eggs possess a hook-like tail which is embedded in host tissue, typically at the posterior or anterior end of the host. In cases of superparasitism, which represented 70% of cases, only a single egg hatches. The first instar, prepupa and final larval instar head capsules are described and illustrated. Many differences between the biology of *Panteles* and of *Stilbops* are discussed. Circumstantial evidence that suggests that *Panteles* may have an alternative host is also presented based on the emergence dates for it and the *Lampronia* together with the size, number and placement of the *Panteles* eggs. DNA sequence data additionally provide the first record of a eupelmid as attacking a gall-forming incurvariid/parasitoid system, though it is not clear whether this was an hyperparasitoid on the *Panteles* or a primary on the incurvariid.

Keywords: Hymenoptera, larval head capsule, *Panteles schnetzeanus*, superparasitism, *Stilbops*, Stilbopinae, galls

Introduction

Short (1978) elevated the banchine tribe Stilbopini to subfamilial rank to include the Holarctic and Neotropical genus *Stilbops* and the Chilean genus *Notostilbops*, though another genus now placed in the Stilbopini, *Panteles* Förster, was left at that time within the Banchinae (see Townes and Townes 1978). Wahl (1988) reassessed the relationships of the genera of Banchini, concluded that *Panteles* did not belong there, and transferred it to the Stilbopinae, though noting that the characters uniting it with *Stilbops* and *Notostilbops* were not very strong. Although *Notostilbops* is rare and nothing is known of its biology, *Stilbops* species are sometimes very common and their biology is interesting because they are one of the few ichneumonid genera that are egg-larval parasitoids, attacking various species of Incurvariidae. The monotypic genus *Panteles*, known only from the West

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Palaeartic, has been recorded as a parasitoid of the univoltine incurvariid moth, *Lampronia fuscata* (Tengström), which is unusual for its family in that its larva forms galls on twigs of *Betula* trees (Roman 1925). However, the biology of *Panteles* is not known in detail, and in particular, it was not even known whether it is an ecto- or endoparasitoid. Through his association of it with the Stilbopinae, Wahl (1993) boldly stated that “Species of *Panteles* and *Stilbops* are endoparasitoids of Incurvariidae (Lepidoptera); oviposition is into the host egg...”, thus creating the impression that there was biological evidence for both genera when there was not.

Although the Stilbopinae are part of the large, almost entirely koinobiont endoparasitoid “Ophioniformes” group of subfamilies (Wahl 1991; Belshaw et al. 1998; Quicke et al. 2000a), the ovipositor apex of *Panteles* is very different from that of other members of this predominantly endoparasitoid assemblage in that it lacks a pre-apical dorsal notch, and instead has a pair of dorsal teeth. Superficially at least, it therefore more closely resembles those of many of the ectoparasitoid taxa (Belshaw et al. 2003). Further, the final instar larvae of *Stilbops* have several features, such as papilliform antennae, that are typically associated with ectoparasitoid taxa, and molecular and combined molecular and morphological phylogenetic studies place *Stilbops* near *Panteles* close to the base of the Ophioniformes (Belshaw et al. 1998; Quicke et al. 2000a), and therefore near the transition between ecto- and endoparasitic groups. Thus, knowledge of the biology and the larval instars of *Panteles* would be especially interesting.

The biology of *Lampronia fuscata* was briefly described by Fassnidge (1939). The moth is univoltine and emerges as an adult in May and June (Heath 1983). Its larva completes development before the end of the year, and then chews an exit hole out of the twig gall, which it seals (caps) with silk camouflaged externally by reddish brown frass. In the UK pupation occurs in April. The moth supposedly prefers small birch trees though this could reflect sampling bias. Parasitized larvae were reported by Fassnidge (1939) to fail to complete and cap the exit hole presumably because the adult parasitoid can chew its own way out, though it is worth noting that the mandibles of adult *Panteles* are not especially robust unlike those of many other ichneumonoids that have to egress from within wood. More recent observations, however, show that capped galls are also quite often parasitized (below and K. P. Bland, personal communication).

Materials and methods

Putative twig galls were collected from small birch trees (*Betula* spp.) in the vicinities of Sunningdale and Virginia Water, Berkshire, UK, from the second week of February to late March 2003. They were carefully dissected in a laboratory within 3 days of collection and *Lampronia* larvae were removed for photography and dissection. Dissections were carried out in ca 20% ethanol to render host tissues slightly opaque. Photographs were made using Automontage®. Molecular procedures were as described by Belshaw and Quicke (2002).

Microscope slides of larval head capsules were prepared by dissolving soft tissues in ca 5% potassium hydroxide solution at 50°C, followed by thorough washing in distilled water, dehydration through to dry ethanol (dried over anhydrous cupric sulphate), transfer to Histoclear® (National Diagnostics), and mounting in Histomount® (National Diagnostics). In addition to the final instar larval skin prepared here, a second specimen was prepared from a gall from which an adult *Panteles* had emerged, in the collection of the National Museums of Scotland, Edinburgh.

Microscope slide preparations are deposited in the collection of the National Museums of Scotland, Edinburgh.

Molecular identifications of parasitoid larvae

In order to determine whether the parasitoid larvae found were indeed *Panteles schnetzeanus*, individuals recovered from within a host *Lampronia* larva, and ones found externally with *Lampronia* remains in a gall, were sequenced for the 28S D2-D3 rDNA gene fragment. The sequences obtained were compared with one obtained from an adult *P. schnetzeanus* reared the previous year from *Betula* galls from the same location (EMBL/Genbank accession no. AJ302877; Belshaw and Quicke 2002), and when no match was found, the sequence was BLAST searched against the EMBL/Genbank databases.

Biological observations

A total of 15 *Lampronia fuscatella* galls from the current year were obtained (out of more than 1000 gall-like swellings dissected). Eleven of these were occupied by a single living *Lampronia* larva (Figure 1), and three by single small, hairy parasitic wasp larvae that were lying close to the caterpillar head capsules (Figure 5A, B), and one, collected on 29 March, by a larger prepupal parasitoid (Figure 4A). All but two of the host larvae obtained were or had been parasitized (Figures 2, 3).

DNA sequence data showed that the endoparasitic larvae (Figure 3A, B) recovered were *Panteles schnetzeanus*, the sequence being identical with that obtained previously from an adult parasitoid. However, the sequence obtained from one of the small, setose larvae (Figure 5A, B) found external to the remains of a *Lampronia* caterpillar was very different, and the BLAST search showed it to have a high match to those deposited in EMBL/

Figure 1. Diagrammatic representation of distributions of *Panteles* eggs within the dissected *Lampronia* hosts.

Figure 2. Host, *Lampronia fuscata*, and parasitoid, *Panteles schmetzianus*. (A–C) Mature, singly parasitized host larvae, the parasitoid egg case is visible as a dark mark at the posterior of the body (A, and detail B) and between the first and second abdominal segments (C); (D, F) hatched *Panteles* egg cases showing apparent white modification to tail associated with tissue embedding (D) and typical larval emergence cap (F); (E) head capsule of caste skin of first instar *Panteles* larva with arrow indicating level of mouthparts with small mandibles.

Genbank for various *Eupelmus* species. Given that only five genera of Eupelmidae are recorded from Britain (Gokhman and Quicke 1995; J. Noyes, personal communication), and of the three Eupelminae only the genus *Eupelmus* has been recorded more than twice, it seems highly likely that these were indeed larvae of a *Eupelmus* species.

Figure 3. (A) Dissected superparasitized *Lampronia* larva showing group of eggs (three out of five visible) with “tails” embedded in host tissue near the rectum, and with a mid-instar *Panteles* larva to left of host gut in mid-region (arrow); (B) detail of the mid-instar *Panteles* larva from this caterpillar.

Biology of *Panteles*

Parasitoid eggs were 0.45 mm long (maximum linear dimension), dark red-brown to black and had a strongly recurved tail (Figure 2D, F); both hatched and intact eggs were clearly visible through the cuticle of the living hosts (Figure 2A–C). In all cases, at least the recurved tail was embedded in host tissue including in some cases the rectum and Malpighian tubules, and in one case, in which the egg was located laterally between first and second abdominal segments, it was completely embedded in host tissue tentatively identified as fat body. Hatched *Panteles* eggs had a neatly cut, but still attached, cap at the broad end of the egg (Figure 2F). The end of the curved tail was distinctly narrowed at least in some cases and appeared to have a translucent whitish apex (Figure 2D; possibly modified chorion). Unhatched eggs were often (ca 50% of cases) deflated. There was never any indication of an immune response against hatched or unhatched eggs or larvae, and I was unable to see any sign of an oviposition mark on the host cuticle.

Figure 4. (A) Female *Panteles* prepupa showing very well-developed pupa with pigmented eyes still inside final larval instar skin; (B) final larval instar head capsule (unstained); (C) eggs of *Panteles* incorporated in *Panteles* silk cocoon.

Figure 5. Eupelmid parasitoid of *Lampronia*. (A, B) Larva *in situ* in *Lampronia* gall showing long setae (A) and brown gut contents (B); (C) whole head capsule with strong sclerotized mandibles but with little other sclerotized skeleton; (D–F) details shown at three different focal planes: (D) showing toothless mandibles, (E) showing opening of salivary glands with single circular orifice (arrowed), and (F) showing serrate ridge (edge of clypeus) over mandibles (at level of midlength of right mandible blade).

Superparasitism by *Panteles* was observed in 55% of cases in which it could be determined (including in the case of the pre-pupal specimen), with a maximum of seven parasitoid eggs in a single host; the distributions of eggs in hosts is shown diagrammatically in Figure 1. Parasitoid eggs were usually clumped at either the posterior or anterior end of the host (in one case the second cluster of eggs was largely within the host's head capsule). Only in one case was a *Panteles* egg found at the anterior of the abdomen (Figures 1, 2C).

In all cases of superparasitism, only one of the parasitoid eggs had hatched (as indicated by the partially separated anterior cap). In four cases it was possible to find the shed skin of the first instar parasitoid larva and this was always very close to the cluster of parasitoid eggs at the rear of the host. At the times of dissection the single *Panteles* larva (tentatively a second instar based on size and failure to find other shed skins) was always located parallel to the host gut at the mid-length of the host larva (Figure 3A).

Description of first instar Panteles larva. This description is based on a cast skin recovered from one superparasitized host (Figure 2E).

Caudate; head capsule moderately large, approximately as long as basally wide and well sclerotized, occupying approximately 0.25 of total larval length. Mandibles very small, not protruding, located sub-apically, 0.25 length of head capsule from apex. Segments with a transverse row of small spines dorsally.

Panteles prepupa. The prepupa of a female *Panteles*, collected on 29 March, is shown in Figure 4A. The pupal wasp cuticle has formed and is separated from the intact final instar larval cuticle and the compound eyes of the pupal wasp are already coloured reddish brown. Division of the body into head, thorax and metasoma, and the ovipositor can be seen clearly.

Description of final instar Panteles larval head capsule. Description based on that shown in Figure 4A, B and a preparation made from remains recovered from an emerged Scottish gall.

Antennae large, flat, disc-shaped oval; without papilla or obvious seta or sensilla; margins well sclerotized. Epistoma represented only by part ventral to anterior tentorial pit. Pleurostoma narrow and weakly sclerotized with no obvious anterior processes; posterior process distinct and well sclerotized. Mandibles long, overlapping for approximately 0.4 length, well sclerotized, each with a single row of small teeth. Hypostoma well sclerotized. Hypostomal spur long and thin, approximately 12 times longer than basally wide, nearly straight, arising approximately at mid-length of hypostoma, crossing stipital sclerite near its middle. Cardo weakly sclerotized but distinct. Stipital sclerite approximately as long as hypostoma, slightly shorter than mandible, less sclerotized laterally. Labial sclerite strongly sclerotized. Salivary orifice U-shaped. Prelabial sclerite present, ventrally forming a broad plate without medial projection, the dorsal arms weakly diverging and very strongly sclerotized. Prelabium with three pairs of setae. Maxillary palp with three sensilla; labial palp with three sensilla. Spiracle with closing mechanism large and separated from atrium by approximately its own length of trachea. Cuticle with very fine rows of weakly toothed ridges.

Cocoon. The *Panteles* prepupa was in a thin (apparently composed of a single layer), whitish silk cocoon within a capped *Lampronia* gall. The cocoon had a few pieces of host frass included in it and also the remains of two *Panteles* eggs (Figure 4C), one hatched, the other not. Although it was probably just fortuitous, it serves to illustrate the durable nature of these eggs.

Biology of eupelmids

Three galls collected in early to mid-March contained the eaten remains of a *Lampronia* larva and a moderately large (ca 2 mm long) eupelmid larva (as identified by DNA; see above). The parasitoid larva's midgut could be seen to be filled with a red-brown slurry

(Figure 5B), unlike the yellowish green contents of the *Panteles* larvae that were dissected from within the host caterpillar. The appearance of these gut contents was, superficially at least, very similar to those found in the gut of the *Lampronia* host. Microscopic examination showed the slurry to be largely composed of cocciform bacteria. One of these parasitoid larvae was transferred to a Petri dish and maintained in a shaded outdoor shed; after 2 weeks it was still alive but had not moulted.

Description of eupelmid larva. Moderately densely long setose (Figure 5A, B). Head capsule weakly sclerotized with only the mandibles obviously so (Figure 5C). Mandibles short with curved, toothless blade (Figure 5D). Salivary ducts uniting before single, circular salivary orifice (Figure 5E, arrow). With an irregularly toothed, transverse ridge (exact anatomical identity uncertain) covering most of mandibles like an upper lip (Figure 5F; at level of upper edge of mandible blade). This appears to be the same as the serrate anterior clypeal edge described by Askew (1961) for *Eupelmus urozonus* Dalman.

Discussion

Natural history of Panteles

The observations made clearly show that *Panteles* is a koinobiont endoparasitoid of the larva of its host. However, contrary to published inferences based on the biology of the putatively related genus *Stilbops*, the large size of its eggs (0.45 mm long), the presence of up to seven eggs in a single host (see Figures 1, 2A), and the apparently precise placement of these eggs both in clumps at posterior and/or anterior (extreme posterior of body cavity or head/cervical region) end of the host with their recurved tails embedded in particular host tissues, collectively indicate that it must be a larval and not an egg-larval parasitoid. Further, the eggs of *Panteles* are so large that it seems unlikely that they could be comfortably accommodated even within a freshly hatched *L. fuscicollis* larva whose body diameter is not likely to be much greater than the length of the parasitoid's egg (sadly the egg and early instars of *L. fuscicollis* do not appear to have been described in the literature). All this leads to a conundrum, because both the host moth and the parasitoid are known to be on the wing at the same time of year [rearing records based on Scottish material in the National Museums of Scotland have emergence dates from early April to mid-May, and the two field-collected adults in that collection were taken in May and June; cf. May/June flight period for adult *L. fuscicollis* in England (Heath 1983)]. Given the unlikely use of first instar *L. fuscicollis* as hosts, the possibility has to be entertained that *Panteles* actually has an alternative host that is more mature at that time of year. This proposition is also supported by consideration of the morphology of the ovipositor in *Panteles*. The presence of protuberances (nodi) at the apex of the upper ovipositor valve is strongly correlated with penetrating hard substrates against which these nodi engage, thus allowing the lower valves to be forced further in (Vincent and King 1995; Quicke et al. 2000b). Such features are unknown in the ovipositors of known ichneumonoid egg-larval parasitoids and might also reasonably be expected to cause unnecessary injury to the host if it is a delicate early instar. The presence of ovipositor nodi in *Panteles* is thus suggestive that the ovipositor has to be used to penetrate a tough substrate such as an already-developed *Betula* gall, and that would not be necessary if it were attacking either *L. fuscicollis* eggs or early instars which had only just started chewing their way into the plant tissue.

The well-developed eye pigment of the *Panteles* prepupa suggests that metamorphosis through the pupal stage may be rapid. In many ichneumonoids, the prepupa before

moulting to the pupa proper often has a trace of eye pigment, often forming a crescentic mark, however, the condition in *Panteles* is very advanced. Similarly advanced development has been noted in the ichneumonid *Acaenitus* and in the cynipid *Diplolepis triforma* (Shaw and Wahl 1989; Shorthouse and Leggo 2002), both of which have to be active early in the year, so it is likely that in these cases the developmental stages of the pupa are advanced to maximize the chance that the wasp will be able to emerge as an adult sufficiently early.

Superparasitism

The present observations show that both single and superparasitism occurs in *Panteles*, though it is not known whether the instances of superparasitism represent self-superparasitism, non-self-superparasitism or a mixture of the two. Nevertheless, superparasitism is clearly a regular occurrence having been observed in 55% of parasitized hosts. In most cases where it is known, first instar larvae of solitary parasitic wasps eliminate supernumeraries resulting from superparasitism by combat, and in these cases the first instar larvae are usually equipped with especially large mandibles (=mandibulate type: Salt 1961; Hagen 1964; Godfray 1993; Quicke 1997; Pexton and Mayhew 2002). However, in the case of *Panteles*, the first instar larva has only tiny mandibles (Figure 2F) which seem unsuited to larval-larval combat. Further, the observation that when hosts had been superparasitized only one of the eggs hatches suggests that the first parasitoid larva can kill or curtail development of the other eggs.

No evidence was found of any physical damage to the unemerged eggs (i.e. there were no obvious holes, lesions or areas of host immune response such as encapsulation). Together with the small mandibles of the first instar larva, this suggests that physiological suppression through the release of toxins that specifically inhibit the development and/or hatching of potential rival eggs may be involved, as has been shown in a few cases including in some other ophioid ichneumonids (Salt 1961; Fisher 1971).

Investigation of cases in which females of solitary species routinely self-superparasitize hosts has shown that this strategy may be adaptive and perhaps involved in circumventing host immune responses. This has been shown in several systems, especially involving hemipteran hosts (Streams 1971; Blumberg and Luck 1990; Sagarra et al. 2000), though such actions do not appear to have been reported for any Ichneumonidae. Other adaptive features may also be involved. For example, in the solitary aphid parasitoid *Monoctonus*, Mackauer and Chau (2001) have shown that although siblicide occurs, the survivor may benefit because such hosts contain larger numbers of teratocytes because both parasitoid embryos have produced them, and also perhaps because superparasitized hosts are induced to feed more. Another possibility is that the supernumary eggs could have had a nurse egg role through releasing compounds useful to the survival of the first to hatch.

That in some superparasitized hosts, the parasitoid eggs were located in two clusters, one at the posterior end and the other in or near the head, could indicate that these were instances of non-self-superparasitism, with the second female selecting an oviposition site remote from that of the first, perhaps in an attempt to escape any physiological suppression. Study of the relatedness of the *Panteles* eggs in these cases would help provide a clue.

Systematic considerations

Apart from the fact that *Panteles* is a larval rather than an egg-larval parasitoid, its final instar larva also differs from that of *Stilbops* in that the latter has papilliform antennae, a

sclerotized pleurostoma, has the hypostoma longer and the hypostomal spur originating more medially (Short 1957, 1978). For all these head capsule features *Stilbops* probably displays the plesiomorphic state, and there are no apparent larval synapomorphies uniting it with *Panteles*. Given that molecular analyses also fail to recover *Stilbops* and *Panteles* as a monophyletic group (Belshaw and Quicke 2002), and that the putative adult morphological synapomorphies mentioned by Wahl (1988) are all homoplastic within the Ophioniformes, it seems likely that although closely related, these taxa should not be included in the same subfamily. Detailed genus-level, combined molecular and morphological analyses in preparation will hopefully help resolve the relationships of these genera with greater certainty (G. R. Broad et al., in preparation).

Eupelmidae attacking Lampronia

No previous published records of any eupelmid attacking either *Lampronia* or any other gall-forming Incurvariidae are known (Noyes 1998, 2001). Although it is not possible to be certain about the identity of the species, it is quite possibly one of two highly polyphagous and common British species that have both previously been reared from galls, *Eupelmus vesicularis* (Retzius) or *E. urozonus* (J. S. Noyes, personal communication). Apart from *Panteles*, and the eupelmid reported here, *L. fuscatella* galls are also known to be attacked by a *Bracon* Fabricius species (Braconidae: Braconinae) (M. R. Shaw, personal communication) which are presumably idiobiont ectoparasitoids. Larvae of *Bracon* differ considerably from those of the eupelmid and so should be easily recognizable: *Bracon* larvae have extensive head capsule sclerites including epistome and hypostome, and are not setose.

Parasitization rate

The very high level of parasitism observed (82%) may go some way towards explaining why, at least in the UK, *Lampronia fuscatella* is reputedly a rare moth (Heath 1983), though this is probably partly due to the relatively inconspicuous nature of the moth and its galls (sometimes these may even be on birch trunks rather than on twigs; K. P. Bland, personal communication). It is also worth noting that the level of parasitism observed here is apparently rather typical and K. P. Bland has encountered 100% parasitism in Scotland ($n=7$) (personal communication). Even though parasitism rates are really only truly assessable in situations where hosts are located in special sites such as leaf mines and galls that can in principle be accurately surveyed, the possibility of sampling bias cannot be ignored. In the present study, galls were discovered visually and no doubt sampling may have been biased to the more apparent ones. If apparency to the human were to correlate with apparency to the parasitoid, then the measured parasitization rates might be exaggerated.

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