Труды Русского энтомологического общества. С.-Петербург, 2014. Т. 85(1): 122–132.
Proceedings of the Russian Entomological Society. St Petersburg, 2014. Vol. 85(1): 122–132.

Illustrated notes on the biology of two European species of *Euceros* Gravenhorst (Hymenoptera: Ichneumonidae: Eucerotinae)

M.R. Shaw

Иллюстрированные заметки по биологии двух европейский видов *Euceros* Gravenhorst (Hymenoptera: Ichneumonidae: Eucerotinae)

М.Р. Шоу

National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, United Kingdom. E-mail: markshaw@xenarcha.com

Abstract. Observational notes and photographs taken in the course of rearing *Euceros albitarsus* Curtis and *E. pruinosus* (Gravenhorst) in captivity from the egg stage are given. The bizarre biology of these obligate hyperparasitoids involves a planidial larval stage that attaches to caterpillars or sawfly larvae, followed by a short phase of internal parasitism of a primary parasitoid if already or subsequently present, followed in turn by the principle growth period of external parasitism on the primary parasitoid, as shown by Tripp (1961). Observations on aspects of this that were not illustrated by Tripp are given and, although these transitions are not fully elucidated here, it is speculated that the number of larval instars had hitherto been overestimated. Investigations on the behaviour and fate of the planidial phase suggest that it is best able to transfer to primary parasitoids that are associated with the prepupal state of the lepidopteran host. Planidia on caterpillars that are not themselves parasitised end up in the host pupa, usually occupying the subalar cavity of the exuvial space (that is, just below the pupal cuticle at the wing cases), but do not develop further in the absence of a primary parasitoid. A summary of some aspects of the biology of *Euceros* that are not yet understood is given: the main uncertainties are the number and feeding positions of larval instars, the timing and nature of the planidium's transfer to the primary parasitoid, and the function of the unusual male antenna.

Key words. Planidium, hyperparasitoid, host relations, life history, *Euceros albitarsus*, *Euceros pruinosus*.

Резюме. Приведены заметки и иллюстрации, сделанные в процессе выведения собранных в природе ихневмонид *Euceros albitarsus* Curtis и *E. pruinosus* (Gravenhorst). Необычная биология этих облигатных гиперпаразитоидов связана с особенностями их первой планидиальной личиночной стадии, развивающейся на первичном паразитоиде бабочки. В статье обсуждаются в первую очередь те особенности биологии этих наездников, которые не были изучены Триппом (Tripp, 1961).

Ключевые слова. Планидия, гиперпаразитоид, связи с хозяевами, жизненный цикл, *Euceros albitarsus*, *Euceros pruinosus*.

Introduction

The ichneumonid subfamily Eucerotinae has a practically worldwide distribution (apparently absent from south east Asia and the neotropics) but contains relatively few species, all – apart from the monotypic Chilean genus *Barronia* Gauld et Wahl – classified as *Euceros* Gravenhorst (Yu *et al.*, 2012).

The known biology of *Euceros* is extraordinary for an ichneumonid, as eggs are laid on vegetation and the resulting first instar larvae are highly specialized; they attach to passing caterpillars or sawfly larvae, but can only complete their development as obligatory secondary parasitoids. Finlayson (1960), following up a pers. comm. from G.S. Walley, was the first to report this, confirmed also by Varley (briefly in 1960, more completely in 1965), but by far the fullest and most detailed account is given by Tripp (1961). He studied and illustrated a Nearctic species, *E. frigidus* Cresson, developing on the primary parasitoids of the diprionid sawfly *Neodiprion swainei* Middleton on *Pinus*, and gave a particularly detailed morphological account of the heavily sclerotised first instar larva, termed a planidium (cf. Clausen, 1940), as well as assessing the further developmental progress of the parasitoid by dissecting sawfly cocoons from which *Euceros* had emerged. Apart from host data given by Barron (1976, 1978) in his taxonomic revision of world *Euceros*, no further biological details appear to have been published. Kasparyan (1996), however, discusses the biology of *Euceros* in an evolutionary light in a far-reaching essay that, among other things, emphasises the importance as well as the difficulties of the use of sawfly hosts in the early evolution and progression of parasitism by Hymenoptera.

In 1990 and 1995 I had the opportunity to make limited biological observations on two European species, *E. albitarsus* Curtis and *E. pruinosus* (Gravenhorst) respectively, both parasitising the primary parasitoids of Lepidoptera. At the time my aim was rather trivial: just to see if I could successfully rear these species from egg to adult under entirely captive circumstances, and unfortunately I was unable to give the project sufficient undivided attention to attempt to solve the riddles that remained (in particular the precise number of larval instars and the manner of their development). Nevertheless, some of the incidental observations made extended or slightly disagreed with those given by Tripp (1961), and the photographs I was able to take sometimes covered different aspects of the life history and, although mostly of regrettably low quality, they do illustrate it clearly enough to be worth presenting. This paper simply recounts those experiences, drawing attention to departures from (or extensions to) Tripp's (1961) observations.

Material and methods

Two adult females of *Euceros albitarsus* emerged on 22 and 23.IV.1990 from cocoons of *Ophion minutus* Kriechbaumer (Ichneumonidae: Ophioninae) resulting from larvae of *Agriopis aurantiaria* (Hübner) collected at Fontainebleau (France: Seine-et-Marne) on 15.V.1989 by T.H. Ford, that had been given to me as *O. minutus* cocoons. A single adult female of *E. pruinosus* was swept at Chippenham Fen NNR (England: Cambridgeshire) on 9.V.1995 by M.G. Fitton, and the eggs laid by her, on 12–14.V.1995, were sent through the post and received by me on 22.V.1995. These females and their progeny were the source of all observations recorded here.

The females were confined individually in 7.5×2.5 corked glass tubes, onto the inside of which small spots of dilute honey were touched and replenished daily. At intervals estimations of the eggs laid were made, and a fresh tube was supplied. After the planidial larvae had hatched, Lepidoptera larvae were passed briefly into the tube and examined for adhering planidia. In all the cases from which adult *Euceros* were later reared, these caterpillars were cultured from the egg stage in captivity and had previously been parasitised by captive reared females of a regular parasitoid: in the case of *E. albitarsus*, the geometrid *Theria primaria* (Haworth) parasitised by the campoplegine ichneumonid *Dusona erythrogaster* (Foerster); for *E. pruinosus*, the geometrid *Operophtera brumata* (Linnaeus) parasitised by the tryphonine ichneumonid *Netelia* (*Bessobates*) *latungula* (Thomson). In both cases supposedly parasitised caterpillars resulted from observed single apparent ovipositions by the primary parasitoid, but only in the case of the ectoparasitoid *Netelia* Gray was it possible to be certain that oviposition had actually occurred, or indeed that a primary parasitoid larva successfully established itself. A range of other potential caterpillar hosts (collected wild in England at Gait Barrows, North Lancashire on 13.V.1990, and Chippenham Fen, Cambridgeshire on 9.V.1995) were also introduced and received planidia of *E. albitarsus* and *E. pruinosus*, respectively, but were either unparasitised or produced only the primary parasitoid they already contained; however, they are the source of some of the observations and photographs recorded, and the rearing results in the case of those exposed to *E. albitarsus* will be briefly enumerated.

Caterpillars were fed on suitable foliage, and all livestock was maintained in a shaded and airy detached shed and carefully monitored under nearly outdoor conditions (cf. Shaw, 1997).

Results

1. *Euceros albitarsus* Curtis, 1837

The females started to oviposit two to three days after emergence, then for about the next ten days they increasingly copiously laid white eggs about 0.22 mm long attached to a fine white pedicel about 0.35 mm long or a little longer at one, presumably the caudal, end (Figs 1, 2). Although difficult to measure, pedicel length seemed rather uniform; however, the angle of the egg with respect to the pedicel varied (possibly changing over time) from distinctly tilted upwards (Fig. 1) to horizontal (Fig. 2). It appeared that at least 200 and perhaps more than 300 eggs were laid in most 24 hour periods within this time, but accurate daily checks were not made. Subsequently very few eggs were laid over the next week, despite the females feeding well on dilute honey, after which one female died but the other lived on and resumed ovipositing (about 150 eggs on the 20th day after emergence; a few on others days, sporadically) but died on the 32nd day after emergence following 12 days of at most very low egg production. The total number of eggs laid was probably not more than 3000 by either female, but it is not clear if this corresponds to a real maximum.

Figures 1–6. *Euceros albitarsus*. 1 – eggs on pedicels, tilted upwards; 2 – egg on pedicel, horizontal; 3, 4 – development of planidium inside egg; 5, 6 – planidium on pedestal.

The egg was depressed dorsally, and after a few days the planidium could be seen developing within, the head evidently at the other end from the pedicel (Figs 3, 4). This orientation would be expected from Hallez's (1886) Law, which predicts that the caudal end of the egg would issue first from the female, and it is clear from Tripp's (1961) figures that the end attached to what becomes the pedicel issues first. About six days after oviposition, the planidium hatched from the egg, but unfortunately this event was not witnessed directly. However, in doing so the planidium must somehow reverse its orientation, possibly by hatching on its back and looping over, to rest on the platform formed by the collapsed chorion with its head now at the pedicel end (Figs 5, 6), and in fact usually projecting slightly beyond it. This is the position in which the planidium waits for its carrier host and, in response to any activity in its immediate environment, the planidium projects further, rearing and waving its head end around. Mostly the planidia remained on their platforms, from which they efficiently transferred to passing caterpillars

Figures 7–12. *Euceros albitarsus*. 7, 8 – planidia on abdominal intersegmental membranes of *Orthosia gothica*; 9 – planidium on anal proleg of *Orthosia gothica*; 10, 11 – planidium in *Theria primaria* pupa, under wing cases; 12 – planidium in *Operophtera brumata* pupa, near antennae and legs.

(and were very easily able to move along setae, when present, to reach the host's body). Some, however, were seen moving on the sides of the tubes, having left their pedestals for unknown reasons (perhaps accidental, or as a result of suboptimal conditions), and these too were able to transfer to caterpillars – though less readily than those still on their platforms. Dismounted planidia placed manually on hosts also attached successfully. Some unattached planidia were still alive and able to transfer at least 40 days after hatching, but there was appreciable mortality well before this (though possibly the result of suboptimal conditions in the tubes), many of the dead planidia still being on their pedestals. After transferring to the caterpillar, the planidium moves over its body until it settles on an integumental membrane, most often intersegmental and laterally (Fig. 7 shows two planidia, one at each of two adjacent intersegmental membranes, in these especially favoured sites), where it forms a small pocket (Fig. 8), but sometimes ventrally around the prolegs (Fig. 9) and occasionally the true legs or behind the head. At rest and before settling, the planidium is about 0.2 mm long, almost as long as the egg (0.22 mm), but once it settles on a suitable host membrane it imbibes a little haemolymph and swells slightly, to about 0.3 mm at rest (green fluid then being visible in its gut). A small darkened lesion on the host also betrays this activity (Fig. 9). Settled planidia stay in situ without growing further, but are able to survive host ecdysis by boring through the old and attaching to the fresh cuticle; the great majority of settled planidia under observation before and after host ecdysis were seen to have accomplished this successfully and without other displacement.

Planidia settled on unparasitised caterpillars remained in situ until host pupation, but were then seen to be quiescent inside the host pupa, just beneath the cuticle. The planidia observed in (3 different) *Theria primaria* pupae were each near or under the wing case (Figs 10, 11), but one in *Operophtera brumata* was among the antennae and legs (Fig. 12). The use of this exuvial space, and in particular the subalar cavity, is seen also in various early instar Diptera parasitoid larvae [e.g. the tachinids *Gonia cinerascens* Rondani (Baronio, Sehnal, 1980) and *Senometopia pollinosa* (Mesnil) (Herrebout, 1969), and the bombyliid *Villa brunnea* Becker (Du Merle, 1979)]. The *Euceros* planidia were not so easily visible through the pupal cuticle after it had hardened; however, it is presumed that they remained in that position until the moths emerged, when planidia were certainly not left behind in the pupal exuvium. They had presumably transferred to the adult moths (cf. Tripp, 1961), but (following a search that was only rather cursory, and much hampered by the copious scales of the adult moths) they were not rediscovered on the moths that emerged successfully (1, *O. brumata*) or developed to the pharate adult stage and died (1, *T. primaria*) the following spring. The two other pupae with planidia in situ were preserved.

The main experimental host was *Theria primaria* parasitised by *Dusona erythrogaster*, and, of the 27 exposed to planidia in spring 1990 and reared normally, eight died as *Theria* prepupae without parasitism being evident (this level of mortality and its timing is not unusual in routine cultures of *T. primaria*, which has a somewhat prolonged prepupation period, and they probably had not contained viable *Dusona* parasitoids). A further six of the 27 produced moth pupae (of which three had no visible planidia and were allowed to progress to produce adult moths, a further one with a planidium died as a pharate adult, and two with planidia were preserved), and 13 produced *Dusona* cocoons. Of the latter, ten were kept intact, to yield a series of five males of *E. albitarsus*, emerging between 22 and 29.IV.1991, and two male *D. erythrogaster*, emerging between 13 and 15.V.1991, leaving three from which nothing emerged: by the time they were opened it was unclear what had befallen the *Dusona* prepupa that had died inside, but there was no clear evidence of the presence of *Euceros*. These results indicate firstly that not all of the *Dusona* apparent ovipositions were successful (whether failing at attempted oviposition or within the host), and secondly that the *Euceros* planidia were not always successful in establishing themselves in or on the primary parasitoid. Three further *Dusona* cocoons were opened in an effort to trace the development of the *Euceros*.

The first *Dusona* cocoon was opened on 6.VII.1990, about 6 weeks after exposure of the caterpillar to both *Dusona* and *Euceros*, and probably about 5 weeks after the *Theria* had formed its cocoon. Transversely just under the cuticle of the head capsule of the *Dusona* prepupa was a planidium about 0.35 mm long, but almost certainly this was a cast skin (Fig. 13). What appeared to be a *Euceros* larva, evidently having shed its planidial stage skin, but apparently not having grown much if at all, was faintly visible in the still living *Dusona* prepupa, just under the cuticle, dorsally, and about two thirds towards the caudal end of the *Dusona* (Fig. 14) – though the interpretation of this observation is not certain. The *Dusona* prepupa was then placed in a gelatine capsule. On 14.VIII,1990, after a period during which I was unable to make observations, the *Dusona* prepupa had spun a quantity of white silk and defecated, and was now dead, with a small but similarly now dead ectoparasitoid on its head (it is unclear whether or not this position is only coincidentally near the cast skin of the planidium) with a rather pronounced and rounded head capsule about 0.25 mm wide (Fig. 15). It appeared that this larva had fed, and probably also moulted, near that position – but again this interpretation is not certain. If the supposed observations are correct, however, it might suggest that the post-planidial larva had moved around and spent some time inside the host, but then erupted and moulted (with or without first feeding internally, for which there is no evidence either way), and that the dead larva in Fig. 15 was third instar (i.e. two instars beyond the planidial stage). The size of the head capsule suggests that it must be at least two instars after the planidium, and its small body size as well as the only slight extent of its feeding externally on the *Dusona* prepupa would suggest that it was not more advanced than that, although if it had died without much feeding since its last moult it could conceivably have been at the very start of its fourth instar. All of this is, however, conjectural.

Figures 13–18. *Euceros albitarsus* (13–17) and *Euceros pruinosus* (18). 13 – planidium (probably its cast skin) in head capsule of prepupal *Dusona erythrogaster*; 14 – probable post-planidium instar larva within prepupal *Dusona erythrogaster*; 15 – dead larva, ectoparasitoid phase, on prepupal *Dusona erythrogaster*; 16, 17 – prepupa; 18 – planidia on venter of *Amphipyra pyramidea*.

The second *Dusona* cocoon was opened on 2.X.1990, and contained prepupal remains and faeces of the consumed *Dusona*, and a *Euceros* prepupa that had not yet defecated, although with the development of imaginal features (eyes) well visible (Figs 16, 17). A third *Dusona* cocoon was opened on 24.III. 1991 and by that time contained a *Euceros* pupa, which went on to produce a normal adult male on 23.IV.1991.

Among the wild-collected caterpillars exposed to the planidia were several that produced primary parasitoids which either developed successfully to the adult stage, or at any rate did not produce *Euceros*. These were (Geometridae): three *Epirrita dilutata* (Denis et Schiffermüller), one *Operophtera brumata* and one *Agriopis marginaria* (Hübner) that all produced Tachindae; four *A. marginaria* that produced *Casinaria* sp. (2), *Hyposoter clausus* (Brischke) (1) and *Protapanteles immunis* (Haliday) (1); one *O. brumata* that produced *Netelia (Bessobates) latungula*; 26 *Theria primaria* that produced *Aleiodes* sp. (15), various small solitary Microgastrinae (9) and *Hyposoter brischkei* (Bridgman) (2); and (Noctuidae) one *Orthosia gracilis* (Denis et Schiffermüller) that produced *Scirtetes robustus* (Woldstedt). While many of these primary parasitoids may have been simply too small to support *E. albitarsus* (at least *Scirtetes* and *Netelia*, however, should certainly be big enough), a high proportion did in fact get to the adult stage (including the *Scirtetes* and *Hyposoter*) [although not always emerging from the cocoon successfully; however, this is believed to be simply an artefact of suboptimal conditions], suggesting a failure of the *Euceros* to transfer to them successfully. Almost all of the above (except *Netelia*; also the Tachinidae, from which, however, *Euceros* appears never to have been recorded) killed the caterpillar host before it had completed its feeding. While it is true that in many cases the primary parasitoid then spun its cocoon substantially away from the host remains, perhaps thereby isolating itself from the planidium, this was not the case for the numerous *Aleiodes* that killed *Theria* larvae and pupated inside the dead host's skin. It may be that biochemical cues associated with the caterpillar's pupation are what normally induces the *Euceros* to attempt transfer – including entering freshly pupal Lepidoptera if no fully fed primary parasitoid arises within its pupation chamber. This is slightly supported by the observation of planidia still active on the outside of *Aleiodes* mummies, having evidently failed to bore through the caterpillar's cuticle to reach the primary parasitoid that was mummifying it at a time when it was still only partly grown and not in proecdysis. It is also supported by the observation that planidia were still on the outside of rather advanced prepupae (this was best observed in *Orthosia* species, which do not construct such tight cocoons as *Theria*), suggesting that the planidium probably only moves to enter the host at the exact time of pupation – soft fresh cuticle then being available for penetration. Although a possible cue for this (that could function also if a primary parasitoid were to erupt) might be simply the host's movement or the rupturing of its skin, biochemical cues seem more probable.

Penultimate instar larvae of the nematine sawflies *Pristiphora crassicornis* (Hartig) and *Nematus lucidus* (Panzer) (Hymenoptera: Tenthredinidae) were also exposed to the planidia, which attached and successfully transferred to the final instar, but primary parasitoids were absent and only adult sawflies resulted. Unfortunately no observations were made concerning the position of the planidium in or on the sawfly pupa.

2. *Euceros pruinosus* (Gravenhorst, 1829)

Observations with this species were less extensive, but generally did not materially disagree with the findings reported above for *E. albitarsus*, with the possible exception of the behaviour of the planidium in relation to its eggshell.

Ovipositions took place in daylight mostly on the side of the glass tube and its cork facing the light (a *Quercus robur* leaf placed in the tube was hardly used), but continued in darkness and eggs were then placed apparently at random (M.G. Fitton, pers. comm.). No comparable observations on this were made for *E. albitarsus*.

The egg was more aligned with the pedicel than in *E. albitarsus*, deviating by at most only about 30°. Measurements were not made at the same time (nor in the same way) but it appeared to be slightly smaller, at 0.18 mm, and on a slightly shorter pedicel, 0.31 mm, than found for *E. albitarsus*. The planidium was also measured to be smaller, at 0.16×0.05 mm. Iwata (1960) estimated a total egg load of about 5000 for this species, but no estimation could be made in the present case, not least because the adult female was collected from the wild and may already have been ovipositing (although in captivity she did not do so over the first three days).

A possibly major difference between the two sets of observations was that by the time the tubes containing the eggs of *E. pruinosus* reached me (see Methods, above), the eggs had all hatched and the *Euceros* planidia were all dismounted, actively moving on the sides of the tubes, leaving the collapsed eggshell unoccupied and indeed not really seeming to comprise a secure platform through not being horizontal. This might suggest that, unlike *E. frigidus* (Tripp, 1961) and *E. albtarsus*, this species habitually actively searches for hosts by crawling. However, the possibility cannot be ruled that the dismounting that occurred (although extensive) was just the result of a traumatic journey through the post: indeed, some of the planidia were seemingly dead on arrival. Whatever the reason, it did mean that in the present study the planidia of *E. pruinosus* more usually gained initial access to an experimentally introduced caterpillar via its venter [Fig. 18, on *Amphipyra pyramidea* (Linnaeus)] as it walked among them, and it was notable that settlement was much more likely to occur around the prolegs and true legs than was seen in *E. albitarsus*.

Figures 19–21. *Euceros pruinosus*. 19 – planidia inside (small arrows) and remaining external on (large arrows) pupa of *Theria primaria*; 20 – many planidia on arrested prepupa of *Theria primaria*; 21 – adult male.

By far the majority of various wild caterpillars exposed to the planidia proved to be unparasitised. The only adult *E. pruinosus* reared was a male that emerged unobserved in spring 1996, from a cocoon of *Netelia* (*Bessobates*) *latungula* that resulted around 24.VI.1995 from an *Operophtera brumata* larva bearing an egg as a result of exposure to a female *N.* (*B.*) *latungula* before exposure to the planidia on 23.V. 1996. From another (similar) sequence of exposures, a *Netelia* cocoon from which there had been no emergence was opened several years later, and was found to contain a dead *Netelia* prepupa with a dead seemingly intact planidium externally, possibly attached, near its caudal end; and at the head end an external dead *Euceros* larva with a rounded head capsule 0.51 mm wide. This *Euceros* larva was about 0.10–0.15 times the bulk of the remaining mass of the *Netelia* larva.

As with *E. albitarsus*, planidia in unparasitised Lepidoptera pupae were seen immediately under the wing case, and were easily seen only when the host pupa was still fresh and had not fully darkened. In one instance a *Theria primaria* pupa was seen to have planidia still mobile on the outside (Fig. 19, large arrows), presumably having failed to join the two or possibly more that were visible within the pupa, having entered during the window of opportunity as it pupated (Fig. 19, small arrows). It is unclear whether these external planidia were by then certainly doomed, having missed all chances, or whether they might have been able to transfer to a late-arriving ectoparasitoid should one arise. However, it seems improbable that they would live long enough to do so and that the individuals internally settled in the host's exuvial cavity would be in a better position in that event. This bears on the findings of Finlayson (1960) and Tripp (1961) that *E. frigidus* could successfully develop on idiobiont cryptine ectoparasitioids parasitising the cocooned stage of *Neodiprion swainei* Middleton. The subject of Fig. 19 died as a pharate adult, but in other cases adult moths emerged successfully from pupae of both *Theria primaria* and *Operophtera brumata* that contained planidia. In none of these cases were the planidia left inside the pupal exuvium, but neither were they recovered from the bodies of the adult moths where, it is presumed (cf. Tripp, 1961), they must have ended up; however, the search for them externally on adult moths was much hampered by scales and setae, and was not thorough.

Largely because the planidia were mostly crawling on the walls of the tube, some experimental exposures were done by rolling a caterpillar around in the tube – sometimes with the result that large numbers of planidia were picked up. In many cases the planidia did not seem to distribute themselves on intersegmental membranes, although (quite apart from the issue of competition) the viability of such individuals may have been poor: unsettled planidia were certainly lost in large numbers during host ecdysis. It was also seen that large loads of planidia had an adverse effect on the host, sometimes arresting its development in an early prepupal state (Fig. 20). The reason for this is unclear, but (in retrospect) it may also have occurred in some of the exposures of caterpillars to excessive numbers of *E. albitarsus* planidia.

Discussion

These observations complement those of Tripp (1961), perhaps helping to account for some of the anomalies he perceived (such as finding planidia both on and in unparasitised hosts), and also extending knowledge in some directions. Rather than summarise the results in relation to Tripp's (1961) work in detail, this discussion concentrates on the uncertainties that remain.

Tripp (1961) concluded that *Euceros frigidus* has seven or eight larval instars, but the evidence he presented for this was not strong. It seems clear from his work that there is at least one post-planidium instar that lives within the host, but his estimation of three such instars before an external moult, to be followed by a further three or four external instars, seems excessive. The perceived number of internal instars in particular appears to have been deduced just from the large disparity in widths of the heads of planidial and the first detected external instars; however, this might alternatively be explained by the vastly different functions of these larval stages. Although in the present work very little was done to shed light on this, the external instar of *E. albitarsus* seen was still small, and the consumption of the host by that time had been very slight. The same was true of the only external larva of *E. pruinosus* that was seen: although larger and probably more advanced to judge from its head width, this larva had by then also consumed only a rather small proportion of its host. It seems most likely that the *E. albitarsus* seen represented the earliest actively feeding ectoparasitoid instar, probably having just moulted from a single post-planidium internally feeding instar (but note that it is simply a parsimonious assumption, based on minimum functional necessity, that there should be only one such instar; no other evidence is advanced here). If Tripp's lower estimation of three externally feeding instars is accepted, this would amount to just 5 instars, including the planidium, which seems more in line with Ichneumonidae in general. However, this suggestion requires testing, a task that could only realistically be undertaken during a study in which each carrier host was constrained to bear just one planidium. Unfortunately the remains that are to hand from the present study are not in this category, and also they are now mostly in rather poor condition.

It has been clear in the present work that the planidium stays on the exterior of its lepidopteron carrier until (if no primary parasitoid is present) the latter pupates, when the planidium immediately enters the host pupa and rests in its exuvial space. When primary koinobiont endoparasitoids are present it seems only (or at any rate, best) able to transfer to those that erupt from the prepupal lepidopteron (as many primary parasitoid taxa do), which might suggest that it comes under the influence of the same broad suite of hormonal and biochemical changes that lead to this timing in the relationship between many primary parasitoids and their host (e.g. Baronio, Sehnal, 1980; see also Schneider, 1950, 1951). The planidium then presumably enters the fully-grown primary parasitoid larva. However, this process was not actually observed, and the possibility that a parasitised carrier host is entered, and the primary parasitoid is sought, at an earlier stage – although seeming unlikely – has not been positively ruled out. Although no *Euceros* adults resulted from endoparasitoids that erupted from, or mummified, partially grown caterpillars bearing planidia, these primary parasitoids might simply have been too small for the *Euceros* to use. It would be of interest to repeat the trials using a clearly large enough species of koinobiont primary endoparasitoid that leaves the host only partially grown – though it is difficult to think of a suitable candidate.

In the case of development of *E. pruinosus* on *Netelia*, which is a koinobiont ectoparasitoid that undergoes practically all of its larval development on a cocooned prepupa, there is no certainty about the timing of the planidium's transfer to the primary parasitoid, and knowing this would obviously be of considerable interest. All that is clear is that the *Netelia* was able to reach full growth and construct its cocoon, as in the case of the koinobiont endoparasitoids, although finding a (dead) planidium on the exterior of a (dead) *Netelia* prepupa (that had been partially consumed by another, externally feeding, *Euceros* larva) might be taken as weak evidence that the planidium does not transfer to *Netelia* until the latter is fully grown. The same lack of information is true of transfer to idiobiont ectoparasitoids such as the Cryptinae found by Finlayson (1960) and Tripp (1961) to be able to serve as the primary parasitoid host of *E. frigidus* in cocoons of *Neodiprion swainei*; it might be presumed (but is not certain) that the planidium had rested either on the sawfly prepupa or, if it had pupated, in its pupal exuvial space prior to parasitism by the cryptine, but there is nothing to suggest the timing and nature of its transfer to the latter, which undergoes its full development in the sawfly cocoon. *Euceros* species are also recorded from larval-pupal endoparasitoids such as Anomaloninae (Finlayson, 1960; Yu *et al.*, 2012), and again there are similar interesting questions arising from this relationship that are completely uninvestigated.

The position, in the head capsule, of the only planidial exuvium (of *E. albitarsus*: Fig. 13) seen inside a primary parasitoid in this study might or might not have significance. First instar endoparasitoid larvae of some ichneumonid taxa are known to migrate to the anterior end of the host, either to come together for the elimination of supernumary competitors (Jørgensen, 1975), to disrupt further host development by destroying its brain (Führer, Killincer, 1972), or to enter the head for unclear reasons (Heitland, Pschorn-Walcher, 2005). Whether the head is a site for dealing with supernumary competitors by *Euceros*, or whether the planidium's presence there in some way prevented its host's further development, are both unknown – although in the present case the host certainly spun more silk (presumably in response only to being removed from its cocoon) and defecated following the entry of its head capsule by the planidium.

It is disappointing that the relationship between the planidium and its eggshell in *E. pruinosus* remains tantalisingly unclear: this simple matter of whether the planidium of this species waits on a platform comprising its eggshell, or habitually leaves it to seek its carrier host by crawling, could rather easily be elucidated by anyone fortunate enough to rear or collect a fecund adult female of this species alive.

Finally, as far as I am aware there has been no investigation of the use, presumably in courtship, of the extraordinary flattened and expanded male antennae (Fig. 21), developed to a differing extent in all species of *Euceros*.

Acknowledgements

I am grateful to the late Tom Ford for giving me the cocoons from which *E. albitarsus* emerged, to Mike Fitton for providing the adult female of *E. pruinosus* and its eggs, to Rob Petley-Jones, Kevin Warrington and English Nature (now Natural England) for permission to do field work at Gait Barrows NNR and Chippenham Fen NNR, and to Mike Rothnie, Diane Bolger and Nadine Lee for help with digitising and manipulating images. Finally, I am grateful to Dmitry Kasparyan for our many years of happy and productive friendship, and also for his prodigious output of invaluable taxonomic research on Ichneumonidae that, among other good things, has led to this Festschrift and thus the stimulus for me to put these notes together.

References

Baronio P., Sehnal F. 1980. Dependence of the parasitoid *Gonia cinerascens* on the hormones of its lepidopterous host. *Journal of Insect Physiology*, **26:** 619–626.

Barron J.R. 1976. Systematics of Nearctic *Euceros* (Hymenoptera: Ichneumonidae: Eucerotinae). *Naturaliste Canadien*, **103:** 285–375.

Barron J.R. 1978. Systematics of the world Eucerotinae (Hymenoptera, Ichneumonidae). Part II: non-Nearctic species. *Naturaliste Canadien*, **105:** 327–374.

Clausen C.P. 1940. *Entomophagous insects*. New York and London: McGraw-Hill (Reprinted 1972. New York: Hafner Publishing Company). x + 688 p.

Du Merle P. 1979. Biologie de la larve planidium de *Villa brunnea*, Diptère Bombyliidae, parasite de la processionnaire du pin. III. Le début de la vie endoparasitaire du planidium, les réactions de l'hôte et les échecs du parasitisme. *Annales de la Société Entomologique de France (N.S.)*, **15:** 525–551.

Finlayson T. 1960. Taxonomy of cocoons and puparia, and their contents, of Canadian parasites of *Neodiprion sertifer* (Geoff.) (Hymenoptera: Diprionidae). *The Canadian Entomologist*, **92**: 20–47.

Führer E., Killincer N. 1972. Die motorische Aktivität der endoparasitischen Larven von *Pimpla turoniella* und *Pimpla flavicoxis* in der Wirtspuppe. *Entomophaga*, **17:** 149–163.

Hallez P. 1886. Loi de l'orientation de l'embryon chez les insectes. *Compte Rendu de l'Academie des Sciences*, *Paris*, **103:** 606–608.

Herrebout W.M. 1969. Some aspects of host selection in *Encarcia rutilla* Vill. (Diptera: Tachinidae). *Netherlands Journal of Zoology*, **19:** 1–104.

Heitland W., Pschorn-Walcher H. 2005. Biology and parasitoids of the peculiar alder sawfly, *Platycampus luridiventris* (Fallen) (Insecta, Hymenoptera, Tenthredinidae). *Senckenbergiana Biologica*, **85:** 215–231.

Iwata K. 1960. The comparative anatomy of the ovary in Hymenoptera. Part V. Ichneumonidae. *Acta Hymenopterologia*, **1:** 115–169.

Jørgensen O.F. 1975. Competition among larvae of *Pimplopterus dubius* Hgn. (Hymenoptera: Ichneumonidae), a parasitoid of *Epinotia tedella* Cl. (Lepidoptera: Tortricidae). *Zeitschrift für Angewandte Entomologie*, **79:** 301–309.

Kasparyan D.R. 1996.The main trends in evolution of parasitism in Hymenoptera. *Entomologicheskoe Obozrenie*, **75:** 756–789. (In Russian. English translation in *Entomological Review*, **76:** 1107–1136.)

Schneider F. 1950. Die Entwicklung des Syrphidenparasiten *Diplazon fissorius*, Grav. (Hym., Ichneum.) in uni-, oligo- und polyvoltinen Wirten und sein Verhalten bei parasitärer Aktivierung der Diapause-larven durch *Diplazon pectoratorius* Grav. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **23:** 155–194.

Schneider F. 1951. Einige physiologische Beziehungen zwischen Syrphidenlarven und ihren Parasiten. *Zeitschrift für Angewandte Entomologie*, **33:** 150–162.

Shaw M.R. 1997. *Rearing parasitic Hymenoptera*. Orpington: Amateur Entomologist's Society. 46 p.

Tripp H.A. 1961. The biology of a hyperparasite, *Euceros frigidus* Cress. (Ichneumonidae) and description of the planidial stage. *The Canadian Entomologist*, **93:** 40–58.

Varley G.C. 1960. No title. *Proceedings of the Royal Entomological Society of London (C)*, **25:** 7.

Varley G.C. (1964) 1965. A note on the life-history of the ichneumon fly *Euceros unifasciatus* Voll. with a description of its planidium larva. *Entomologist's Monthly Magazine*, **100:** 113–116.

Yu D.S.K., van Achterberg C., Horstmann K. 2012. *Taxapad 2012, Ichneumonoidea 2011*. Database on flash-drive. www.taxapad.com, Ottawa, Ontario, Canada.