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Systematic Entomology (1989) **14,** 117–125

The biology, egg and larvae of *Acaenitus dubitator* (Panzer) (Hymenoptera, Ichneumonidae: Acaenitinae)

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ABSTRACT. *Acaenitus dubitator* (Panzer) is found to be a koinobiont endoparasitoid of the larva of an endophytic beetle, *Cleonis piger* (Scopoli) (Curculionidae), in Britain, suggesting a similar mode of development for the ichneumonid subfamily Acaenitinae as a whole. The parasitoid can overwinter in its cocoon in one of two ways. Individuals overwintering as essentially unaltered mature larvae do not become adult the following summer, while those that overwinter as morphologically distinct prepupae are committed to pupate and become adult immediately afterwards. The change from mature larva to prepupa takes place in late summer, soon after the time of cocoon formation, but a proportion of mature larvae lie over in the first year, and perhaps subsequently. This appears to be an adaptation to life in a particularly harsh and uncertain environment. The egg, prepupa, and first, second and final instar larvae are described and figured. Previous interpretations of the cephalic sclerites of final instar acaenitines are revised.

Introduction

Of the thirty-one ichneumonid subfamilies currently recognized (Gauld & Bolton, 1988) the Acaenitinae is one of the least known biologically, despite the large size and striking appearance of most of the included species. The subfamily is centred in the Old World tropics but extends to most areas except South America (Townes, 1971). There are only a few infrequently encountered European species, of which six are known from Britain, generally from single or very few captures (Fitton, 1981; Shaw, 1986). There are a few rather vague rearing records in the world literature, usually citing wood-inhabiting cerambycid beetles but also including various other holometabolous insects living in similar substrates, and some partial descriptions of the final instar larvae (mostly prepared from exuviae found in cocoons). However, the lack of circumstantial detail or informative accounts of the developmental biology of any species has led to a disparity of opinion expressed in the literature as to whether Acaenitinae are endoparasitoids or ectoparasitoids (reviewed by Gauld, 1984b and by Wahl, 1986). Clarification of this point, as well as the examination of fresh larval material, is needed to provide firm information on which the higher classification of the subfamily can be based.

For these reasons, Fitton's (1981) sole localized British record of *Acaenitus dubitator* (Panzer) from Aberlady Bay, Lothian, Scotland, as recently as 19 May 1960 seemed well

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worth following up, as the site is close to the place of work of one of us (M.R.S.) and because the impoverished nature of the Scottish fauna offered a good prospect of successfully guessing the host. Professor A. F. G. Dixon, the captor cited by Fitton, and Dr R. A. Crowson, his collecting companion at the time, were able to confirm that on 19 May 1960 they had been collecting exclusively in the treeless area of tidal mudflats, sand dunes, freshwater marsh and grassland that is currently administered as Aberlady Bay Local Nature Reserve by East Lothian District Council.

The genus *Acaenitus* contains only this one species, for which there are no literature rearing records. However, guessing its host was not difficult as species of *Phaenolobus*, which is the most closely related genus (Townes, 1971), have several times been recorded from the larvae of cerambycid beetles such as *Obera* and *Phytoecia* species (see Aubert, 1969, 1978; Scaramozzino, 1986), which live in the relatively narrow stems of shrubs and field layer perennials and biennials. While it is improbable that any cerambycid of any kind breeds there (R. A. Crowson, pers. comm.), the large endophytic weevil *Cleonis* (=*Cleonus* auctt.) *piger* (Scopoli), whose larva feeds in a gall in the upper part of the tap root of *Cirsium arvense* (L.) Scopoli (Compositae), is abundant at Aberlady Bay L.N.R. where its life history has been investigated by Cawthra (1958). When the site was visited the supposition that *C.piger* would be the host was easily confirmed and, at least at the sites investigated, the parasitoid appears to be monophagous.

C.piger has at times been recorded from many inland sites both in Britain and in Europe, and its current virtual restriction to coastal sites in Britain probably reflects only that our inland open sandy biotopes have not survived; a distributional distortion known in other British 'arenacious' insects (Morris, 1987 and pers. comm.). The weevil overwinters as an adult and oviposits in spring as the growing shoots of *C.arvense* start to appear above ground. It oviposits just below ground level, but only beside plants growing on rather bare sand and, at Aberlady and other coastal sites nearby, it is therefore more or less entirely restricted to the poorly fixed areas of dune in the more exposed situations relatively close to the sea. *C.arvense* plants penetrated by the first instar weevil larvae soon start to develop a gall, manifested as a more or less localized thickening of the tap root, in which the four larval instars and the pupal stage are passed. The host plant is usually prevented from flowering, and the adult weevil emerges in about August/September (Cawthra, 1958). *C.arvense* stems die back each autumn, and the weevil's vacated feeding and pupation chamber is easily detected in the roots of the dead stems throughout the following winter and, rather less easily, into the succeeding summer.

Methods

The presence of *A.dubitator* at particular sites was straightforward to assess as its cocoon is always formed within the host's pupation chamber and all cocoons overwinter at least once. Dead stems of *C.arvense* that had harboured *C.piger* were found at the following sandy coastal sites near Edinburgh, which were searched on the dates indicated:

Aberlady Bay L.N.R. (Lothian: NT 4682); 16.iii.1986; 20.vi.1986; 2.i.1987
Gullane Bents (Lothian: NT 4783); 23.iii.1986
Yellow Craigs, Dirleton (Lothian: NT 5185); 31.iii.1986
John Muir Country Park, Belhaven Bay (Lothian: NT 6479); 3.iv.1986
Tentsmuir Point National Nature Reserve (Fife: NO 5027); 9.v.1987.

Living cocoons of *A.dubitator* collected in this way were immediately transferred to 2.5×7.5 cm corked glass tubes and kept in a partly open and unheated detached outdoor shed in a fully shaded situation in an Edinburgh garden. Some were opened and the contents preserved by placing them in cold water which was brought rapidly to the boil and boiled for 2 min before they were transferred to 70% alcohol in which they were shipped to D.B.W. for description and illustration. The contents of other opened cocoons were transferred to similarly sized clear gelatine capsules and kept under observation. Otherwise cocoons were kept intact until adult *A.dubitator* emerged.

Living *C.piger* larvae in growing *C.arvense* roots were collected at Aberlady Bay L.N.R. on 20 June and 7 July 1986, and all hosts were dissected and searched for parasitoids. The endoparasitoids found were preserved in 70%

alcohol and shipped to D.B.W. for description and illustration.

The methods of Wahl (1984) were used for the preparation of early stages, and specimens were examined unstained and without special illumination. Description of general body form follows Michener (1953). Terminology of cephalic structures follows Finlayson (1975) and Short (1959), except that *parietal band* is used instead of 'ocular line' (Short, 1959) or 'sclerotized crescent' (Finlayson, 1975), and *hypostomal-stipital plate* refers to the structure formed by the fusion of the hypostomal spur and stipital sclerite.

All material from this study is deposited in the National Museums of Scotland, Edinburgh.

Results and Discussion

Distribution of A.dubitator

A.dubitator was easily found in 20–60% of galls at Aberlady Bay L.N.R., Gullane Bents and Yellow Craigs, sites that are within 8 km of each other, but appeared to be absent from the outlying host populations at John Muir Country Park and Tentsmuir Point N.N.R. (n=150 and 40 host galls examined, respectively). The only other locality for *A.dubitator* in Britain known to us is Anglesey, Gwynedd, on the strength of one damaged female found unidentified in Manchester Museum labelled only 'Anglesey dead on sea-shore O. Gilbert'. *C.piger* is known to occur on the coastal dunes at Newborough Warren N.N.R., Anglesey (M. G. Morris, pers. comm.).

The only other insect parasitoids found in the samples taken were a few broods of a gregarious ectophagous species of *Bracon* (Braconidae) that had attacked third and fourth instar hosts at Aberlady Bay L.N.R. In addition, possibly entomophagous nematodes were found in asssociation with a small number of freshly dead early instar *C.piger* larvae in the living *C.arvense* material collected at the same site on 7 July 1986. There was, however, nothing to suggest why *A.dubitator* was absent from some of the other sites.

Overwintering of cocooned stages

The tough and densely spun cocoons of *A.dubitator* are smooth, parchment-like and usually of a rather uniform light sandy brown colour, though sometimes a little darkened from the ends. They are cylindrically ovoid, with mean measurements *c.* 12.9×5.4 mm (range 11.0×4.5 to 14.5×6.1 mm, n=18).

The fourteen *A.dubitator* cocoons opened during their first winter were found to contain final instar larvae in two distinct stages of development. Six were present as essentially unaltered larvae, not yet having defaecated and with a darkened gut line visible through the dorsum for most of their length. We refer to these as mature larvae (Figs 7, 8). Three were kept under at least intermittent observation (from 5 January 1987) throughout the summer: one remained unchanged and lived into the following winter; one spun a little more silk at the capital end (only) of its gelatine capsule, defaecated, and became prepupal (see following paragraph) unobserved sometime during August and subsequently overwintered in that stage; and the other became partly prepupal, with the areas of compound eye pigmentation visible but without defaecating, and had obviously died in this condition by October.

In addition to these mature larvae, eight of the individuals removed from their cocoons in the first winter were present as prepupae (Fig. 10) with a clearly modified shape, including sexual differences, and compound eye pigmentation visible externally. All had defaecated, though they were still capable of larval mandibular movement. Four prepupae were kept under observation through the following summer: one (♀) pupated on 30 April and eclosed on 28 June; one died in a semi-pupal state, probably in early May; and the other two failed to develop further and were obviously dead by early July. The failure of the latter to develop may have been the result of disturbance: in any case there was no indication that the prepupa is capable of living through the later part of summer and delaying further development until the following year.

From the above it is clear that the winter is passed in the cocoon in one of two well-defined ways: as an essentially unmodified mature larva, or as a highly modified prepupa. Either the mature larva becomes prepupal late in its first summer, or it can hibernate (and can possibly complete one or more subsequent cycles of aestivation and hibernation unchanged) before developing to the prepupal stage late in the following summer, to hibernate again as a prepupa. The prepupa, on the other hand, appears to be committed to develop to the adult stage in the summer following its only hibernation as a prepupa. In addition to the evidence above, this conclusion is supported by the collection of the previous year's cocoons made on 20 June 1986 at Aberlady Bay L.N.R., by which time that summer's adult emergence period had finished. Of nine cocoons collected, five had recently emerged (i.e. at their first opportunity, presumably having overwintered as prepupae) and two others were opened and found to contain mature larvae. One of the remaining two unopened cocoons gave rise to an adult the following year (i.e. presumably having overwintered once as a final instar larva and once as a prepupa), demonstrating without doubt that delayed emergence occurs regularly in the wild. Taking into account all fifty cocoons collected, at least nineteen (including twelve that in one way or another became adults) were evidently already prepupal in their first winter, and at least sixteen (including eight that became adults *c.* 22 months after forming their cocoons) passed their first winter as mature larvae. The remaining fifteen intact cocoons were allowed to enter their third winter unopened: even though they were all by then quite severely desiccated and many were probably dead, it seems probable that most, at least, of these had spent their first winter alive as mature larvae rather than as prepupae.

Although analagous delayed imaginal development is not uncommon in many groups of holometabolous insects, the habit of overwintering as a cocoon more than once is very unusual in temperate Ichneumonoidea. The present case is of particular interest in that two dissimilar modes of overwintering are shown to exist, each representing an irreversible predetermined control over events yet to take place in the ensuing summer.

Adult phenology and longevity

The specimens collected in 1960 by Dixon were caught on 19 May, and in 1986 it was clear that emergence had finished in the field at Aberlay Bay L.N.R. by 20 June: indeed, host larvae collected on that date already contained first instar parasitoid larvae as well as eggs. However, in the cool, late summers of both 1986 and 1987 emergence in captivity took place mainly in the last few days of June (mean 26, median 27, mode 29 June), considerably later than in the field. This discrepancy was strongly at variance with the highly coincident results regularly obtained in other rearing programmes conducted under the same semi-natural environmental conditions. Presumably the cocoons are incubated partly by the heat of early summer sunshine on the bare sand of their coastal biotope, in which case emergence in the wild might be expected to vary considerably from year to year. In captivity eclosion had always taken place before the first daily inspection at 7.30 a.m.

Adults that emerged in 1986 (from cocoons that had overwintered only once) were found to have low and ponderous activity but remarkable longevity under semi-natural, outdoor shade, environmental conditions. Except when exposed to sunshine they were clumsy and slow, looking incapable of flight, and yet without access to either food or water the males lived an average of 18 days ($n=4$) and the females an average of 27 days ($n=3$) in the shade.

A. dubitator seems to possess an unusual suite of biological characteristics, including a strong dependence on sunshine, the potential to withstand long periods of sub-optimal environmental conditions, and the bet-hedging strategy of staggering emergence over more than one season. Taken together, these may reflect the extreme harshness and uncertainty of poorly fixed dunes as a habitat for both host and parasitoid, as well as the parasitoid's rather uncertain prospect of close synchronization with its host in any given year.

Host stage attacked

On the first (20 June 1986) of the two occasions when larval *C. piger* were collected, most were in their second instars but no third instar larvae could be found. Eggs, many of which appeared to be recently laid, and first instar larvae of *A. dubitator* were found floating free in the haemocoel of both first and second instar hosts, strongly suggesting that oviposition is into both. Several hosts contained two or more parasitoids, although (if larval) invariably only one was alive, suggesting that avoidance of superparasitism, if it happens at all, is inefficient.

On the second occasion (7 July 1986) most hosts were in their fourth instars, though third instars were common and a few second instar hosts could still be found. In the sample dissected, only two out of twenty fourth instar hosts were parasitized, as opposed to seven out of twelve of the third instars and one of two second instars. Superparasitism was again frequent. Although all parasitoids were still very small, no eggs were found and there was therefore no indication that hosts had been at all heavily attacked subsequent to their second instars. Rather, it appears that hosts become retarded, even at that early stage, by being parasitized mainly in their first and second instars.

Unfortunately it was not possible to visit the site later in July, when the middle and late instar parasitoid larvae should have been present. Observations by Cawthra (1958) indicate that parasitoid larvae, thought by her to be dipterous but almost certainly in fact those of *A. dubitator,* kill the host larva during late July or early August, at a time when most healthy hosts have already pupated, again suggesting that the parasitoid retards the host's development.

The discovery that *A. dubitator* is a koinobiont (see Askew & Shaw, 1986) endoparasitoid suggests that the subfamily as a whole probably develops in this way and predicts for it a rather more conservative host range than is recorded in the literature. Unsubstantiated rearing records of Acaenitinae from endophytic hosts other than Coleoptera (e.g. siricid Hymenoptera and sesiid Lepidoptera) should therefore be regarded as particularly in need of confirmation.

Morphology of early stages

Egg (Fig. 1). Four eggs dissected from first and second instar hosts were examined: all were about the same size and shape as the one shown in Fig. 1. The egg is elongate and tapered at one end, and is of the acuminate-type (Hagen, 1964) found in ichneumonids that possess long ovipositors and oviposit in or near concealed hosts. While three of the eggs showed no discernable contents, one had a developing embryo of approximately the size of the first instar.

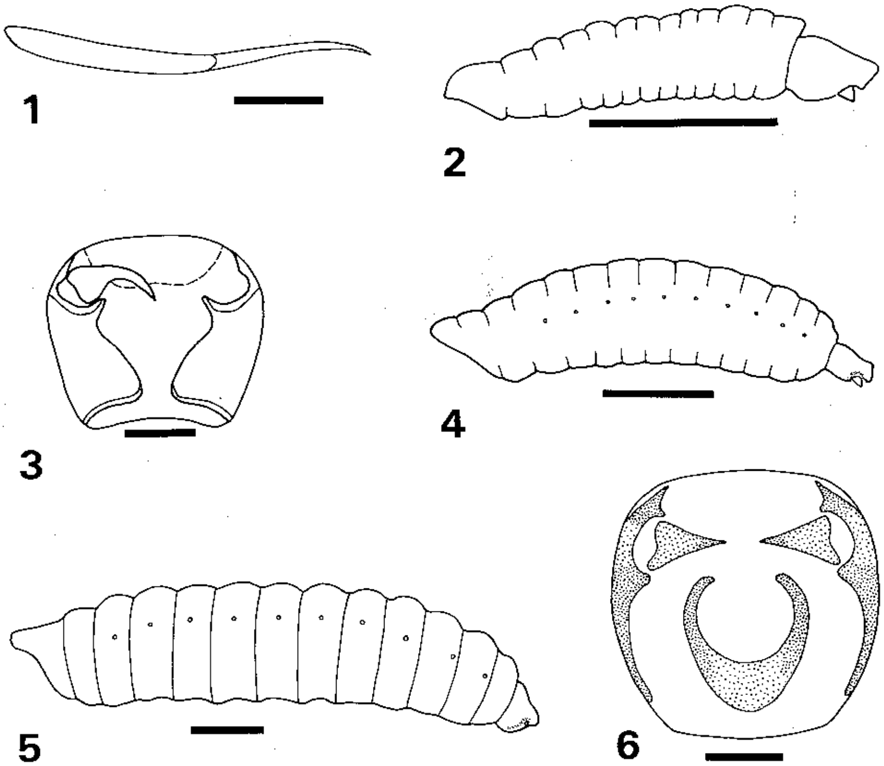
First instar (Figs 2–4). Nine larvae with the same habitus and size as that shown in Fig. 2 were examined following dissection from first, second and third instar host larvae. Observations made at the time of dissection indicate that a caudal appendage (approximately 0.3× the total larval length) was present but subsequently lost in handling. A ventral concavity on abdominal segment 10 is the presumed site of attachment.

The larva is simple and cylindrical, 1.2–1.6 mm long, with a well-developed head capsule. Long setae, spines, or tubercles are lacking. No spiracles could be discerned at 80× magnification. The body is whitish-translucent and the head capsule is light amber. Fig. 3 shows the ventral aspect of the head capsule and the long, well-sclerotized mandibles. The dashed line represents a lighter coloured area on the dorsal surface which is apparently the labrum.

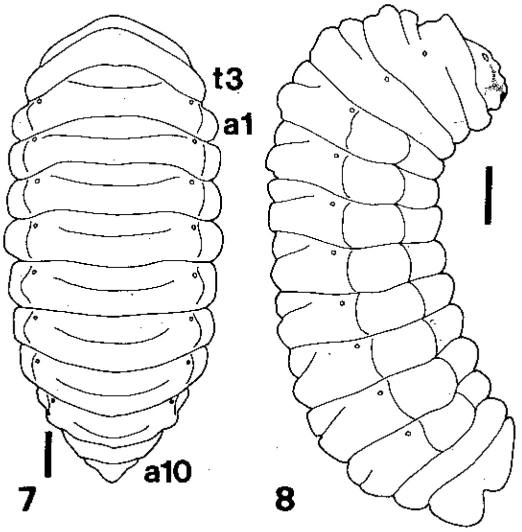
Four larvae of the same habitus and size range as in Fig. 4 were examined following dissection from first and second instar hosts. Although they are longer (1.8–2.0 mm in length) and more inflated than the previously discussed larvae, the head capsule is of the same shape and size in both forms. Mandibular morphology is the same as well and it seems that these larger larvae are merely a more developed form of the same instar. Ten pairs of spiracles are present, two (meso- and meta-) thoracic and eight abdominal.

Second instar (Figs 5, 6). Four larvae similar to that shown in Fig. 5 were dissected from third and fourth instar hosts. The length is about 3.6 mm. The body is similar to later stages of the first instar, but segmentation is somewhat more pronounced. Spiracular distribution is the same as in the previous instar, and the concave depression on the ventral surface of abdominal segment 10 is also present. The head capsule (Fig. 6) is quite different from the previous instar, most notably in the reduction of the mandibles to simple triangular structures and in the appearance of a definite hypostoma and labial sclerite.

Mature larva (Figs 7, 8). Three mature larvae were examined after being removed from their cocoons. Figs 7 and 8 illustrate the dorsal and lateral aspects. The larva is robust with very pronounced transverse ventrolateral tubercles on abdominal segments 1–8. Intersegmental lines are distinct. The dorsal surface of the meso- and metathoracic segments and abdominal segments 1–8 are divided into distinct cephalic and caudal annulets. Only widely scattered minute setae are present. Ten pairs of well-developed open spiracles are present, with the distribution being the same as in previous instars. The overall colour is creamy white with the spiracular peri-



FIGS 1–6. *Acaenitus dubitator*: 1, egg (scale=0.5 mm); 2, first instar larva (scale=0.5 mm); 3, head capsule of first instar larva (scale=0.1 mm); 4, presumed first instar larva after growth (scale=0.5 mm); 5, second instar larva (scale=0.5 mm); 6, head capsule of second instar larva (scale=0.5 mm).



FIGS 7–8. *Acaenitus dubitator*, mature larva: 7, dorsal aspect (t3=metathorax, a1=abdominal segment 1, a10=abdominal segment 10, scale=1.0 mm); 8, lateral aspect (scale=1.0 mm).

tremes and sclerotized cephalic structures brownish.

The cleared, slide-mounted cephalic structures are shown in Fig. 9(a). DESCRIPTION: Cephalic sclerites strongly to moderately sclerotized. Epistoma incomplete medially. Labral sclerite absent. Hypostomal spur and stipital sclerite fused to form triangular plate. Labial sclerite approximately ovoid; ventral portion deep, about 0.6× as long as entire sclerite and moderately sclerotized. Silk press in form of horizontal slit. Prelabial sclerite absent. Maxillary and labial palpi each bearing one large and one small ovoid sensillum. Mandibular base large and well-sclerotized; blade about 0.7× as long as mandible, without teeth, and strongly sclerotized only at extreme apex. Antenna disc-like, weakly sclerotized; central papillus absent. Parietal band only weakly sclerotized.

Spiracle as in Fig. 9(b), with atrium spherical and atrial opening reduced; closing apparatus adjacent to atrium.

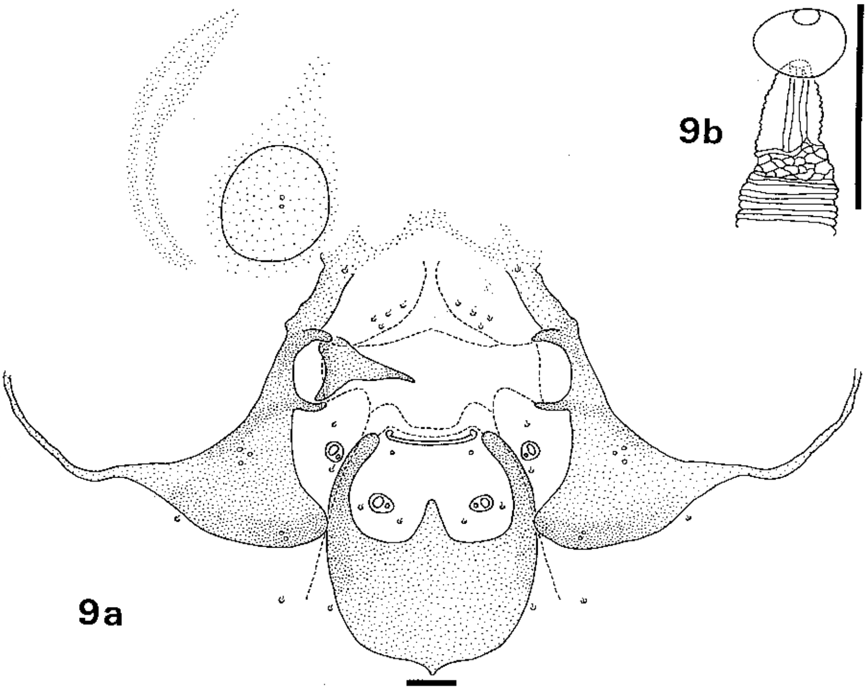


FIG. 9. *Acaenitus dubitator,* mature larva: (a) cephalic sclerites (scale=0.1 mm), (b) spiracle (scale=0.1 mm).

Skin with densely packed small round protuberances and with widely scattered small setae.

Prepupa (Figs 10, 11). Three prepupae were examined; Fig. 10 shows the lateral aspect. It differs from the mature larva in that: (a) it is not as robust; (b) the dorsal surfaces of the metathorax and abdominal segments 1–8 exhibit a more complex pattern of annulets; (c) the ventrolateral tubercles are smaller and ovoid; and (d) abdominal segments 9–10 are produced dorsally. The colour is the same as that of the mature larva except that the brownish red pigment of the developing imaginal compound eye shows through in the vicinity of the mesothorax. As overwintering occurs in this stage it would appear to represent the pronymphal phase of the prepupa (Hagen, 1964).

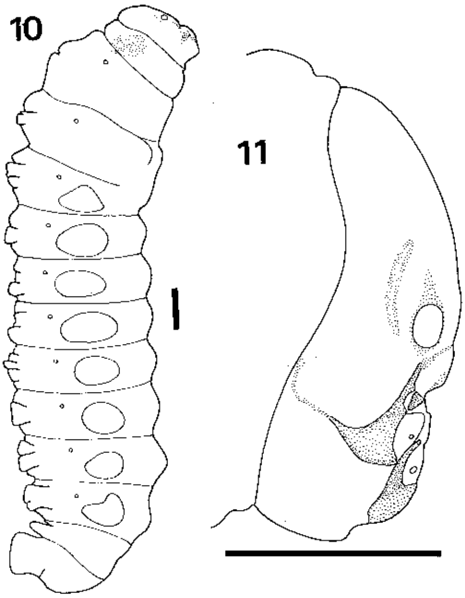
The cephalic sclerites are the same as in the mature larva. Fig. 11 shows the lateral aspect of the head.

Comments on the early stages

Five larval instars have usually been recorded for Ichneumonidae (Gauld, 1984a). The size relationships of the first instar to the egg, and of the first to the second instar were the factors that led us to assign the larval material to these instars. This leaves the third and fourth instars unknown. These might be of some use in understanding the ontogeny of the hypostomal-stipital plate.

Very little is known about overall morphology of ichneumonid larvae and adequate illustrations are rare. The prepupa of *A.dubitator* closely resembles the larva of *Coleocentrus excitator* (Poda) that is figured in Baumann (1933). The latter's relatively elongate habitus, upturned abdominal segment 10, and Baumann's designation of it as 'kokonlarve' makes it probable that his specimen was a prepupa.

The cephalic sclerites of *A.dubitator* closely conform to the morphology of known acaenitine larvae and the prediction that acaenitines are endoparasitoids, based on inferences from larval morphology (Wahl, 1986), is now firmly upheld. Discovery of the larva of *A.dubitator*, as well as examination of the larva of *Arotes amoenus* Cresson (Wahl, unpublished), has led to a reappraisal of earlier conclusions (Wahl, 1986)



FIGS 10–11. *Acaenitus dubitator*, prepupa: 10, lateral aspect (scale=1.0 mm); 11, lateral aspect of head capsule (scale=1.0 mm).

regarding the labral sclerite in acaenitines. It now appears that the suspensorium of the hypopharynx had been misinterpreted as the labral sclerite in *Phaenolobus* and *Spilopteron*. Thus Short (1978) was indeed correct when he stated that the labral sclerite was absent in *Spilopteron*. Loss of the labral sclerite can be postulated as a synapomorphy of the Acaenitini, to which *Acaenitus, Arotes, Phaenolobus* and *Spilopteron* belong. Retention of the labral sclerite in *Coleocentrus* corresponds with a number of adult plesiomorphies in that genus as well.

As stated earlier, it is most likely that all acaenitines are koinobiont endoparasitoids. Acaenitinae is one of a monophyletic group of subfamilies that includes Oxytorinae and Orthocentrinae (Wahl, 1986) and perhaps also Diplazontinae (Wahl, unpublished). Diplazontines are well known as koinobiont endoparasitoids of predatory Syrphidae, though some taxa oviposit into host larvae in their final instars (Rotheray, 1981). Oxytorinae and Orthocentrinae are known to be endoparasitoids, but little else is known of their biology beyond scattered host records. The indications are that they, too, will be found to be koinobionts.

Acknowledgments

We are grateful to R. A. Crowson, A. F. G. Dixon and M. G. Morris for the helpful information indicated in the text, to C. Johnson for access to the collections in Manchester Museum, to M. Duncan and East Lothian District Council for permission to do fieldwork at Aberlady Bay L.N.R. and John Muir Country Park, and to P. Kinnear and the Nature Conservancy Council for permission to sample at Tentsmuir Point N.N.R.

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Accepted 1 March 1988