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Biology, early stages and description of a new species of *Adelognathus* Holmgren (Hymenoptera: Ichneumonidae: Adelognathinae)

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Abstract

Adelognathus leucotrochi Shaw & Wahl sp. nov. is described from Britain where it is a univoltine slightly gregarious koinobiont ectoparasitoid of late stage larvae of the tenthredinid sawfly *Nematus leucotrochus* Hartig feeding on *Ribes uva-crispa*. Defensive reactions by the host to prospecting females are described. The developmental biology of *A. leucotrochi* is described in detail: the host is only temporarily paralysed by the injection of a venom that has no other effect on the host, and eggs are laid on the host's dorsum without involvement of the ovipositor—that is, the egg issues direct from the genital opening. Prior to oviposition the adult female parasitoid prepares the site by spreading an adhesive substance from her ovipositor. Host-feeding by adult females occurs on haemolymph and sometimes also other tissues obtained at the site of a wound made always by the mandibles, but appears not to be obligatory. It may be concurrent or non-concurrent with oviposition; in the latter case, it may be either destructive or non-destructive. Larval development is very rapid, taking about 70 hr at 18–22ºC, and the host continues to feed for approximately the first half of this period. Five larval instars were detected, and their cephalic sclerites are described and illustrated, as are those of the final instars of a further three species of *Adelognathus* for comparison. The rather featureless final instar larva is also figured, as is the tough cocoon in which the winter is passed as a prepupa. The biology of some idiobiont *Adelognathus* species is discussed in comparison with that of *A. leucotrochi*, and several other instances of eggs not issuing from the ovipositor in non-aculeate ectoparasitoid Hymenoptera, whether koinobionts or idiobionts, are briefly reviewed. It is concluded that this habit seems to arise rather easily when there is direct bodily contact between the adult and the host/prey, as indeed is the case in all carnivorous aculeates that do not practice continuous provisioning.

Key words: parasitism, Tenthredinidae, *Adelognathus chrysopygus,Nematus leucotrochus*, host-feeding, oviposition, ovipositor use, koinobiont, larval development, larval morphology, Britain

Introduction

The enigmatic ichneumonid subfamily Adelognathinae consists of the single genus *Adelognathus* Holmgren, with 46 described species occurring in the Holarctic (Yu *et al.* 2012). Its relationship to other subfamilies has been unclear, with Townes (1969: pp. 32–33) considering adelognathines somewhere near the Pimplinae, Tryphoninae, Labeninae, Xoridinae, and Agriotypinae. Quicke *et al.* (2009) placed it as the sister-group to Cryptinae, but that work is based upon only one gene and an inadequate morphological data set. Preliminary results from a more comprehensive molecular and morphological study (A.M.R. Bennett *et al.* in prep.) place it as the sister-group to a clade consisting of Ichneumoninae, Cryptinae, and Microleptinae.

Adelognathus species are all small insects, generally under 4 mm in length, and as far as is known they are exclusively external parasitoids of the larvae of sawflies (Hymenoptera: Pamphilioidea and Tenthredinoidea). Development may be solitary or in small gregarious broods (Fitton *et al.* 1982). While it is possible that strictly solitary species exist, most species are probably best regarded as fundamentally gregarious, with brood sizes of one to a few, in some cases with variation according to generation (Kopelke 1987). Although many *Adelognathus* species parasitize exposed hosts, some are associated with hosts that feed in more concealed sites (Fitton *et al.* 1982), in one case in a gall (Kopelke 1987). Both the large whitish eggs and the parasitoid larvae are, at least when

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laid dorsally on exposed hosts, highly conspicuous (illustrated by Fitton *et al.* 1982), and larval development is usually extremely rapid.

Having made limited observations on the larval development of at least four *Adelognathus* species, Fitton *et al.* (1982) generalized that the host larva carries on feeding after the parasitoid has oviposited on it, and often continues to do so through the early part of the parasitoid's larval development; i.e. that *Adelognathus* species are clearly koinobiont parasitoids. One of these species, *Adelognathus chrysopygus* (Gravenhorst) nec auctt (= *A. granulatus* Perkins: Kasparyan 1990), has subsequently been studied by Rahoo & Luff (1987: as *granulatus*) as a parasitoid of the tenthredinid sawfly *Pristiphora pallipes* (Lepeletier) found feeding on cultivated gooseberry, *Ribes uva-crispa* Linnaeus, in NE England. From laboratory studies, they reported that the host did not recover feeding activity after being stung and paralysed prior to oviposition, although in the wild parasitized larvae could evidently be collected from the foliage of their foodplant. Although their methods did not clearly differentiate the effect of single attacks from repeated ones, Rahoo & Luff (1987) suggested that a more severe effect of the adult parasitoid's venom was correlated with a different egg placement, ventral rather than dorsal, on the host in their study. The wild-collected brood of purportedly the same species that had been observed (although on a different, but unidentified, tenthredinid host) by Fitton *et al.* (1982: as *granulatus*) had exhibited neither of these features.

Partly to try to reconcile these apparent differences, a search of wild (or possibly in some cases feral) stands of *Ribes uva-crispa* growing in and adjoining ancient woodland in NW England was undertaken during May 1991. Larvae of three species of nematine tenthredinid sawflies, *P. pallipes*, *Nematus ribesii* (Scopoli) and *Nematus leucotrochus* Hartig, were found, the first very sparingly but the last two in abundance. In the event *A. chrysopygus* was not found and only *N. leucotrochus* was parasitized by an *Adelognathus* species. However, its incidence was high: numerous adults were reared, and observations were made on the host-parasitoid interactions in culture in the following generation. The main purpose of this paper is to record these biological observations, but as no existing name could be found for the *Adelognathus* species it is first formally described below as *Adelognathus leucotrochi* Shaw & Wahl, **sp. n.**

Material and methods

Sawfly larvae were collected from stands of *Ribes uva-crispa* growing in ancient semi-natural woodland sites and adjoining hedgerows in the neighbourhood of Beetham, Cumbria between 24 and 28.v.1991. Several shaded stands supported especially final, and a very few penultimate, instar *N. leucotrochus* larvae, feeding semi-dispersed, while similarly sized *N. ribesii* larvae, in tighter aggregations, were only found feeding on a few of the more exposed stands, from which *N. leucotrochus* was generally absent. Only final instar larvae of *N. leucotrochus* supported *A. leucotrochi* larvae or (more often) eggs, and in most stands the majority of the final instar larvae of this species seen were parasitized. The two *Nematus* species differ greatly in appearance, *N. ribesii* being by far the more heavily spotted. The number of *P. pallipes* larvae found (three) was too small to tell if there was a habitat preference, but none was parasitized.

All rearings of wild-collected material were carried out under near-natural conditions of day length and outdoor shade temperatures (in Edinburgh), in an unheated, detached and completely shaded garden shed with strong through draught (Shaw 1997). Sawfly larvae not bearing *Adelognathus* were reared in groups on *Ribes uva-crispa* leaves in closed clear plastic boxes (14 × 8 × 6 cm) with a copious lining of absorbent tissue (lavatory roll), and allowed to enter the tissues for cocoon formation. Cocoons were later recovered and stored under the same conditions until adult emergence. Sawfly larvae parasitized by *Adelognathus* were reared singly on *Ribes uva-crispa* in upright 7.5 × 2.5 cm corked glass tubes, with tissue pressed into the base. Faeces were removed daily, as necessary, and the parasitoids were allowed to make cocoons in the folds of the tissue or (in about half the cases) among strands of sphagnum moss also provided. After cocoon formation (May/June) half of the corks were replaced by taught fine nylon mesh (ladies' tights) through which a mist of water was sprayed at irregular intervals (ca weekly) until April: adult emergence success was equally high under the two treatments.

Adult parasitoids were confined in 7.5 × 2.5 cm corked glass tubes and fed droplets of honey-water (supplied daily, ca 1:4 but drying) *ad libitum* from their date of emergence. They were between 20 and (exceptionally) 46 days old during observations of host contact. Most females were deliberately killed while in good health, but some were kept alive for about 50 days before they started to die of general infirmity. Males were deliberately killed after

25 days, with little prior mortality. Some of the females used in experiments were virgin, but others had been kept with males during their first two weeks of life (though no matings were actually witnessed): both groups of females laid eggs, and no difference between them was observed in any aspect of their behaviour.

Experimental hosts were always offered in feeding positions on *Ribes uva-crispa* leaves in 7.5 × 2.5 cm corked glass tubes. Experimental rearings were conducted indoors at 18–22°C: the times measured between developmental events would undoubtedly be more prolonged in the field, where night-time temperatures would often fall to as low as 5ºC at that time of year. Both *Nematus leucotrochus* and *Nematus ribesii* were used as experimental hosts, the former cultured in captivity from virgin females (i.e. an all male progeny), but the latter collected wild in the egg or an early larval stage (i.e. possibly both sexes). "Final" and "penultimate" instar hosts refer to feeding instars (i.e. do not account for the eonymph stage). Host-feeding and oviposition events were followed under a low-power binocular microscope.

The specimens examined in this study were borrowed from or are deposited in the following collections:

AEIC	American Entomological Institute: Gainesville, Florida, U.S.A.
HNHM	Hungarian Natural History Museum: Budapest, Hungary
NHML	The Natural History Museum: London, United Kingdom
RMNH	Naturalis Biodiversity Center (former Nationaal Natuurhistorische Museum): Leiden, The Netherlands
RSME	National Museums of Scotland (former Royal Scottish Museum): Edinburgh, United Kingdom
ZINC	Zoological Institute, Russian Academy of Sciences: St. Petersburg, Russia

The morphological terminology is mostly that of Townes (1969). However, *anterior transverse carina* and *posterior transverse carina* are used (respectively) for "basal transverse carina" and "apical transverse carina", *epicnemial carina* for "prepectal carina", *gena* for "temple", and *supraclypeal area* for "face". Wing vein terminology is that of Mason (1986). *Mesosoma* and *metasoma* are used to refer to the apparent thorax and abdomen, respectively. *T1, T2,* etc., are used for the first metasomal tergite and following tergites. When the lengths of the body and wing are given, the values in parentheses are those of the holotype. Reference to metasomal color in the description applies only to the tergites and first sternite unless otherwise indicated.

The terminology for the cephalic sclerites of the mature larva is that of Wahl (1990) and Sime & Wahl (1998); methods of preparation are those of Wahl (1989). Congo Red was used to stain some weakly sclerotized preparations. Scale lines in the illustrations represent 0.1 mm unless otherwise indicated. Wahl's notation for larval preparations follows the museum acronym. It consists of his initials, the day, month, year, and a letter designating the individual preparation.

Images of adult specimens were taken with an EntoVision micro-imaging system. This system consists of a Leica M16 zoom lens attached to a JVC KY-75U 3-CCD digital video camera that feeds image data to a desktop computer. The program Archimed 5.3.1 is then used to merge an image series (representing typically 30–50 focal planes) into a single in-focus image. Lighting was provided by an EntoVision dome light. A Medical Nikkor 120 mm lens with automatic flash attached to a standard SLR camera body was used with Fuji 35 mm color transparency film for the images of the early stages.

Adelognathus leucotrochi Shaw & Wahl, sp. n.

(Figs 1–7)

Type material: Holotype: UNITED KINGDOM, England, Cumbria, Beetham: ♀ "*Nematus leucotrochus* on *Ribes uva-crispum* with 2 ectos, 26.5.1991, em. 21.4.1992; NMSZ 1993.143" (*M.R. Shaw*) (RSME). Condition of holotype: intact. **Paratypes**: **similar data as holotype** but often different brood size, collection and emergence dates (collection dates of 24.v.1991, 25.v.1991, 26.v.1991, and 28.v.1991, emergence dates in iv.1992), 36♀, 20♂ (AEIC, HNHM, NHML, RMNH, RSME, ZINC); **UNITED KINGDOM, Scotland, Edinburgh, Grange (suburbs)**, from same host species, collected 6.vi.1998 and 13.vi.1998, emerged iv.1999 (*M.R. Shaw*), 6♀ (RSME). Non-paratype material: 2♀ collected in England (North Yorkshire, Tadcaster, 24.iv.2011 (*W.A. Ely*)) and Scotland (Edinburgh, Grange, 3.v.1990, (*M.R. Shaw*)).

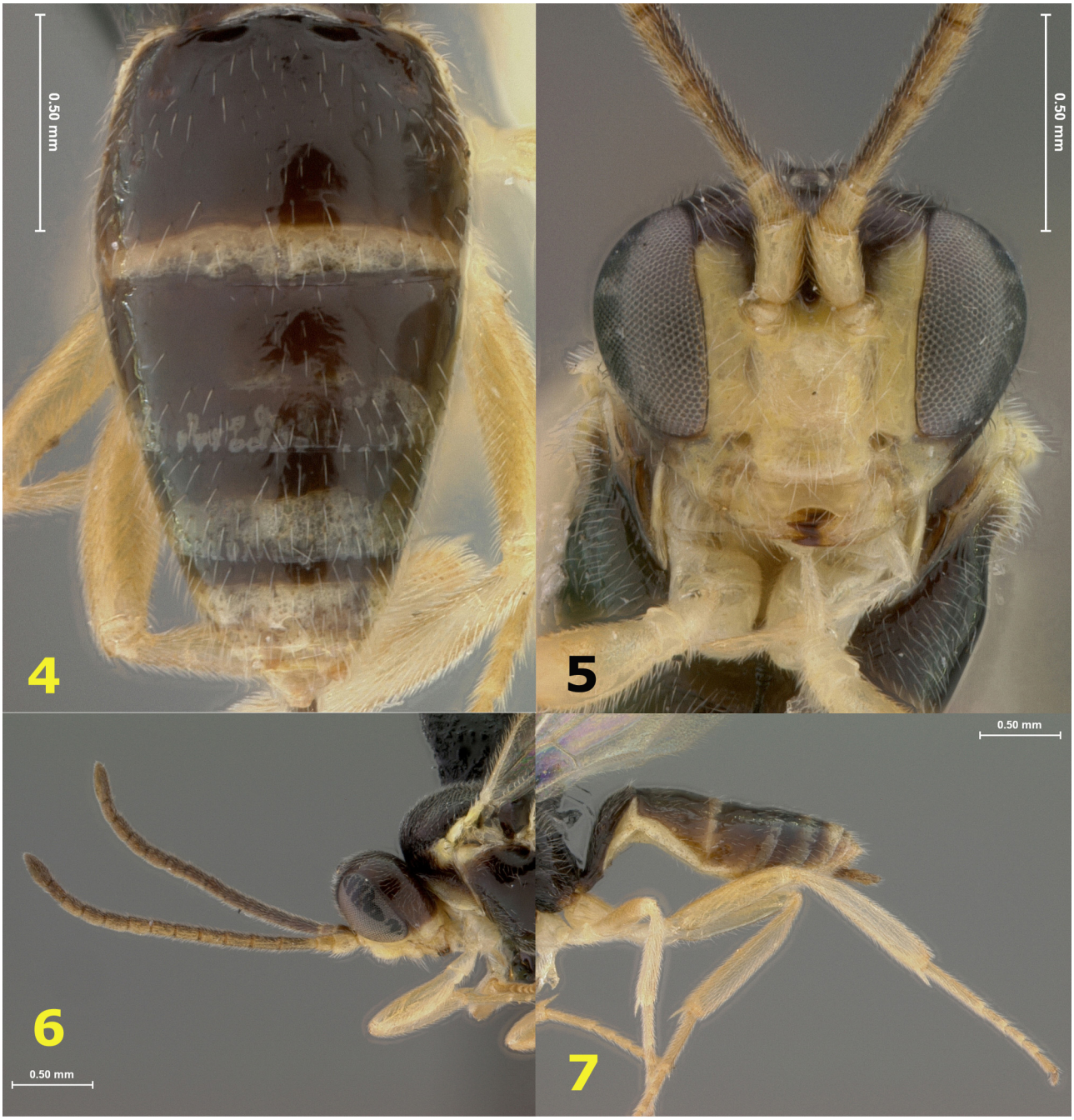
Diagnosis. This species (Fig. 1) can be recognized by the following combination of characters: clypeus, supraclypeal area, and paraocular area yellow (Fig. 5); clypeal apex truncate; flagellomere 4 about 2.2 × as long as wide; subocular sulcus absent; mesoscutum smooth and evenly setose; mesopleuron centrally glabrous; hind coxa white ; hind leg with tarsomere 2 about 1.1 × as long as tarsomere 5; vein 3rs-m of fore wing spectral (and areolet superficially appearing open in many specimens); T1 smooth; T2 smooth and with widely scattered minute setiferous punctures medially and laterally, mediolaterally impunctate.

Description. Female. *Structure*. Scape about 2.0 × as long as pedicel (measured on ventral surface); flagellum about 0.8 × length of hind wing; 12 flagellomeres, flagellomeres 7–12 distinctly thickened (Fig. 6); flagellomere 4 about 2.2 × as long as wide. Clypeus smooth with weak transverse grooves, apex truncate and narrowly reflexed (Fig. 5). Labrum extending beyond clypeus, its apical margin distinctly concave (Fig. 5). Supraclypeal area granulose. Malar space about 0.3 × as long as basal mandibular width. Subocular sulcus absent. Occipital carina not elevated as lamella. Hypostomal carina joining occipital carina before base of mandible. Propleuron weakly convex. Mesoscutum smooth, with minute setiferous punctures separated by 3.0–5.0 times their diameter (Fig. 2); lateral lobes weakly and shallowly foveolate. Epicnemial carina complete, its dorsal end touching anterior margin of mesopleuron. Mesopleuron smooth and centrally glabrous (Fig. 3). Propodeum with anterior and posterior transverse carinae absent, anterior 0.5 of median longitudinal carina absent; anterior 0.3–0.5 smooth, posterior 0.5–0.7 with numerous more or less longitudinal rugulae on granulate surface (Fig. 2). Tarsomere 4 of fore leg about 1.8 × as long as wide; hind leg (Fig. 7) with tarsomere 2 about 1.1 × as long as tarsomere 5. Vein 3rs-m of fore wing spectral (and areolet superficially appearing open in many specimens). T1 1.3–1.5 × as long as apical width, appearing subpetiolate in dorsal view (Fig. 2), smooth and shining; S1 about 0.2 × as long as T1 (Fig. 7). T2 smooth and with widely scattered minute setiferous punctures medially and laterally (punctures separated by at least 1.0 × setal length), mediolaterally impunctate (Fig. 4). *Color*. Black, the following yellow: mandible except for dark brown apex, gena immediately adjacent to mandible, labrum, clypeus, supraclypeal area, paraocular area (extending 0.6 × distance between antennal socket and apex of eye), ventral surfaces of scape and pedicel, ventral 0.5 of propleuron, ventral 0.7 of anterior edge and dorsal posterior corner of lateral area of pronotum, subalar ridge and immediately adjacent area of mesopleuron, tegula, apical 0.2 of T2, apical 0.4 of T3–4, apical 0.5–0.6 of T5, and following tergites. Flagellum with ventral surface light brown, dorsal surface dark brown. Legs with coxae, trochanters, and trochantelli white, except for diffuse light brown of basal 0.1 of hind coxa; femora, tibiae, and tarsi brownish-yellow. Pterostigma of fore wing light brown. *Length*. 3.4–3.7 mm (3.6 mm); fore wing 3.7–3.9 mm (3.8 mm).

Male. *Structure*. As in female, except flagellomeres 6–8 with elevated linear tyloids. *Color*. As in female, except: yellow of paraocular area extending to 0.8–0.9 × distance between antennal socket and apex of eye; ventral surface of flagellum brownish-yellow; lateral area of pronotum yellow but for brown stripe extending from median area to center of lateral area. *Length*. 3.1–3.5 mm; fore wing 2.9–3.2 mm.

Comments. In Fitton *et al.* (1982), the female of *A. leucotrochi* runs to couplet 9, where it founders due to the short antenna, and yellow supraclypeal area and paraocular area. In Kasparyan (1990), *A. leucotrochi* will go smoothly to couplet 56, which leads to *A. brevicornis* Holmgren and *A. rufithorax* Kasparyan. However, the combination of the length of flagellomere 4 and color patterns of the supraclypeal area, propleuron, and mesopleuron rules out placement in either species. Comparisons with determined material (including specimens used by Kasparyan) and published descriptions convince us that *A. leucotrochi* cannot be construed as belonging to any described species. It can be distinguished by the combination of: distinctly thickened flagellomeres 7–12, flagellomere 4 about 2.2 × as long as wide, color pattern of anterior head surface (Fig. 5), regularly punctate mesoscutum (thus appearing evenly setose in pristine specimens), black mesopleuron and propodeum, length of S1 about 0.2 × length of T1, and smooth surface of T2. In particular, female *A. leucotrochi* differ from *A. brevicornis*, the closest species to it morphologically, in its completely yellow supraclypeal area, more extensively yellow portion of the gena immediately adjacent to the mandible, more extensive yellow markings on the propleuron and pronotum, and almost entirely yellow hind coxa (usually extensively brown in *A. brevicornis*). In males, the pronotal and propleural coloration of the two species is more similar, but in *A. leucotrochi* the yellow paraocular area extends further dorsally (about 0.8 × the distance between the antennal socket and the apex of the eye, against 0.5 × in *A. brevicornis*). In addition, *A. brevicornis* has a later flight period in Britain (June through July, possibly also August through September) and different hosts (found several times on an undetermined tenthredinid on *Betula*).

FIGURES 1–3. *Adelognathus leucotrochi* **sp. n.**, ♀. 1. Habitus, lateral; 2. Mesosoma and first metasomal tergite, dorsal; 3. Mesosoma, lateral.



FIGURES 4–7. *Adelognathus leucotrochi* **sp. n.**, ♀. 4. Metasomal tergites from second, dorsal; 5. Head, anterior; 6. Head and antenna, lateral; 7. Metasoma and hind leg, lateral.

Yellow to whitish apical banding is found on the tergites of many species of *Adelognathus*. In *A. leucotrochi*, the apical bands in tergites 3+ appear to be caused by a particularly thin epidermis, as they are often degraded to the point where a good portion of a band is missing in a mottled and irregular fashion.

Etymology. The specific name derives from that of the host, *Nematus leucotrochus* Hartig.

The larvae of Adelognathinae

(Figs 8–16)

Introduction. Prior to this study, the larvae of Adelognathinae were known for two species: Short (1978) illustrated the cephalic sclerites of the mature larvae of *A. brevicornis* Holmgren and *A. pallipes* (Gravenhorst).

They had an unusual mix of characters characteristic of ectoparasitoids (papillate antenna, denticulate mandibular blade, spiracular atrium separated from closing apparatus by section of trachea) and endoparasitoids (labral sclerite absent, skin with setae short and widely scattered), although it should be noted that these associations are subject to exceptions (Wahl 1986; Shaw & Wahl 1989). The numerous long fine mandibular denticles are found elsewhere in the Ichneumonidae only in the Lycorininae (Short 1978; DBW pers. observation).

Preparation of *A. leucotrochi* larval exuviae revealed a character that was not figured by Short for other *Adelognathus*: the struts of the inferior mandibular process are greatly lengthened, with the anterior strut extending dorsally so that its apex is above the dorsal margin of the short pleurostoma. Examination of the original slide preparations used by Short showed that this character was present but not recognized by him in both cases. Below, a new diagnosis is provided for adelognathine mature larvae based upon re-examination of Short's preparations and new material. Following that, each species is briefly treated with regards to characters visible in the preparations. Finally, the various larval stages of *A. leucotrochi* are discussed.

It should be noted that all drawings of ichneumonid cephalic sclerites must involve elements of reconstruction, due to vagaries of the mounting process which result in tears and the resulting skewing of sclerite positioning, as well as structural distortions. The method employed (by DBW, here and elsewhere) is to use a drawing tube to make accurate outlines, and then flip and trace structures so as to produce a bilaterally symmetrical result, which aims to be a faithful rendition of the original. Short's working method is unknown, although he may have utilized an ocular grid. His final results are often at odds with the original mount in terms of proportions and details, as well as including striking misinterpretations of morphology.

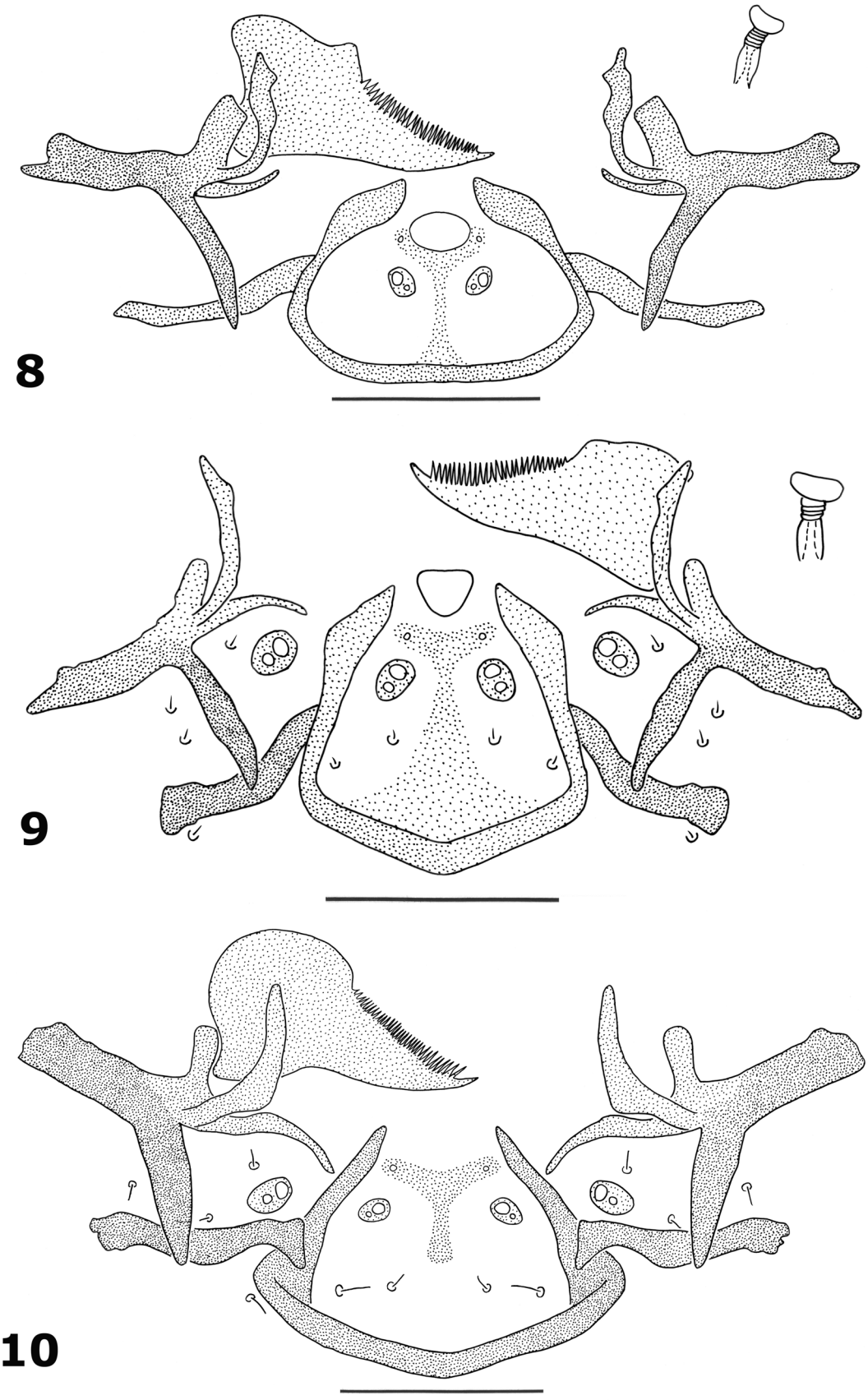
Diagnosis of the mature larvae of Adelognathinae. Cephalic sclerites weakly to strongly sclerotized. Epistomal suture unsclerotized. Labral sclerite absent; clypeolabral plates absent. Pleurostoma with only ventral section sclerotized; struts of inferior mandibular process elongate and narrow, anterior strut extending dorsally with its apex extending above apparent dorsal end of pleurostoma. Hypostoma straight and rather short, posterior end without elongate or upcurved sclerotized processes. Hypostomal spur about 3.0–5.0 × as long as basal width. Stipital sclerite present, straight to gently curved, slightly longer than hypostomal spur. Labial sclerite approximately quadrate. Salivary orifice ovoid. Prelabial sclerite weakly sclerotized, T-shaped. Maxillary and labial palpi each bearing one large and one small ovoid sensillum. Mandible weakly but uniformly sclerotized; blade 0.5–0.6 × as long as mandible, with numerous long fine denticles. Antenna papilliform, disc unsclerotized. Spiracle with closing apparatus separated from atrium by section of trachea; atrium goblet-shaped with large opening. Skin covered with small, bubble-like protuberances; setae short and widely scattered.

The pleurostoma has only a relatively short ventral section present. It does not extend to the region where the superior mandibular process would be normally located in ichneumonids. Given that a small internal projection is present near the apex of the anterior inferior mandibular strut, it is possible that this elongate structure serves as the dorsal articulation point for the mandible.

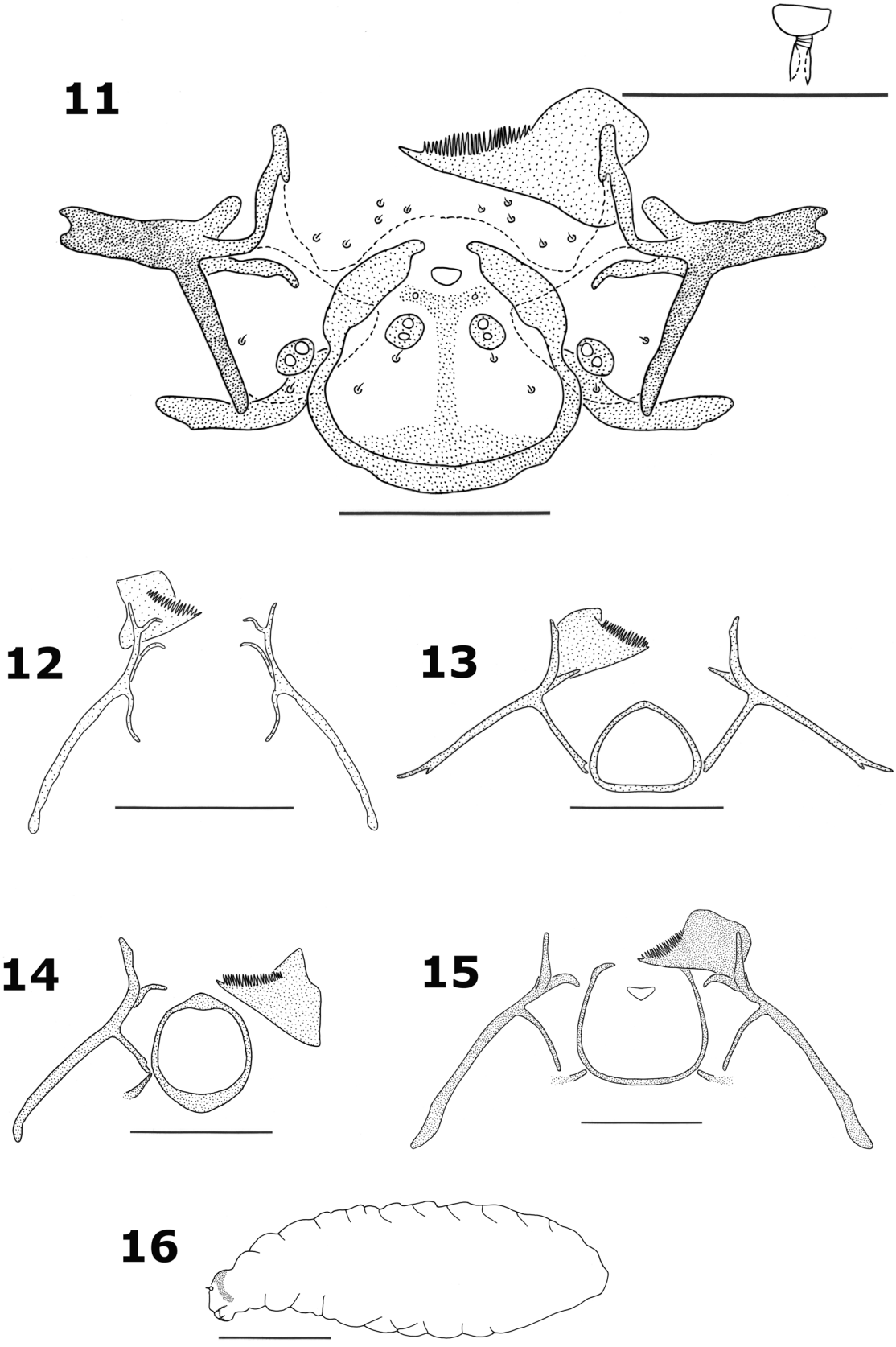
Comments on the mature larvae of individual *Adelognathus* species. a) *A. brevicornis*. Originally figured in Short (1978: 197, Fig. 150); the same slide [RSME] is redrawn here (Fig. 8). While the gross structures are more or less as Short interpreted them, the following apply: (i) the anterior inferior mandibular strut is interpreted by Short as the pleurostoma, (ii) the preparation is so distorted that membranous margins and setae cannot be accurately portrayed, (iii) there is no trace of the antennal disc and the relationship of the papillus to the other sclerites is unknowable, and (iv) there is no trace of the cardo.

b) *A. leucotrochi*. The individual in Fig. 11 [AEIC, DBW 13.v.1998a] is from the paratype series. A fuller discussion of the larval stages of *A. leucotrochi* is given below.

c) *A. pallipes*. Originally figured in Short (1978: 197, Fig. 151). Examination of the original slide [HMOX] revealed it to be so distorted that an accurate reconstruction is impossible. Short's drawing is largely fanciful except for the quadrate labial sclerite and typical mandibular denticles; the antennal papillus is present but there is no trace of the disc. Fortunately, a slide with two well-mounted *A. pallipes* larval exuviae is in the National Museum of Natural History, Washington, D.C. [labeled as "*Catalytus pallipes* Ashmead", "Hym. 794 slide". The synonymy (and homonymy in *Adelognathus*) of this nominal species and *Plectiscus pallipes* Gravenhorst was established by Townes (1944)]. One is figured here (Fig. 9); the larva is the one on the right-hand side of the mount. It should be noted that locality data are missing and the associated adults were not seen in order to verify the determination (although the proportions look roughly the same as in the HMOX specimen, allowing for the distortions in the latter).



FIGURES 8–10. *Adelognathus* larvae. Scale line 0.1 mm. 8–10. Cephalic sclerites. 8. *A. brevicornis*, final instar; 9. *A. pallipes*, final instar; 10. *Adelognathus* sp. indet., final instar.



FIGURES 11–16. *Adelognathus* larvae. 11–15. Cephalic sclerites, scale line 0.1 mm. 11. *A. leucotrochi* **sp. n.**, final instar; 12–15. *A. leucotrochi* **sp. n.**, instars A–D respectively; 16. *A. leucotrochi* **sp. n.**, fully grown (after preservation), scale line 1.0 mm.

d) *Adelognathus* sp. Another larval specimen was found in the HMOX collection, labeled simply as "*Adelognathus* sp." and "12325"; it is illustrated here in Fig. 10. The shapes and proportions of the sclerites, plus the lengths of the cephalic setae, indicate that it belongs to a different species than *brevicornis*, *leucotrochi*, or *pallipes*. Although not shown in the illustration, the antennal papilla is present.

Larval stages of *A. leucotrochi.* Apocritan Hymenoptera are considered to have five larval instars as the plesiomorphic condition (Evans & West-Eberhard 1970) but only a miniscule number of species have been studied in depth. Ichneumonids are no exception, as discussed by Gauld (1984). Four distinctly different exuviae were recovered from the exterior of a dead *Nematus leucotrochus* mature larva (same locality data as for the paratype series, v.1991; AEIC, 23.iii.1992b, Figs 12–15), and it is obvious that they are prior to the mature larva of Fig. 11. Whether these represent the full number of instars is unknown, but it seems certain that the sequence A–D (i.e. Figs 12–15) is correct. The points of interest are:

(i) As with other ichneumonids with known early instars (Aubert 1959, Shaw & Wahl 1989), the cephalic sclerites develop gradually. The earliest of these *A. leucotrochi* instars (Fig. 12), presumably the first instar, lacks the stipital and labial sclerites, and these structures develop later independently (Figs 14 and 15).

(ii) The long fine mandibular denticles are found in all instars.

(iii) The short pleurostoma and well-developed inferior mandibular struts are present in the last in this series of the exuviae (Fig. 15), presumably the pentultimate instar, but the presence of this feature in earlier instars cannot be confirmed.

Aside from its head, the last larval instar is quite featureless, without prominent tubercles or lobes (Fig. 16).

Biological observations

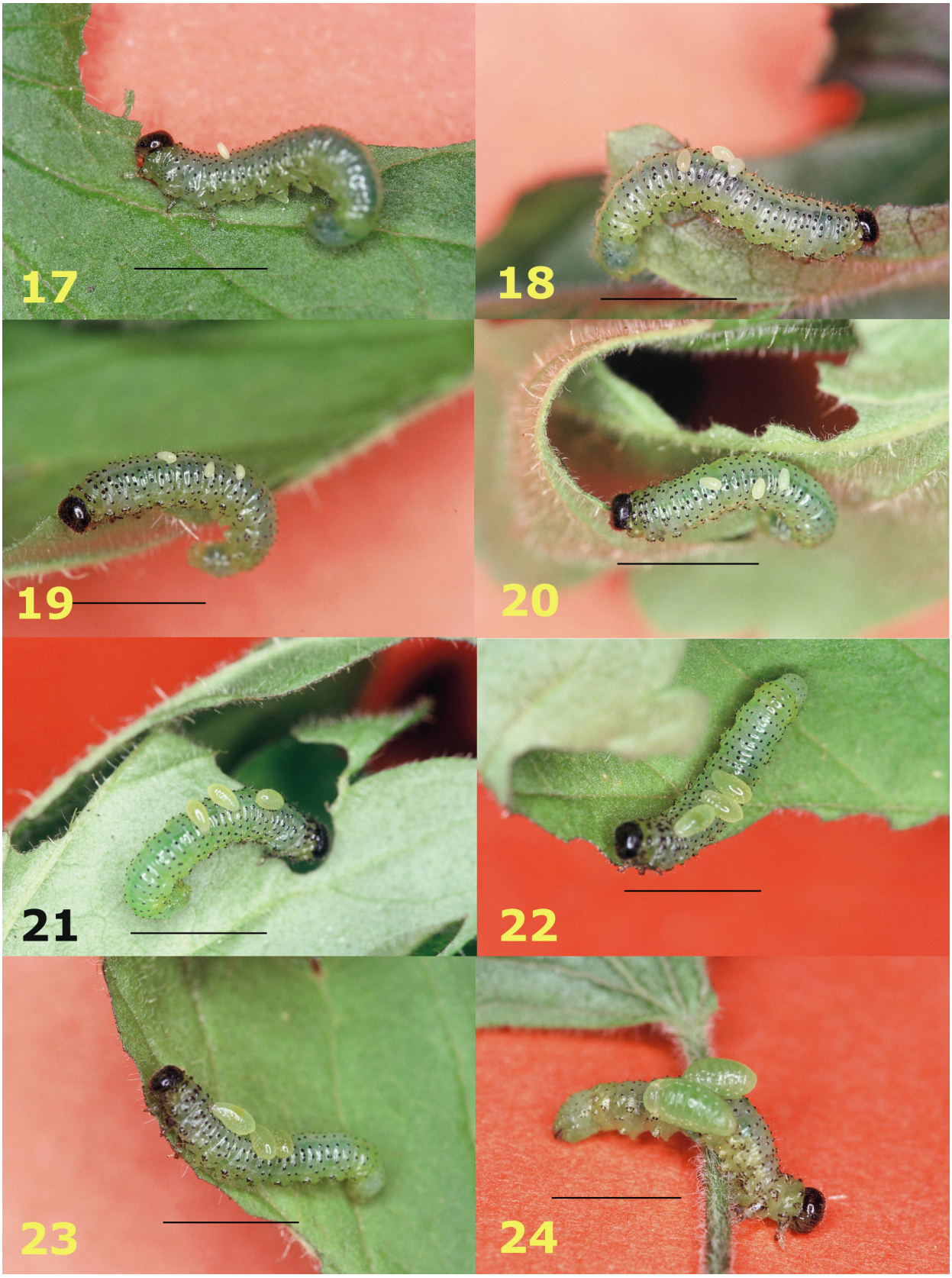
(Figs 17–30)

Gross phenology and host range. *Adelognathus leucotrochi* is strictly univoltine, all 67 adults reared from the wild emerging between 18 and 25 April 1992, the year following cocoon formation in late May or early June: these resulted from 77 parasitoid eggs/larvae on a total of 34 host larvae. Mortality under captive conditions was surprisingly low for a parasitoid needing to spend about 11 months in the cocoon stage. The parasitoid is exactly synchronized with its univoltine host, *Nematus leucotrochus*, but coincides with only the first of the two or three annual generations typically undergone by *N. ribesii*. Its apparent failure to develop on the first generation of *N. ribesii* in the wild, and the failures on this species under experimental conditions (see below), further encourages the view that it may be a strictly monophagous parasitoid of *N. leucotrochus*.

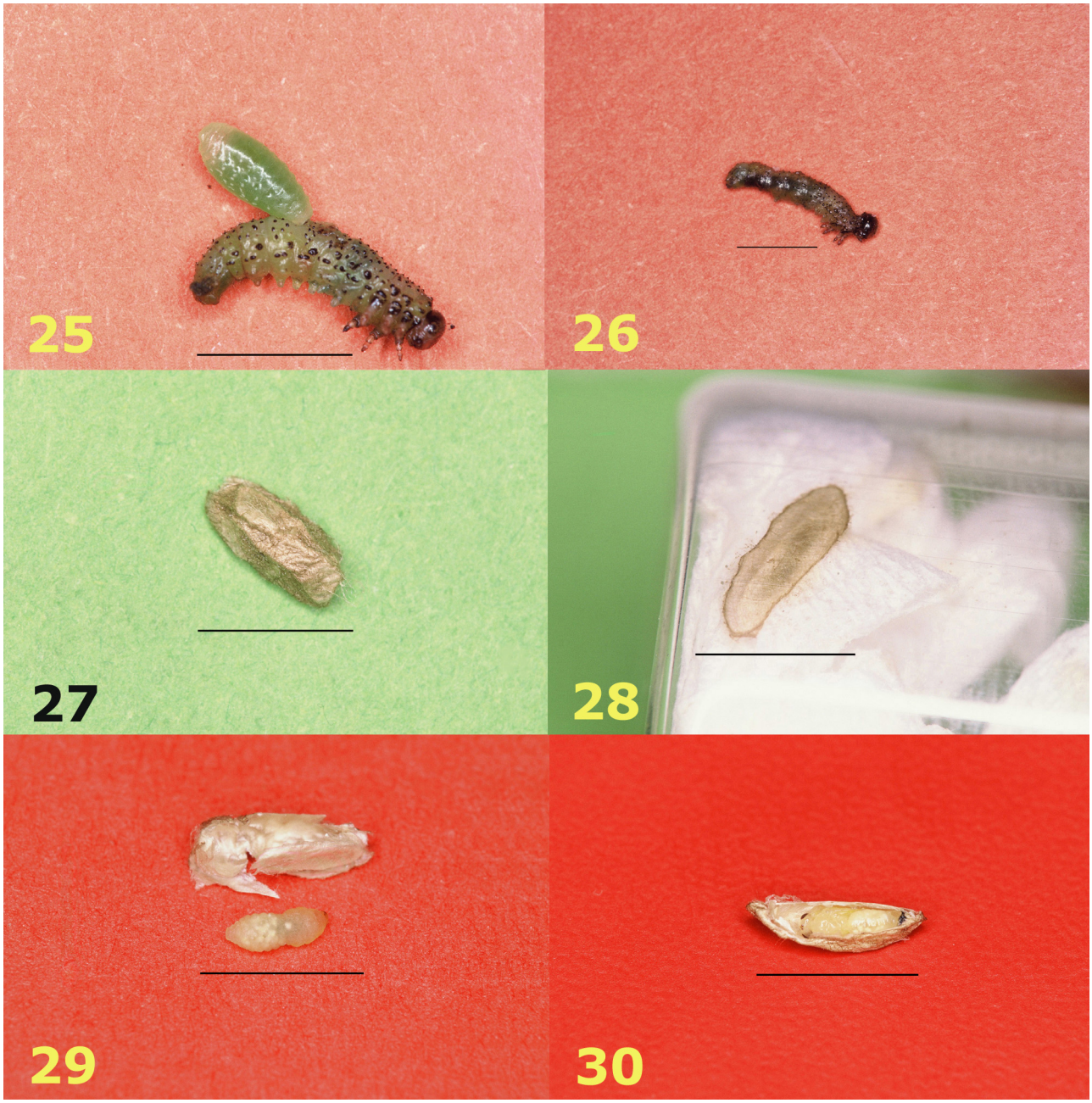
Brood size and sex ratio. Half of the *N. leucotrochus* larvae seen with *A. leucotrochi* eggs or larvae in the wild supported two parasitoids, with rather more supporting three than one (Table 1). A single host was seen to support 5 eggs (from which 2♀ 3♂ normally sized adult parasitoids resulted in due course), but this seems likely to have been due to attack by two different females. Brood sizes in culture were similar (Table 1). The sex ratio of adults reared from wild-collected parasitized hosts was 45♀:22♂. No disproportionate tendency for males to be placed in mixed sex broods was evident (i.e. the distribution of sexes across broods was apparently random, given a 2:1 preponderance of females).

TABLE 1. Brood sizes of *Adelognathus leucotrochi* **sp. n.** on larvae of *Nematus leucotrochus* (*N.l.*) and *Nematus ribesii* (*N.r.*). F = final instar larvae; P = penultimate instar larvae.

Number of *A. leucotrochi* per host	Wild larvae (*N.l.*, F)	Culture (*N.l.*, F)	Culture (*N.r.*, F)	Culture (*N.r*, P)
1	9	1	0	2
2	26	2	3	1
3	17	2	0	0
4	0	0	0	0
5	1	0	0	0



FIGURES 17–24. Development of *A. leucotrochi* **sp. n.** on final instar *N. leucotrochus* larvae. 17. Solitary egg, 2 days old; 18. 3 larvae, just after hatching; 19. 3 larvae, 3 hr after hatching (brood A); 20. 3 larvae, 9 hr after hatching (brood A); 21. 3 larvae, 24 hr after hatching (brood A, host still feeding); 22, 23. 3 larvae, 30 hr after hatching (brood A, host ceasing feeding but still mobile); 24. 2 larvae, 50 hr after hatching and 17 hr before leaving host (brood B). Scale line 5 mm.



FIGURES 25–30. Figs 25–26. Development of *A. leucotrochi* **sp. n.** on final instar *N. leucotrochus* larvae. 25. 1 larva, just before leaving host. 26. Host remains, just after being left by 2 larvae (brood B). Figs 27–30. Cocooned stages of *A. leucotrochi* **sp. n.** Figs 27, 28. Cocoon; 29. Prepupa removed from cocoon; 30. Pupa in opened cocoon. Scale line 5 mm.

Host-feeding. Several females showed no tendency to host-feed, even under conditions in which they eventually starved to death. Others, however, did so regularly. For host-feeding, the wound on the host was invariably made with the mandibles rather than the ovipositor. The following instances of host-feeding were observed: (i) Destructive, on small (second instar) *Nematus ribesii*. After repeatedly antennating the host, the female chewed through its abdominal integument, which took about 5 seconds, and retreated as the host suddenly jerked, whereupon a drop of haemolymph appeared at the wound. Having wiped her mouthparts on the substrate (cork), the female bit the host again, and a second (smaller) drop of haemolymph appeared at this new abdominal site. The female made no attempt to imbibe the haemolymph, but instead moved to the thorax of the dying host and chewed a large wound, feeding on the host's tissues and occasionally pulling strands clear of the host to do so. The female was positioned on the substrate, alongside the host, during this process. After 15 minutes the parasitoid retreated to groom (and cleaned her mouthparts by wiping them on the cork substrate) for a few minutes, then re-

approached the host and chewed another large wound near its caudal end where a similar bout of feeding lasted 20 minutes. By then the host was apparently dead, and the female was so engorged she was incapable of flight. A second female went through a similar cycle with an equivalent host, but fed much less extensively. (ii) Non-destructive, on penultimate instar *N. ribesii*. After antennating the host, which was well into its instar and almost certainly unsuitable for oviposition, the female subdued it by stinging, as though for oviposition (see below). After the host had become somewhat quiescent the female mounted it and bit through its integument, at four sites in fairly close succession, feeding a little at least at the last two (perhaps just on haemolymph). She continued to visit the host, and to antennate it, several times during a further 30 minute period, but neither host-fed nor seemed likely to oviposit. The host was then removed and, despite having lost a lot of fluid, it resumed feeding quite normally within an hour, though its subsequent moult was about 30 hours later than controls. A normal adult male resulted in due course. (iii) Concurrent, on final instar *N. leucotrochus*. One oviposition sequence, in which two eggs were laid, included a period of host-feeding from a small lateral wound towards the caudal end of the abdomen chewed immediately after the first egg was laid. The female remained mounted on the host and imbibed a quantity of haemolymph over 3 minutes, but there was no evident excess bleeding. She then laid another egg near the first one, at an anterior abdominal position on the host's dorsum. The host recovered full activity and the parasitoids developed normally. Concurrent host-feeding is probably unusual: it was not seen during either of the other two oviposition sequences fully witnessed, nor did the appearance of the females' metasomas suggest that it had happened in a further eight unobserved or only partially observed oviposition sequences.

Host acceptance and oviposition. Host larvae in all instars, as well as faeces, cast skins and leaves of *Ribes uva-crispa* partly eaten by the larvae of both *Nematus* species, aroused interest from prospecting females of *A. leucotrochi*, and indeed provoked investigations that sometimes spanned several minutes. On two occasions 2nd instar larvae of *N. ribesii* were used for host-feeding, but otherwise none of the investigations of hosts before the penultimate instar led to any serious attack. Hosts accepted for oviposition were almost always in their final instars, and the behaviour of the parasitoids clearly indicated that this was the preferred instar. However, penultimate instars of both *N. leucotrochus* and *N. ribesii* sometimes elicited stinging reactions from the parasitoid, and the only female (which was becoming aged by that time) to oviposit onto *N. ribesii* did so on three penultimate instar hosts, though less readily than on final instar ones. Because the progress of the host through its instar proved to be important in a way that was not evident at the outset, a fair test of acceptability of penultimate instar *N. leucotrochus* was not really made. The principle objective behind the exposures for oviposition was close observation of successful parasitization; therefore hosts were mostly offered optimally, sparingly and sequentially, and only a few female parasitoids were involved. Four parasitoid females between them laid eleven eggs on five final instar *N. leucotrochus* larvae; one of these females also laid a total of six eggs on three final instar *N. ribesii* and four eggs on three penultimate instar *N. ribesii* (Table 1). Brood sizes on penultimate instar *N. ribesii* were on average smaller than on final instar larvae, but the condition of the aging females as well as the small sample size precludes meaningful interpretation. When *N. ribesii* was the potential host a high proportion of eggs (5 out of 10) were detached as a result of the hosts subsequently rubbing against leaves or the walls of their container, most females failed to oviposit at all, and there was also a high level of mortality of developing larvae (only one of the 5 larvae that hatched on the host (a penultimate instar) attained full growth, but then failed to make a cocoon). None of these problems seriously beset the eggs laid on *N. leucotrochus*, only one of which was wiped off through the host's movements. However, as numbers were small, and as the females were already aging by the time *N. ribesii* became available for experiments, having previously had access to final instar *N. leucotrochus* which were by then no longer available, it is impossible to say for certain (although it is strongly suggested) that this reflects a greater suitability of *N. leucotrochus*. There was no consistent difference between the fates of eggs on final or penultimate instar *N. ribesii*.

When a host larva was encountered—which appeared to result only from chance contact—it was antennated. This caused the larva to lash its body violently and apparently in great alarm: holding on only with its true legs the larva made writhing and sweeping movements with its body, dorsoventrally coiling its abdomen apically and dashing it down onto the parasitoid's positions (or potential positions: the host often continued this behaviour long after a parasitoid had left or been driven away). Several times the sweeping and coiling motion succeeded in snatching up a parasitoid, which then freed itself only with difficulty and usually literally limped away for a lengthy groom following its mauling. On other occasions the parasitoid was batted off the leaf by these violent host reactions. Most often, however, the parasitoid either repeatedly withdrew sufficiently in time to dodge the blows or

else simply weathered the host's violence, and eventually leapt onto the host's dorsum inflicting a rapid sting as it did so. It appeared that the earlier antennation served only to recognize host suitability at the taxon level, for almost all hosts encountered received this sting and those that were well into their instar were sometimes then rejected without further investigation. The initial sting was not always sufficient to subdue the host into a more-or-less complete temporary paralysis: often the parasitoid withdrew for a minute or two and then remounted the host to sting it again, but sometimes the parasitoid kept a grip on the thrashing host until it subsided, with or without administering a second sting. In either case, the parasitoid usually withdrew a little and groomed during the host's greatest period of torpor, and returned to the host only as its activity started to increase again (ca 5–20 min). The association with the host rarely reached this point unless the host was within the first 6 hours or so of its instar—soon after having resumed feeding. Hosts further into their instar were rejected, apparently at least in part during the stinging process, and were then judged unacceptable by antennation if subsequently encountered in a semi-paralysed state. Occasionally, however, such hosts were stung again after a few hours, and again rejected.

As their activity was gradually returning, suitable hosts—i.e. those that had recently shed their skins—were mounted by the parasitoid, which antennated them carefully and finally adopted a more-or-less median dorsal position. The apex of the parasitoid's abdomen could be seen to pulse, presumably as gland reservoirs were being activated. The ovipositor was separated from its sheaths (which played no part in guiding it) and the host's integument was externally probed by the apical half of the ovipositor, repeatedly, until a favourable site was found. No consistency was discerned in this, except that eggs were generally laid near the middle of a segment, and positioned more or less dorsally and so as to avoid seta-bearing warts. Most eggs were laid on the middle third of the host's body, but a few were placed in more anterior positions. When a suitable site had been selected, the whole length of the ovipositor was pressed flat across the host integument; the parasitoid usually adopting a transverse stance on the host's dorsum, sliding its ovipositor transversely in a dorsolateral direction between lines of warts. The ovipositor in this position was moved gently back and forth for short distances, and by this means a liquid secretion could be seen being applied to the surface of the host. At no time during the oviposition process *per se* did the ovipositor pierce the host's integument. The genital opening of the parasitoid, below the base of the ovipositor, was practically in contact with the host's integument during this process, and the ovoid egg issued from it entirely free from the ovipositor to make contact with the end of the strip of adhesive put down by the ovipositor. The end of the egg that issued first and was attached to the host's integument became the caudal end of the parasitoid larva. Sometimes the parasitoid withdrew a little from the host between laying eggs on it, but when the bout was really over the female left the area very much more decisively. Between one and three eggs were laid by females during the oviposition bout, as found in the wild. Within this range the number appears to be in part a function of how active the host is becoming as it recovers from its paralysis: if the host's activity is too high the parasitoid is deterred from continuing to oviposit. Although females were often left with hosts on which they had just oviposited, they never increased the egg load once the first bout was over and the host was fully left. Surprisingly, in view of the need to find the host very early in its instar, female parasitoids showed no tendency to remain close to hosts in proecdysis, nor even to those whose cuticles were still relatively pale and soft immediately following ecdysis. In all, six ovipositions were closely observed under a low-power binocular microscope (involving three females), on four hosts (two final instar *N. leucotrochus*, and both final and penultimate instars of *N. ribesii*). In total, 21 eggs were laid by four females in captivity, one of the virgin females supplying 13 of them. Eggs could be detached very easily from hosts, even after the adhesive had set (in which case a wisp of white material, looking falsely rather like a pedicel, generally came away with it). They normally remained projecting from their caudal end until hatching (Fig. 17), but in some cases they become more or less pressed to the host's body (but possibly only as a result of high humidity under captive conditions: wild-collected eggs were all projecting).

Egg and larval development. The eggs hatched after 50–70 hours at 18–22°C, by which time the host larvae had consumed a quantity of vegetation and deposited on average around 160 faecal pellets (final instar *N. leucotrochus*). Eggs removed from the host hatched normally, but the resulting larvae appeared to be unable to establish themselves on either the original or a completely fresh host when placed on it. The parasitized hosts continued to feed for a little longer as the parasitoid grew, but deposited only about 70 more faecal pellets (final instar *N. leucotrochus*, as above) before ceasing to feed about 30–35 hours after egg hatch, and then remaining quiescent while the parasitoid larvae gradually consumed them over the next 35 or so hours (Figs 18–26, showing various stages of this process; see captions). Even though, in the case of hosts bearing only one parasitoid, considerable host tissue sometimes remained (Fig. 25), hosts were always dead by the time the larva was fully

grown (about 70 hours after egg hatch at 18–22°C, irrespective of the number of parasitoid larvae). The fully fed larvae then sometimes remained on the host for a period before they usually crawled, occasionally dropped, from the host, moving downwards and commencing cocoon construction in ground debris within the next few hours. The cocoons are parchment-like and those spun in captivity were irregularly spindle-shaped (Fig. 27) and usually flattened against a smooth surface (Fig. 28) with a double envelope construction. Emergence from the cocoon follows aestivation of the larva, hibernation as a prepupa, and pupation in early spring. The cocooned stages persist for a total of around 10–11 months. Cocoons were opened at intermediate dates and had contents as follows: (a) 22.viii.1992: actively mobile larva, gut contents clearly visible mediodorsally as a black line; (b) 1.xi.1992: prepupa, head capsule protruding, waist formed (about which it could waggle sideways), eyes only just discernible, gut contents showing dark a little posterior of waist, no defecation; (c) 11.i.1993 (Fig. 29): as (b) but with pale "urate" spots and less visible gut content; (d) 14.iii.1993 (Fig. 30): pupa, strongly developed eyes, underlying integument still largely pale, "urate" spots in dorsum of metasoma, faeces ejected.

One egg was observed just after the larvae commenced hatching. The process whereby the head end of the first instar larva, which initially would have been remote from the host's integument, engaged the host had unfortunately already taken place, and the structure was already lying flat on the host's body with the first instar larva about a third eclosed when it apparently commenced feeding (when the host suddenly twitched). Over the next 45 minutes the eggshell was gradually moved back and crumpled to form a pad to which the caudal end of the parasitoid remained fixed (Fig. 18). This pad remained, and was added to at successive ecdyses, throughout the feeding period of the parasitoid.

Effect of parasitoid venom on the host. Wild-collected hosts (*N. leucotrochus*) bearing eggs developed absolutely normally if the parasitoids were removed in the egg stage. Both sexes of the adult sawfly resulted from wild-collected host larvae treated in this way. Hosts that had been stung and partly paralysed in culture, including those from which eggs were detached, also developed normally with undetectable time lapses, except for a minority of hosts (*N. ribesii* in unsuitable condition for oviposition) that were actually killed by repeated bouts of stinging resulting from prolonged confinement with female parasitoids.

Discussion

Perhaps the most interesting observation was that the egg is laid from the genital opening, near the base of the ovipositor, and that no part of it travels along the ovipositor—a finding that reconciles the otherwise surprising observation (Kopelke 1987) that in *Adelognathus cubiceps* Roman, a parasitoid of *Pontania* species feeding in leaf galls on *Salix*, the adult parasitoid chews its way through the gall to oviposit on the host larva within. On the face of it, this mode of oviposition is very unusual for Ichneumonoidea, whose abilities to reach and parasitize deeply concealed hosts by virtue of their long ovipositors is well known and based on observations involving a large number of ectoparasitoid subfamilies, as is the use of the ovipositor for injecting one or more eggs into the hosts used by the endoparasitoid groups. However, the egg not passing down the ovipositor appears to be typical of all groups of koinobiont ectoparasitoid Ichneumonidae so far observed. It is universal in the large subfamily Tryphoninae (Kasparyan 1973) and almost certainly Lycorininae (Coronado-Rivera *et al.* 2004, Shaw 2004), in which only a non-embryonic part of the egg passes down the ovipositor with the bulk of the egg remaining external to it; and in the *Polysphincta* genus-group of the ephialtine Pimplinae the egg issues from the genital opening onto a pre-glued patch of the host integument (see Takasuka *et al.* 2009 for a brief review of known occurrence) without involving the ovipositor, much as in *Adelognathus*. These groups of Ichneumonidae are by no means all close relatives (Quicke *et al.* 2009, A.M.R. Bennett *et al.* in prep.). It has been suggested (Shaw 1995) that the braconid genus *Histeromerus* Wesmael (comprising the tribe Histeromerini, uncertainly placed in the subfamily Rhyssalinae) which, like *Adelognathus cubiceps,* chews its way to its hosts, in this case beetle larvae deeply concealed in wood, may also oviposit without the egg passing down the ovipositor, though in the case of *Histeromerus* direct observation of the process was not made. Although *Histeromerus* is an idiobiont, there is the all-important direct bodily contact with the host. It is noteworthy, too, that all aculeates whose ectophagous larvae develop on animal bodies also make direct bodily contact with the prey/host, and this presumably accounts for that group having similarly dispensed with the ovipositor as an egg-laying device, leaving only the stinging function that is widespread in Apocrita.

Precise and accurate observation of the mechanics of oviposition in the Hymenoptera has not been undertaken on a broad, phylogenetically informative front, but it may replay closer attention, in particular to reconcile the few scattered and apparently overlooked observations in the older literature, such as those by Morice (1912) who recorded that in *Phymatocera* Dahlbom, a tenthredinid sawfly, the egg was at first seen to issue externally from the genital opening and then to enter the base of the ovipositor (= saw) to be transported internally; and by Buckell (1928), who reported that eggs of the eulophid *Melittobia* Westwood issue ribbon-like from the ovipositor along its whole length, the bulk finally erupting from the basal third. It has also long been recorded that the eggs of certain elachertine eulophid koinobiont ectoparasitoids pass largely externally along a groove formed by the partial separation of the lower valves of the ovipositor (Gadd & Fonseka 1945, Gadd *et al.* 1946), to which more recently MacDonald & Caveney (2004) have added the observation that the egg of the related *Elachertus* Spinola also passes externally down the ovipositor. In all of these ectoparasitoid Eulophidae the adult is able to make direct bodily contact with the host.

It is also of interest that *Adelognathus* has valvilli within the "egg canal" area of the ovipositor (Quicke *et al.* 1992). In this case the valvilli are clearly not functionally involved with oviposition (cf. Rogers (1972), who suggested this function in the campoplegine ichneumonid *Venturia canescens* (Gravenhorst)), but presumably ensure the one way passage of secretions—in this case the venom causing temporary paralysis, and also the egg-holding glue that is spread from the ovipositor—as is believed to be their function in Aculeata (Mason 1983 unpublished: see Gauld & Bolton 1988, Quicke *et al.* 1992).

The use of mandibles for host-feeding by females is seen in a number of Ichneumonoidea, including the ichneumonid subfamily Tryphoninae (*Netelia* Gray: Shaw 2001). The more interesting observation on host-feeding is that different patterns were seen in *Adelognathus leucotrochi*, conforming to "non-concurrent destructive", "non-concurrent non-destructive", and "concurrent" modes in the terminology of Jervis & Kidd (1986). Some individuals lived apparently full lives (including successful ovipositions) on diluted honey alone. So much variation suggests that caution should be exercised over the interpretation of limited behavioural data: species may not be as easy to classify unequivocally as has been supposed. There seemed even to be variation in what the females ate, some apparently taking only haemolymph and others more substantial tissue. Not surprisingly in view of their lower nutritional requirements, the few males tested were not in the least interested in hosts (even though they could presumably have fed in the same way as females).

The venom used by *A. leucotrochi* was shown, conclusively, to have no role other than to subdue the host at the time of oviposition. This is similar to the situation in the tryphonine genus *Netelia* (Shaw 2001), in sharp contrast to the venoms used to control subsequent host development in taxa such as *Eulophus* Müller (Eulophidae) and *Clinocentrus* Haliday (Braconidae: Rogadinae) (Shaw 1981). In timing, oviposition attacks were always very early in the host instar, within a few hours of the host's resumption of feeding. This, and not a venom effect, was the means by which the female parasitoid ensured that the host would be overwhelmed, through development of the parasitoid larvae, before it could reach its next ecdysis. Although only final instar hosts were found to be parasitized in the wild, very few penultimate instar hosts were seen and the lack of parasitoids on them may not be meaningful. Indeed the experiments performed with a related but probably unsuitable host suggested that penultimate instar hosts might be used, though less enthusiastically, but this could neither be confirmed nor refuted in culture as a result of constraints that only became evident with hindsight. Against this is the possibility that, even if they were accepted, the period of the penultimate instar may prove to be too short, so that host ecdysis could take place before sufficient damage had been inflicted.

The original, though frustrated, purpose of embarking on this study was to test Rahoo & Luff's (1987) conclusion that in their species, *Adelognathus chrysopygus*, the host does not recover feeding activity. Three points seemed to suggest that their conclusion may be unsound: (i) They recorded that the parasitized hosts used to set up the parasitoid culture were collected in the wild from foliage of the foodplant. (ii) Their experimental conditions were such that captive host larvae were exposed to large numbers of female parasitoids, observation was not continuous, and it was not stated what kind (or consistency) of recovery from paralysis was seen. (iii) In the present experiments with *Adelognathus leucotrochi*, when interactions were allowed to result in multiple or repeat stingings, the hosts were less able to recover activity and, indeed, often died. However, more recently, F.D. Bennett (*in litt.* 1999) has made observations, at our request, on a population of *A. chrysopygus* parasitizing *P. pallipes* on his garden *Ribes* in the Isle of Man (British Isles) that fully corroborate the study by Rahoo & Luff (1987). Bennett found that the female *A. chrysopygus* (i) may spend hours near a prospective host larva before subduing it, initially

by stinging it at an apparently random position during a split-second attack, then (ii) she waits nearby for up to half an hour until the host becomes quiescent, when (iii) she revisits it and probes with the ovipositor, stinging the host on both sides behind the head (presumably into ganglia). Oviposition then proceeds onto the fully paralysed host, which does not subsequently recover sufficient activity to resume feeding, and more-or-less paralysed host larvae bearing eggs could be found in the wild on *Ribes* foliage. Bennett also reported (*in litt.*1999) that, as in *A. leucotrochi*, the egg issues direct from the genital opening without passing down the ovipositor in any sense, and that host-feeding was at wounds inflicted by the mandibles. It should be emphasized that the hosts of *A. leucotrochi* were often only stung once and that, when additional stinging was needed to temporarily subdue the host, there was no effort made to sting the host at a precise site. Subsequently a further species, *Adelognathus differmis* Holmgren, has been recorded by Heitland & Pschorn-Walcher (2005) to be an idiobiont, in this case as a parasitoid of the nematine sawfly *Platycampus luridiventris* (Fallén) feeding on *Alnus*. As in the case of *A. chrysopygus*, eggs were deposited on the ventral surface of the paralysed host, though it is reported that eggs of the other certainly known idiobiont, *A. cubiceps*, are placed in a lateral position (Kopelke 1987)—but in that case on a concealed host.

The four female specimens (in RSME) of the koinobiont recorded by Fitton *et al.* (1982) as *A. granulosus*, now correctly *A. chrysopygus*, have been re-examined in comparison with female specimens of *A. chrysopygus* deposited in RSME that resulted from the studies of both Rahoo & Luff (3♀) and Bennett (6♀) as parasitoids of *P. pallipes*. The material from *P. pallipes* is very constant, but the koinobiont series differs by having the lower gena next to the mandible mostly dark (strongly yellow in the material from *P. pallipes*) and the second segment of the hind tarsus a little less elongate. The moderately extensive non-reared European material present in RSME separates rather cleanly along these lines. Both segregates run only to *A. chrysopygus* in Kasparyan's (1990) key, but it appears likely that two different species are involved. The resolution of this is, however, beyond the scope of the present work.

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References

Aubert, J.F. (1959) Les hôtes et les stades immatures des ichneumonides *Pimpla* F., *Apechthis* Först. et *Itoplectis* Först. *Bulletin Biologique de la France et de la Belgique*, 93, 235–259.

Buckell, E.R. (1928) Notes on the life-history and habits of *Melittobia chalybii* Ashmead (Chalcidoidea: Elachertidae). *Pan-Pacific Entomologist*, 5, 14–22.

Coronado-Rivera, J., González-Herrera, A., Gauld, I.D. & Hanson, P. (2004) The enigmatic biology of the ichneumonid subfamily Lycorininae. *Journal of Hymenoptera Research*, 13, 223–227.

Evans, H.E. & West-Eberhard, M.J. (1970) *The Wasps*. University of Michigan Press, Ann Arbor, 265 pp.

Fitton, M.G., Gauld, I.D. & Shaw, M.R. (1982) The taxonomy and biology of the British Adelognathinae (Hymenoptera: Ichneumonidae). *Journal of Natural History*, 16, 275–283. http://dx.doi.org/10.1080/00222938200770221

Gadd, C.H. & Fonseka, W.T. (1945) *Neoplectrus maculatus* Ferrière—a predator and parasite of *Natada nararia* Mo. and other nettlegrubs. *Ceylon Journal of Science,* Section B (Zoology), 23, 9–18.

Gadd, C.H., Fonseka, W.T. & Ranaweera, D.J.W. (1946) Parasites of tea nettlegrubs with special reference to *Platyplectrus natadae* Ferrière and *Autoplectrus taprobanes* Gadd. *Ceylon Journal of Science,* Section B (Zoology), 23, 81–94.

Gauld, I.D. (1984) *An introduction to the Ichneumonidae of Australia*. British Museum (Natural History), London, 413 pp.

Gauld, I. & Bolton, B. (Eds.) (1988) *The Hymenptera*. British Museum (Natural History), London, 332 pp.

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

Jervis, M.A. & Kidd, N.A.C. (1986) Host-feeding strategies in hymenopterous parasitoids. *Biological Reviews*, 61, 395–434. http://dx.doi.org/10.1111/j.1469-185x.1986.tb00660.x

Kasparyan, D.R. (1973) Ichneumonidae (Subfamily Tryphoninae) Tribe Tryphonini. *Fauna of the USSR*, Hymenoptera, 3 (1),

1–414. [in Russian: translated 1981 Oxonian Press, New Delhi and distributed by E.J. Brill, Leiden, 1989, 414 pp.]
Kasparyan, D.R. (1990) Ichneumonidae. Subfamily Tryphoninae: Tribe Exenterinae [and] Subfamily Adelognathinae. *Fauna of USSR*, New series (No 141 Insecta Hymenoptera), 3 (2). 1–341. [in Russian, Nauka, Leningrad,]
Kopelke, J.-P. (1987) *Adelognathus cubiceps* Roman 1924 (Ichneumonidae: Adelognathinae)—ein ungewöhnlicher Parasitoid der gallenbildenden *Pontania*-Arten (Tenthredinidae: Nematinae). *Senkenbergiana biologica*, 67 (1986), 253–259.
MacDonald, K.E. & Caveney, S. (2004) Unusual life history characteristics of *Elachertus scutellatus* Howard (Hymenoptera: Eulophidae), a koinobiont ectoparasitoid. *Environmental Entomology*, 33, 227–233.
http://dx.doi.org/10.1603/0046-225x-33.2.227
Mason, W.R.M. (1983) The phylogeny of the Apocrita. (Unpublished lecture notes handed out at workshop on the taxonomy and biology of the parasitic Hymenoptera, Gainesville, Florida).
Mason, W.R.M. (1986) Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. *Proceedings of the Entomological Society of Washington*, 88, 1–7.
Morice, F.D. (1912) The president's address. *Transactions of the Entomological Society of London*, 59 (1911), cxvii–clv.
http://dx.doi.org/10.1111/j.1365-2311.1912.tb02772.x
Quicke, D.L.J., Fitton, M.G. & Ingram, S. (1992) Phylogenetic implications of the structure and distribution of ovipositor valvilli in the Hymenoptera (Insecta). *Journal of Natural History*, 26, 587–608.
http://dx.doi.org/10.1080/00222939200770361
Quicke, D.L.J., Laurenne, N.M., Fitton, M.G. & Broad, G.R. (2009) A thousand and one wasps: a 28S rDNA and morphological phylogeny of the Ichneumonidae (Insects: Hymenoptera) with an investigation in to alignment parameter space and elison. *Journal of Natural History*, 43, 1305–1421.
http://dx.doi.org/10.1080/00222930902807783
Rahoo, G.M. & Luff, M.L. (1987) The biology of *Adelognathus granulatus* Perkins (Hym., Ichneumonidae) a parasitoid of the small gooseberry sawfly *Pristiphora pallipes* (Lep.) (Hym., Tentredinidae). *Zeitschrift für angewandte Entomologie (Journal of Applied Entomology)*, 104, 480–484.
http://dx.doi.org/10.1111/j.1439-0418.1987.tb00549.x
Rogers, D. (1972) The ichneumon wasp *Venturia canescens*: oviposition and avoidance of superparasitism. *Entomologia experimentalis et applicata*, 15, 190–194.
http://dx.doi.org/10.1111/j.1570-7458.1972.tb00195.x
Shaw, M.R. (1981) Delayed inhibition of host development by the non-paralyzing venoms of parasitic wasps. *Journal of Invertebrate Pathology*, 37, 215–221.
http://dx.doi.org/10.1016/0022-2011(81)90078-1
Shaw, M.R. (1995) Observations on the adult behaviour and biology of *Histeromerus mystacinus* Wesmael (Hymenoptera: Braconidae). *Entomologist*, 114, 1–13.
Shaw, M.R. (1997) *Rearing parasitic Hymenoptera*. Amateur Entomologist's Society, Orpington, 46 pp.
Shaw, M.R. (2001) Interactions between adults of some species of *Netelia* Grey (Hymenoptera: Ichneumonidae: Tryphoninae) and their caterpillar hosts (Lepidoptera). *Journal of Hymenoptera Research*, 10, 101–111.
Shaw, M.R. (2004) Notes on the biology of *Lycorina triangulifera* Holmgren (Hymenoptera: Ichneumonidae: Lycorininae). *Journal of Hymenoptera Research*, 13, 302–308.
Shaw, M.R. & Wahl, D.B. (1989) The biology, egg and larvae of *Acaenitus dubitator* (Panzer) (Hymenoptera, Ichneumonidae: Acaenitinae). *Systematic Entomology*, 14, 117–125.
http://dx.doi.org/10.1111/j.1365-3113.1989.tb00269.x
Short, J.R.T. (1978) The final larval instars of the Ichneumonidae. *Memoirs of the American Entomological Institute*, 25, 1–508.
Sime, K.R. & Wahl, D.B. (1998) Taxonomy, mature larva, and biology of *Gnamptopelta obsidianator* (Hymenoptera: Ichneumonidae, Ichneumoninae). *Journal of Hymenoptera Research*, 7, 157–164.
Takasuka, K., Matsumoto, R. & Ohbayashi, N. (2009) Oviposition behaviour of *Zatypota albicoxa* (Hymenoptera, Ichneumonidae), an ectoparasitoid of *Achaearanea tepidariorum* (Araneae, Theridiidae). *Entomological Science*, 12, 232–237.
http://dx.doi.org/10.1111/j.1479-8298.2009.00338.x
Townes, H. (1944) A catalogue and reclassification of the Nearctic Ichneumonidae. Part 1. The subfamilies Ichneumoninae, Tryphoninae, Cryptinae, Phaeogeninae and Lissonotinae. *Memoirs of the American Entomological Society,* 11, 1–477.
Townes, H. (1969) The genera of Ichneumonidae, part 1. *Memoirs of the American Entomological Institute*, 11, 1–300.
Wahl, D.B. (1986) Larval structures of oxytorines and their significance for the higher classification of some Ichneumonidae (Hymenoptera). *Systematic Entomology*, 11, 117–127.
http://dx.doi.org/10.1111/j.1365-3113.1986.tb00171.x
Wahl, D.B. (1989) Further notes on preparation of exuviae of parasitic Hymenoptera. *Entomological News*, 100, 181–182.
Wahl, D.B. (1990) A review of the mature larvae of Diplazontinae, with notes on larvae of Acaenitinae and Orthocentrinae and proposal of two new subfamilies (Insecta: Hymenoptera, Ichneumonidae). *Journal of Natural History*, 24, 27–52.
http://dx.doi.org/10.1080/00222939000770041
Yu, D.S.K., van Achterberg, C. & Horstmann, K. (2012) Taxapad 2012, Ichneumonoidea 2011. Ottawa, Ontario, Canada. Database on flash-drive. Available from: http://www.taxapad.com (accessed 3 November 2014)