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The mature larva of *Heinrichiella obscura* (Gravenhorst) and a review of the larval morphology of Ophioninae [Hymentoptera: Ichneumonidae]

DAVID B. WAHL[1*] & MARK R. SHAW[2]
[1.] *Department of Biology, Utah State University, 5305 Old Main Hill Logan, UT 84332, USA*
[2.] *Honorary Research Associate, National Museums of Scotland Chambers Street, Edinburgh EH1 1JF, UK*
markshaw1945@gmail.com; https://orcid.org/0000-0002-6651-8801
**Corresponding author: dr_x@msn.com; https://orcid.org/0000-0002-2230-6639*

Abstract

The mature larva of the western Palaearctic ichneumonid *Heinrichiella obscura* (Gravenhorst) is described for the first time and the morphology is placed in the context of the genus being a basal lineage of the Ophioninae. The described larvae of Ophioninae are reviewed and a new larval diagnosis of the family is provided.

Key words: larval morphology, parasitoid, Geometridae, Ophioninae

Introduction

As discussed by Shaw & Voogd (2019), and see also below, it was concluded by Quicke *et al.* (2009) that *Heinrichiella* (as *Hellwigia*) *obscura* (Gravenhorst) represents a basal lineage within the ichneumonid subfamily Ophioninae. Through the chance first rearing of *H. obscura* from a species of *Horisme* Hübner (Lepidoptera: Geometridae) in the Netherlands (Shaw & Voogd 2019), its cocoon and hence mature larval remains became available for study. In this paper we describe the final instar larva of *H. obscura*, which has provoked a wider review, including discussion of previous findings, of the larval morphology of Ophioninae. *Heinrichiella obscura* represents a basal lineage of Ophioninae and we include it in a new diagnosis of ophionine larval characters.

Materials, methods, and terminology

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

DBWC	David B. Wahl collection: Providence, Utah, USA
NMNH	National Museum of Natural History, Smithsonian Institution: Washington, DC, USA
NMS	National Museums of Scotland (former Royal Scottish Museum): Edinburgh, United Kingdom

Methods of preparation are those of Wahl (1989). The measurements of the labial sclerite and mandible use the landmarks in Finlayson (1975: Figs 2 and 4). 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.

Almost all drawings of ichneumonid cephalic sclerites will involve elements of reconstruction, due to vagaries of the mounting process which can result in tears, skewing of sclerite positions, and 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. For this study, setae have been placed so as to accurately reproduce their position and number.

As will be discussed later in the paper, Short's drawings are often at odds with the original slide mounts in terms of proportions and details. His drawing methodology is unknown, although he may have used an ocular grid.

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The terminology for the cephalic sclerites of the mature larva is that of Wahl (1990) and Sime & Wahl (1998); the sclerites are illustrated in Figs 6–7 of Bennett *et al.* (2019). The spiracular terminology is that of Shaw *et al.* (2022). The area directly below the atrium is referred to as the *subatrial area.* It is typically finely annulated, in contrast to the following more coarsely annulated spiracular trachea. The closing apparatus is located within the subatrial area.

The mature larvae of *Heinrichiella obscura*

A. Diagnosis of the mature larvae of *Heinrichiella obscura*.

NMS; DBW 17.vi.2020a. Cephalic sclerites illustrated in Fig. 1. Cephalic structures generally moderately to strongly sclerotized. Epistomal suture unsclerotized. Labral sclerite absent; two clypeolabral plates present next to anterior clypeolabral margin. Stipital sclerite present, more or less horizontal; cardo present and lightly sclerotized. Pleurostoma lightly sclerotized, ventral portion barely discernable; posterior struts of inferior mandibular processes not connected by band; accessory pleurostomal area absent. Hypostoma long, moderately to strongly sclerotized, lateral end divided in two at posterior tentorial pit and ventral extension well-developed; accessory hypostomal area absent. Hypostomal spur present, about 3.2× as long as its basal width. Labial sclerite ovoid, about 1.5× as long as wide; ventral portion about 0.5× as long as labial sclerite length. Salivary orifice U-shaped. Prelabial sclerite present as crescent, connected to interior ventral margin of labial sclerite by moderately sclerotized projection of labial sclerite. Labial sclerite with 6 setae. Prelabial area with 29 setae. Maxillary and labial palpi each bearing two sensilla. Mandible apically strongly sclerotized and small; blade about 0.3× as long as full mandibular length, without fine denticles. Antenna without papillus. Spiracle unknown. Skin of postcephalic area not recovered; skin of cephalic area without reticulate furrows.

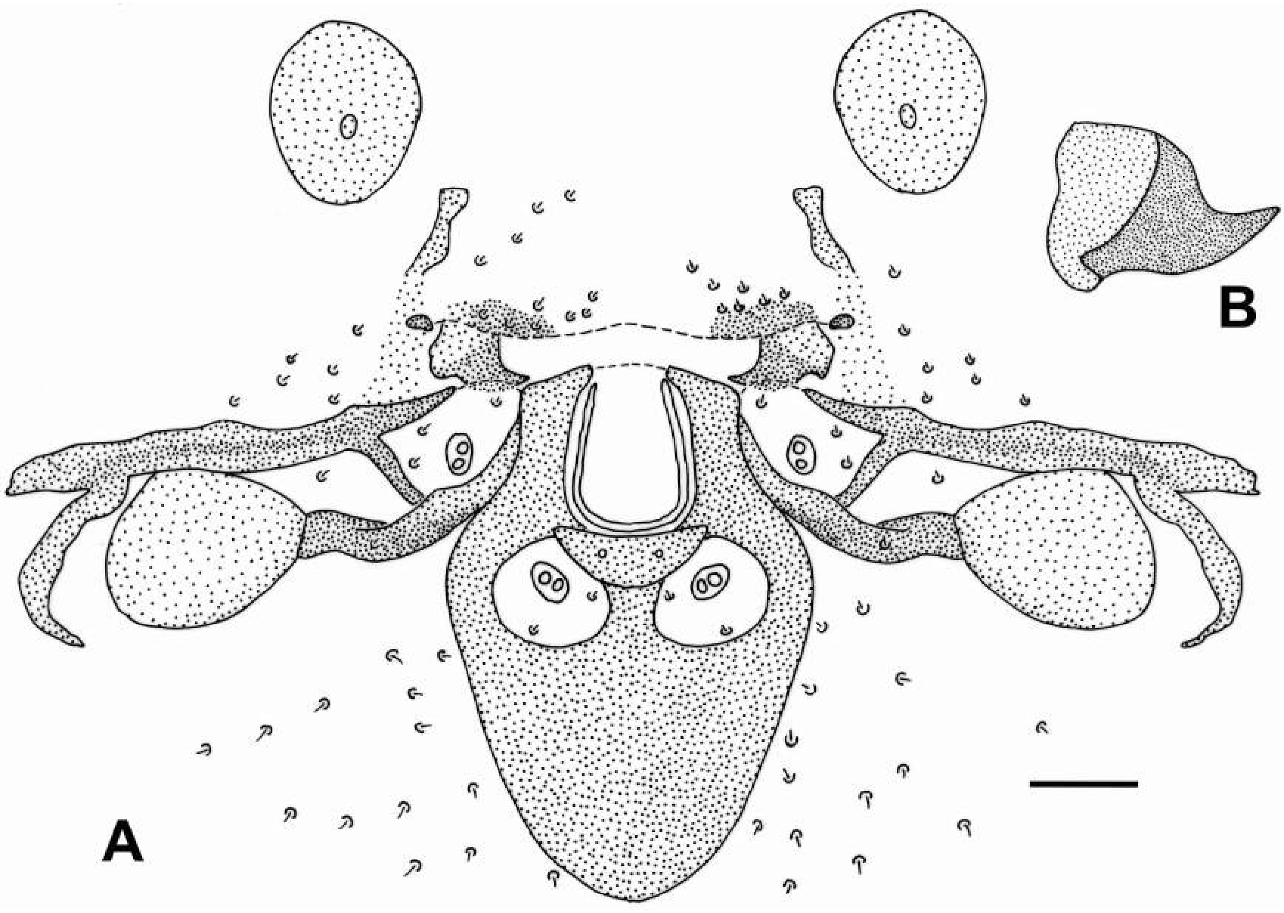


FIGURE 1. *Heinrichiella obscura* mature larva. A. cephalic sclerites, scale line 0.1 mm. B. mandible.

B. Comments

Using the larval subfamily keys of Short (1978) and Finlayson (1987), the cephalic characters of *H. obscura* place it as an ophionine—but neither author critically discussed ophionine larval characters in terms of subfamilial definition. Below is a discussion of the position of *H. obscura* within the subfamily, followed later by a re-examination of ophionine larvae and a new larval diagnosis for the subfamily.

C. The position of *Heinrichiella obscura* within Ophioninae

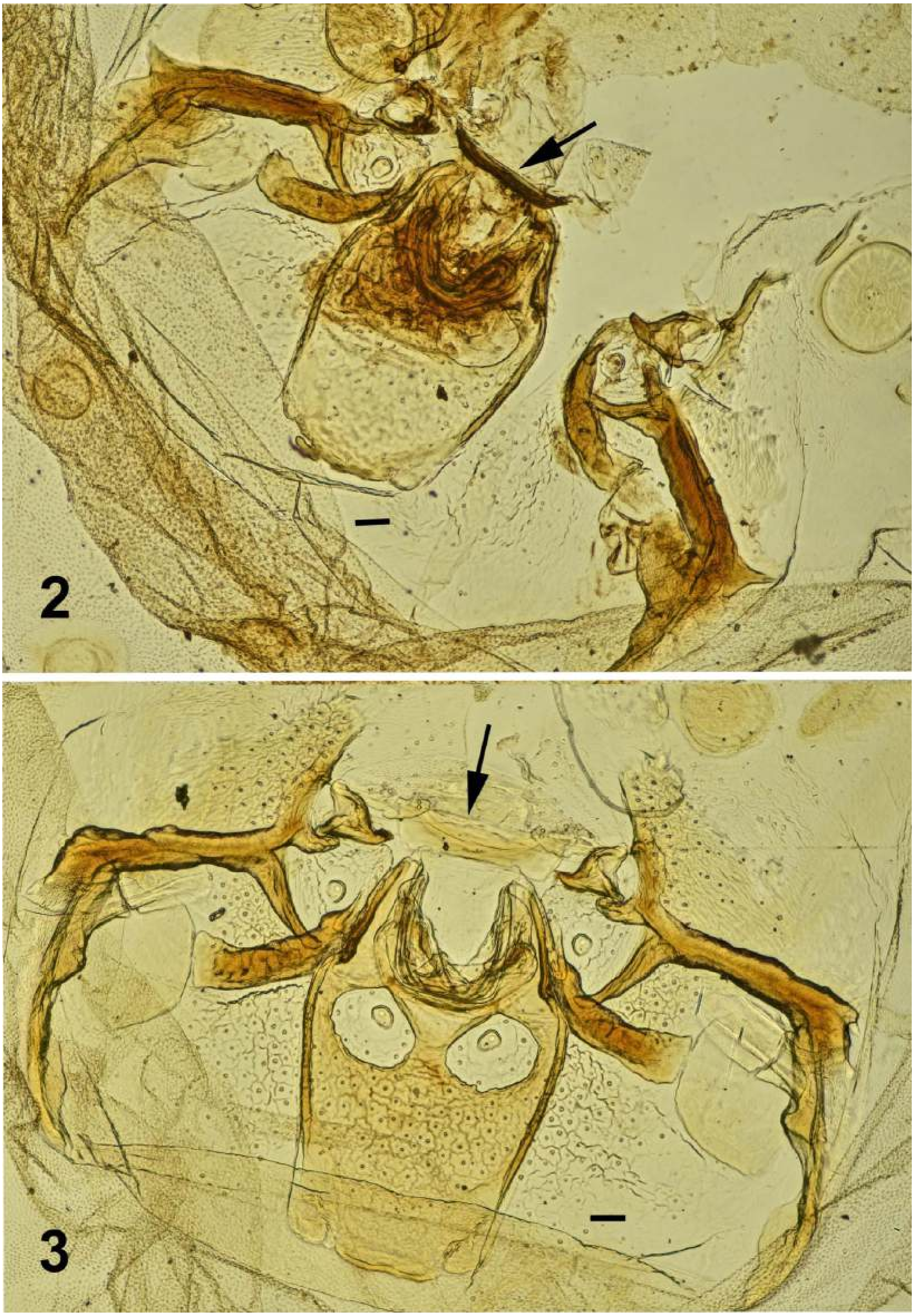
Miah (1998) and Miah & Bhuiya (2001) were the first to demonstrate that the Townesian placement of *obscura* in the Campopleginae was incorrect and that it, *elegans* Gravenhorst, and *Skiapus* Morley formed a clade that was the sister group to Ophioninae; note that at the time *elegans* and *obscura* were both placed in *Hellwigia*. These studies were based solely on morphology. Quicke *et al.* (2005) used simultaneous analysis of morphology and 28S rDNA to also recover *Hellwigia* and *Skiapus* within the Ophioninae, but: 1) they were not found to be sister groups, and 2) *obscura* (as *Hellwigia obscura*) was placed deep within the Ophioninae. Quicke and his colleagues continued simultaneous analysis of morphological and 28S rDNA with a much larger set of ichneumonid taxa (Quicke *et al.* 2009), resulting in *obscura* being the sister group to the rest of the Ophioninae (*Skiapus* was placed as the sister group to the Hybrizontinae). Rousse *et al.* (2016) used an assemblage of 74 ophionine species (representing 24 out of 32 genera) to investigate the internal phylogeny of the subfamily. Morphology, 28S rDNA, and the mitochondrial gene CO1 were used for a variety of analyses. Unfortunately, CO1 data for *obscura* were not available and so this species was included only in the 28S analysis: it was deeply embedded within the subfamily as the sister group to *Dicamptus* Szépligeti + *Enicospilus* Stephens/*Laticoleus* Townes. Rousse *et al.* (2016) treated it as *incertae sedis* within Ophioninae. Finally, Shaw & Voogd (2019) moved *obscura* to *Heinrichiella* based on wide morphological differences between *obscura* and *Hellwigia elegans*, and the relevance of these differences to the aforementioned phylogenetic studies of Ophioninae. We should note Behm (2020) and her curious contention that Shaw & Voogd removed *Heinrichiella* from the Ophioninae: this is an unfortunate misreading.

Perhaps the most authoritative treatment is the forthcoming study by Bernardo Santos and his collaborators, using genomic ultraconserved elements (UCE). Some 500 genera of Ichneumonidae were sequenced, including 12 genera of Ophioninae. The relationships are: *Skiapus* + (*Heinrichiella* + (remaining genera)). *Hellwigia elegans* was not included in the analysis.

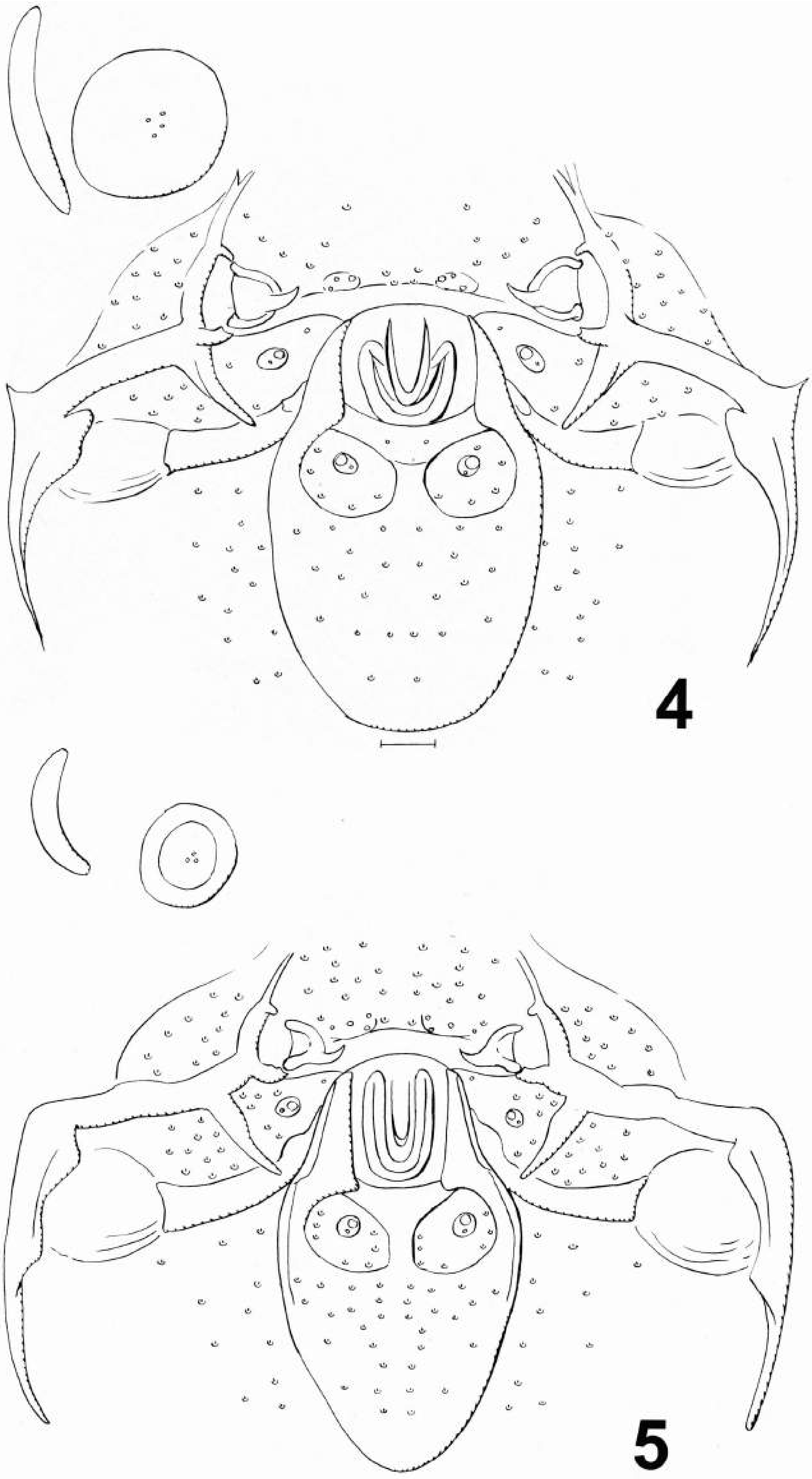
The mature larvae of Ophioninae

The primary sources of our knowledge of ophionine larvae are Short (1978), Gauld & Mitchell (1978, 1981), Gauld (1988), and Tang (1990). The actual slide mounts that we have examined are those of Short in the Smithsonian Institution (National Museum of Natural History), and unpublished ones prepared by DBW from Smithsonian Institution material and his private collection. Short's figures are the most complete, in terms of showing setae and aspects of skin details, followed by Gauld (1988); the other publications show only the sclerites in a schematic fashion. As alluded to above, Short's figures are often quite different from the actual slide, which can be appreciated by comparing the slide mounts of *Enicospilus glabratus* (Say) and *E. texanus* (Ashmead) (Figs 2–3) with Short's drawings (Figs 4–5). In many cases these differences are cosmetic and the relationships between sclerites and/or proportions are still more or less the same. In the two *Enicospilus* examples, the labial length to width is 1.5 in the drawings and 1.6 in the actual slides. The ventral margins of the labial sclerites, however, are quite different: strongly convex in the drawings but truncate in reality. The figure of *E. texanus* in Gauld (1988: Fig. 22) is more similar to the actual Short slide.

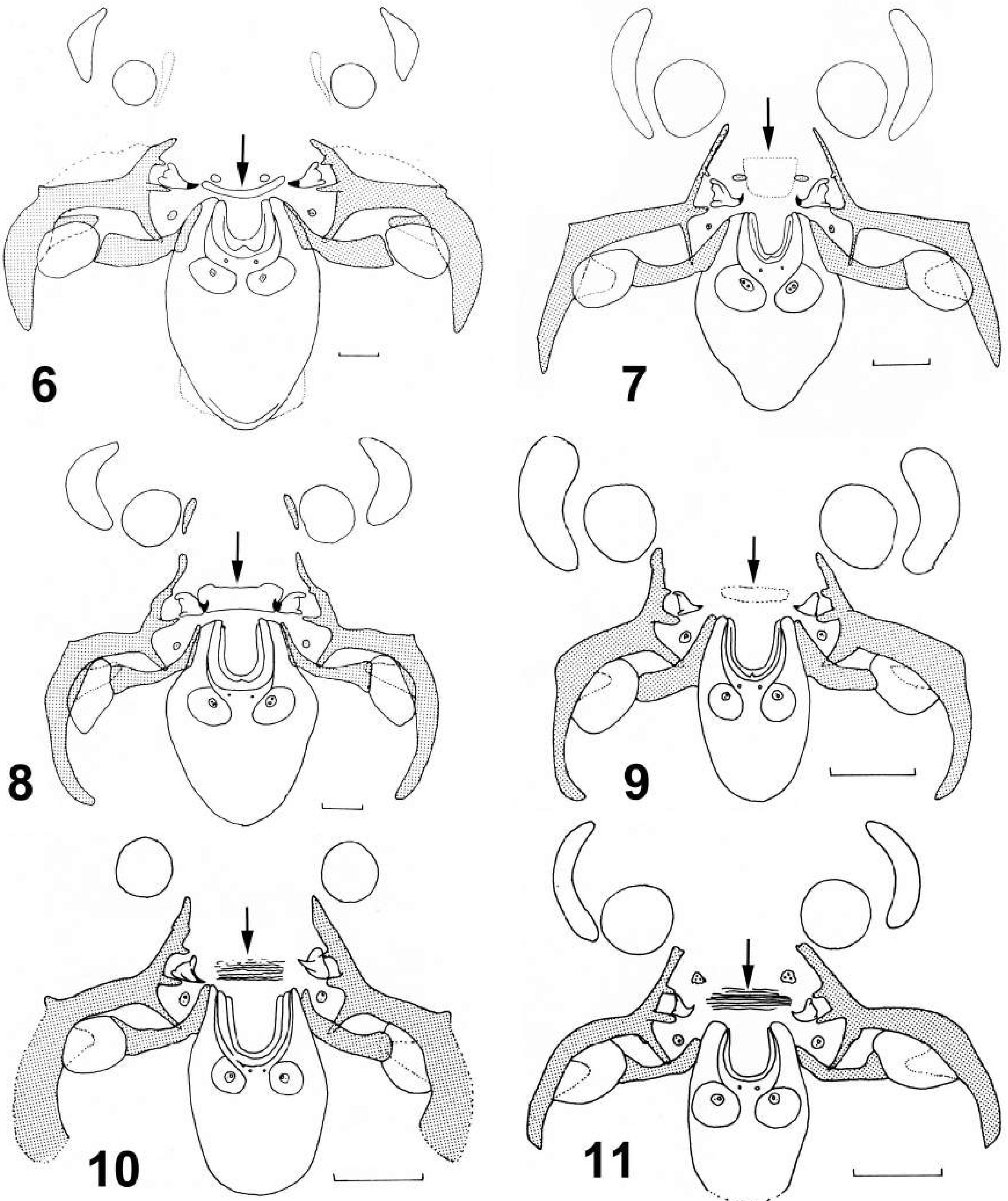
Gauld's larval illustrations show a sclerotized structure between the mandibles and dorsad the labial sclerite (Figs 6–11, arrowed) that varies in shape between linear and roughly quadrate; he refers to this as the 'sclerotized oral bar' (Gauld & Mitchell, 1978: Fig. 5). This is actually the suspensorial sclerite of the hypopharynx (Short, 1952: 37–38) and can be seen in the slide photographs of *E. glabratus*, *E. texanus* , and *Ophion* sp. in Figs 3, 4 and 12 (arrowed). It is present in all ichneumonids and its appearance depends on the vagaries of orientation and preservation. It is of no taxonomic value.



FIGURES 2–3. Cephalic sclerites of mature larvae. 2. *Enicospilus glabratus* [NMNH; J.R.T. Short slide #121]; 3. *E*. *texanus* mature larva [NMNH; J.R.T. Short slide #123]. Scale line 0.1 mm.



FIGURES 4–5. Cephalic sclerites of mature larvae from Short (1978). 4. *Enicospilus glabratus*; 5. *E. texanus*. Scale line 0.1 mm.



FIGURES 6–11. Cephalic sclerites of mature larvae from Gauld & Mitchell (1978). 6. *Enicospilus evanescens* Gauld & Mitchell; 7. *E. nugalis* (Schulz); 8. *E. equatus* Gauld & Mitchell; 9. *E. finalis* Gauld & Mitchell; 10. *E. ruidus* Gauld & Mitchell; 11. *E. sesamiae* Delobel. Scale line 0.1 mm.

Only Short (1978) and Gauld (1988) included setae in their drawings. Setae in the actual specimen are only roughly bilaterally symmetrical and numbers differ between the two halves of the head (Fig. 1). Short's drawings are rather impressionistic: he gave his best indication of the number of setae but also strove for placement symmetry.

We have counted the setae and used the ranges for the ophionine larval diagnosis but the reader should be aware of this problem.

In all, the above five references illustrate the larvae of 63 ophionine species:

Dicamptus Szépligeti: 1 sp.; *Enicospilus* Stephens: 54 spp.; *Euryophion* Cameron: 1 sp.; *Ophion* Fabricius: 14 spp.; *Thyreodon* Brullé: 1 sp. Adding *Heinrichiella* to this assemblage, and on the basis of the Santos *et al.* UCE findings and the combined CO1+28S trees (with or without morphology) from Rousse *et al.* (2016: Fig. 4), the known ophionine larvae provide a broad sampling of morphology across the subfamily. Based upon these illustrations and our examination of larval slides, we provide a new diagnosis of the mature larvae of Ophioninae:

Cephalic structures generally well-sclerotized. Epistomal suture unsclerotized. Labral sclerite absent; clypeolabral plates absent or present; when present, two lightly sclerotized plates present near anterior clypeolabral margin. Stipital sclerite present, more or less horizontal; cardo usually present and lightly sclerotized. Pleurostoma usually lightly to moderately sclerotized, sometimes partially unsclerotized; posterior struts of inferior mandibular processes not connected by band; accessory pleurostomal area occasionally present. Hypostoma long and well-sclerotized, lateral end divided in two at posterior tentorial pit, ventral division often well-developed and elongate, dorsal division short or absent; accessory hypostomal area occasionally present, fused with pleurostomal area to form broad, sheet-like structure. Hypostomal spur present, long to short, 2.1–3.8× as long as its basal width (more than half of species > 2.5×). Labial sclerite ovoid to elongate-ovoid and often with ventral margin truncate, 1.5–3.8× as long as wide (most 2.1–3.8×); ventral portion elongated, length of ventral portion 0.4–0.8× as long as labial sclerite total length; 18–80 setae present. Salivary orifice U-shaped. Prelabial sclerite present as transverse band or triangle, connected to interior ventral margin of labial sclerite by lightly sclerotized projection of labial sclerite. Labial sclerite usually with 22 or more setae (putative groundplan state in ichneumonids is 6 setae). Maxillary and labial palpi each bearing two sensilla. Mandible well-sclerotized, with base relatively large compared to blade (blade usually 0.3–0.5× as long as full length of mandible); blade without fine denticles. Antenna with papillus absent. Prelabium with 8–42 setae (usually ≥ 14). Spiracle with closing apparatus absent. Skin covered with small, bubble-like protuberances; setae present on thorax and abdomen, short and scattered. Cephalic area usually with reticulate furrows, particularly on labial sclerite (Figs 3 and 12).

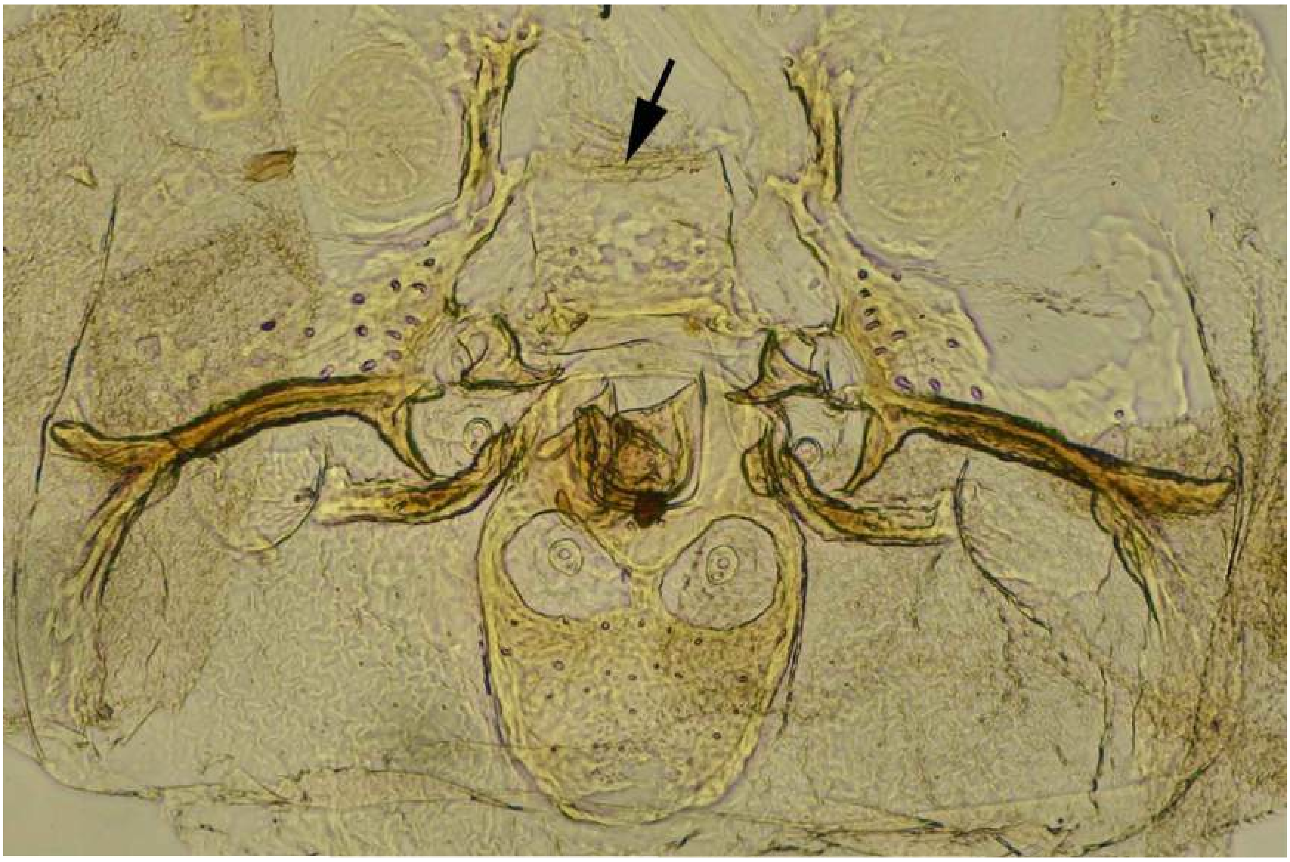


FIGURE 12. Cephalic sclerites of mature larvae of *Ophion* sp. [DBWC; DBW 1985.10.22a]. Scale line 0.1 mm.

Gauld (1985) stated "The cephalic capsules of the larvae of *Enicospilus*, *Dicamptus*, *Euryophion* and *Thyreodon* are clearly more specialized than those of *Ophion* in having a modified hypostoma (Short, 1978)." This was from Short (1978) and his key to separate Ophionini and Enicospilini. Ophionini were partly defined as often having the dorsal and ventral hypostomal extensions less that the ventral extension of the hypostoma, while the Enicospilini usually had at least one of the extensions ≥ the stipital sclerite's length. Re-examination of Short's NMNH specimens depicted with a short ventral extension (*O. flavidus* Brullé and *O. idoneus* Viereck) revealed the extensions to actually be the same length as the stipital sclerite. An undetermined *Ophion* species from Florida (DBWC; DBW 1985.x.22a) has the ventral extension length > the stipital sclerite length (Fig. 12). Pending re-examination of all Short *Ophion* slides, it would appear that this character is not useful for defining groups of ophionine genera.

Most ophionine larval characters are those of the higher Ophioniformes (as used by Bennett *et al.* (2019): Anomaloninae, Campopleginae, Cremastinae, Ophioninae). In these, plesiomorphies include the lack of a labral sclerite and antennal papillus, a U-shaped salivary orifice, a circular to ovoid labial sclerite, a triangular to Y-shaped prelabial sclerite, a mandibular blade that lacks denticles, and a spiracle with the closing apparatus absent (Shaw *et al.* 2022).

We believe the following character combination to be unique to the subfamily:

1) Presence of a sclerotized cardo. The lightly sclerotized cardo is expressed sporadically throughout Ichneumonidae: Pimplinae (most Ephialtini and in *Theronia* Holmgren s.l.), Xoridinae, Phygadeuontinae and Cryptinae (a few species), Banchini, Cremastinae (a few species) and Tersilochinae (a few species).

2) Ovoid to elongate-ovoid labial sclerite, with the ventral section 0.4–0.8× as long as the length of the labial sclerite. To our knowledge, the only ophioniform genera that have a similar labial sclerite are in the Campopleginae: *Dusona* Cameron, *Scirtetes* Hartig, *Synetaeris* Förster, *Transosema* Förster, and *Venturia* Schrottky (Short, 1978; Finlayson, 1975). The Santos *et al*. UCE study (in prep.) has these genera scattered throughout the campopleginae and the labial condition does not appear to be part of its groundplan.

3) A rather small mandible with an upcurved blade that is noticeably smaller than found in the other higher Ophioniformes. This is difficult to quantify; perusal of the larval illustrations of these groups in Short (1978) will demonstrate our characterization.

4) Prelabium with 8–42 setae (usually ≥ 14). The ground plan condition for ichneumonid larvae appears to be four setae.

Two widely distributed characters, reticulate furrows in the cephalic area and numerous (18–80) setae on the labial sclerite, are not found in *Heinrichiella*. These might be characters that define the next clade beyond *Skiapus* and *Heinrichiella* (as in the UCE study) or their absence could be autapomorphic for *Heinrichiella*—only the discovery of the larva of *Skiapus* can resolve this question.

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