

Notes on the biology, morphology and generic placement of “*Hellwigia*” *obscura* Gravenhorst (Hymenoptera: Ichneumonidae, Ophioninae)

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Abstract

The ophionine ichneumonid known as *Hellwigia obscura* has been reared for the first time, from larvae of *Horisme* sp. (Lepidoptera: Geometridae) feeding on *Clematis vitalba* in The Netherlands. The cocoon and the parasitoid's means of emergence are figured, as are some features of the adult. On a balance of morphological grounds, including some already discussed in the literature, it is proposed that “*Hellwigia*” *obscura* should be excluded from *Hellwigia* and instead be ascribed to the genus *Heinrichiella* **stat. rev.** as *Heinrichiella obscura* **comb. n.** Reasons for this change as well as for preferring this generic name to *Prothellwigia* Brues are given

Keywords

Hellwigia elegans, *Heinrichiella*, *Prothellwigia*, *Horisme*, cocoon, emergence, systematics

Introduction

Gravenhorst (1823) erected the genus *Hellwigia* to receive two new nominal species, *H. elegans* Gravenhorst (Fig. 1) and *H. obscura* Gravenhorst (Fig. 2). Holmgren (1859) subsequently fixed *H. elegans* as the type species of the genus *Hellwigia*. Further generic



Figure 1. *Hellwigia elegans*, female habitus (Cyprus).



Figure 2. *Heinrichiella obscura* comb. n., female habitus (France).

names introduced for this group were *Diamon* Gistel, 1848 (invalid replacement name for *Hellwigia* Gravenhorst), *Protohellwigia* Brues, 1910 for a new Miocene (or, according to Townes (1966, 1970), perhaps Lower Oligocene) fossil species *P. obsoleta* Brues from the Florissant deposits of Colorado, and *Heinrichiella* Hedwig, 1949 to receive the new nominal species *Heinrichiella monstrosa* Hedwig which was treated by Townes (1966) as a junior synonym of *Hellwigia obscura*. Townes et al. (1965) synonymised both *Protohellwigia* and *Heinrichiella* under *Hellwigia*, though Townes (1970) later stated that the only species certainly included in the genus *Hellwigia* is the type species *H. elegans*. Horstmann (1969, 1981) had concluded more emphatically that two genera were involved and placed the nominal *Hellwigia obscura* in the genus *Protohellwigia*,

following Townes (1966) who pointed out some shortcomings in the description of Brues (1910) and indicated that *Protohellwigia* was a closer fit to *Hellwigia obscura* than to *Hellwigia elegans*. Townes’ (1966) treatment of *Heinrichiella monstrosa* as a junior subjective synonym of *Hellwigia obscura* has been followed by subsequent authors (e.g. Horstmann 1969, 1981, as *Protohellwigia*).

No biological information has been published for any of these taxa, and the main purpose of this paper is to present rearing data, and some limited additional biological information, for the nominal *Hellwigia obscura*. The most appropriate generic name for the species is also considered. The two species described in the genus *Hellwigia* are not only highly divergent from all other Ichneumonidae, but also from each other (Miah 1998). Even though genera are arbitrary human constructs, the issue of whether they should be treated as congeners is sharpened by the assertion that *Hellwigia* per se is a basal member of the Ophioninae (Quicke et al. 2009, Rousse et al. 2016), as the crucial molecular genetic evidence for this was based on the nominal *H. obscura*, not on the type species of the genus, *H. elegans*, which may or may not be closely related.

Methods

Most photographs were taken as single images down one arm of a Wild M5A stereomicroscope with x20 eyepieces using a Canon PowerShot 110. The exceptions (Figs 1, 5) were taken as multiple images by a Canon SLR EOS 5DSR with 65mm macro lens mounted on a copy stand with an automated Z-stepper then stacked using Helicon Focus software version 6.6.1.

Results

Rearing data for the nominal *Hellwigia obscura*

One of us (JV) collected larvae of *Horisme* spp (Lepidoptera: Geometridae) by beating climbing growth of *Clematis vitalba* at a relatively open calcareous site, Eyserbos, with abundant hedgerows and woodland edge at Eys, Limburg, The Netherlands on 7.ix.2017. Altogether 50 *Horisme* spp larvae were collected, in various stages of growth. Three were easily determined as *H. vitalbata* (Dennis & Schiffermüller) and all produced moths. The remaining 47 comprised both *H. radicularia* (de La Harpe) and *H. tersata* (Dennis and Schiffermüller), but the two species could not be separated in the larval stage and they were reared together. Five of these were parasitized by a gregarious species of Microgastrinae (Braconidae) [the adults escaped but by analogy with rearings from *Horisme* species conducted in England by MRS they were probably *Cotesia nothus* (Marshall)] before becoming fully grown. One succumbed to a species of *Netelia* (*Netelia*) (Ichneumonidae: Tryphoninae) that may be undescribed (Broad and Shaw in prep.), and three prepupae produced banded cocoons that autumn from

which adults of the nominal *Hellwigia obscura* emerged during the period 1–7.v.2018 and were passed on to MRS for determination and incorporation into the NMS collection. In addition, five adult *Horisme radicularia* and 33 *Horisme tersata* were reared, the adults of both species emerging between late April and the first half of May 2018. Despite the numerical superiority of *H. tersata* over *H. radicularia* in the host sample from which the specimens were reared, it is unfortunately not yet possible to ascertain which, if not both, of these species serves as host, but it is hoped that this can be pursued in years to come.

The tough cocoon (Fig. 3) is rather stout, ovoid, dark brown with a central paler girdle, and superficially moderately similar to many *Ophion* species except that the girdle is somewhat more raised. The adult emerges in a rather tortuous way that seems quite inefficient: by piercing the cocoon near its capital extremity and cutting a continuous spiral, in the three cases seen of four to six circumferences, to detach a single long, narrow, coiled strip (Fig. 4) to leave a sharply defined terminal opening (Fig. 3) large enough for the adult to emerge.

Generic placement

Horstmann (1969) maintained, and Townes (1970) implied but did not act upon, that the two recent species originally described by Gravenhorst (1823) in the genus *Hellwigia* might best be treated as belonging to separate genera. This is contrary to their present placement both in *Hellwigia* that follows Townes (1970).

At least part of the reason for their still being treated as congeners may stem from the morphological phylogenetic analysis of genera of Campopleginae, which at that time included *Hellwigia*, conducted by Miah (1998; see also a less explicit account by Miah and Bhuiya 2001). In that analysis the two nominal *Hellwigia* species were scored separately, although most campoplegine genera were scored at the generic level, often following examination of multiple species in the genus. The character set was devised to explore the subfamily Campopleginae, and on that basis it is not surprising that the two *Hellwigia* species clustered as sisters (based on 12 supposed synapomorphies, but then diverging with 9 autapomorphies for *H. elegans* and 8 for *H. obscura*). *Hellwigia* + the highly diverging *Skiapus* (23 autapomorphies) emerged as a clade based on 18 synapomorphies, with a clade (*Hellwigia* + *Skiapus*) + Ophioninae (based on a notional taxon) supported by four synapomorphies. It is admittedly difficult to envisage any other taxon as a sister to either of these highly autapomorphic nominal *Hellwigia* species but, in our opinion, their purported sister-group relationship was neither adequately tested nor established by the analysis of Miah (1998), as most of the taxa and characters selected for analysis were inappropriate for that purpose and in some cases characters seem to have been incorrectly scored. Further, even if a sister-species relationship were true, the large number of characters by which the two species differ rather far exceeds generic differences currently applied in ichneumonid taxonomy.



Figure 3. *Heinrichiella obscura* comb. n., vacated cocoon (Netherlands).



Figure 4. *Heinrichiella obscura* comb. n., spiral cut from apex of cocoon (Netherlands).

Similarities between the species include:

- (i) The highly distinctive distal part of the fore wing venation (Figs 5, 6).
- (ii) The widely exposed, sclerotised and coarsely sculptured labrum (Figs 7, 8).
- (iii) The lack of clear separation between clypeus and face (Figs 7, 8).
- (iv) Ovipositor structure (Figs 1, 2).



Figure 5. *Hellwigia elegans*, wings (Cyprus).



Figure 6. *Heinrichiella obscura* comb. n., wings (Netherlands) [combined from two images].

Differences, probably including both autapomorphies and plesiomorphies (un-assessed here) judged to be important by Horstmann (1969), restated or expanded, are:

- (i) The antenna with terminal segments greatly broadening to make the antenna very strongly clubbed in *H. elegans* (true of both sexes but particularly pronounced in the male, Fig. 9) but unmodified in nominal *H. obscura* (in the male, Fig. 10, flagellar segments are just very slightly broadened post-centrally but then the antenna slightly attenuates apically).
- (ii) A genal bridge closing the ventral hypostomal space of *H. obscura* but absent in *H. elegans* (this difference is illustrated by Horstmann 1969: Figs 1, 2). Miah (1998)



Figure 7. *Hellwigia elegans*, mandibles, labrum, clypeus (Turkey).



Figure 8. *Heinrichiella obscura* comb. n., mandibles, labrum, clypeus (Netherlands).



Figure 9. *Hellwigia elegans*, male antenna (Israel).



Figure 10. *Heinrichiella obscura* comb. n., apical half of male antenna (Netherlands).

scores the junction of the hypostomal and genal carinae far distant from the mandible in *H. obscura* as a separate autapomorphy.

- (iii) The epicnemial carina borders the anterior of the mesosternum in an unbroken straight line in *H. elegans*, while it is centrally produced to form a projection towards the space between the fore coxae in *H. obscura*.
- (iv) The apically flared hind leg tarsomeres of *H. elegans*, unmodified in *H. obscura*.
- (v) The sclerotised part of sternite I of the metasoma reaching only to the anterior end of the postpetiole (i.e. level with the spiracles) in *H. elegans* but beyond the middle of the postpetiole (i.e. well past the spiracles) in *H. obscura*.
- (vi) The hypandrium (male subgenital plate) which is greatly expanded and ventrally flat (also bearing strong spines) in *H. elegans* (Fig. 11), but unmodified (small, with a v-shaped cross section as in the preceding sternite, and lacking spines) in *H. obscura* (Fig. 12).



Figure 11. *Hellwigia elegans*, apex of male metasoma (Turkey).



Figure 12. *Heinrichiella obscura* comb. n., apex of male metasoma (Netherlands).

On these grounds Horstmann (1969) placed the two species in different genera, as *Hellwigia elegans* and *Protohellwigia obscura*. Additional characters, including those given by Miah (1998), to support the generic separation are:

- (vii) The mandibles are bidentate with a fairly slender elongate upper tooth and a much shorter lower one in *H. elegans* (Fig. 7) but almost quadridentate with the upper tooth bearing a produced flange below, somewhat like some *Ophion* species, and the lower tooth clearly divided in *H. obscura* (Fig. 8). This difference seems not to have been previously noted.

- (viii) The claws, which are untoothed in both taxa, are evenly curved in *H. elegans* (Fig. 13) but bent at right angles in *H. obscura* (Fig. 14) (Miah 1998). Gauld (1985) regarded a sinuous pectinal comb on tarsal claws as an autapomorphy for Ophioninae.
- (ix) The lack of a spurious vein extending distally close to the wing margin from the posterodistal corner of the first subdiscal cell in *H. elegans* (Fig. 5) but its presence in *H. obscura* (Figs 6, 15). The presence of this vein has been regarded as a strong autapomorphy for Ophioninae (cf. Gauld 1985, Broad et al. 2018), and the difference between the two species seems not to have been previously noted.
- (x) The lack of basal hamuli in *H. elegans* (Fig. 5), but their presence in *H. obscura* (Fig. 6) (Miah 1998).

Many of the features in which the two species differ are illustrated but without comment by Choi et al. (2011).

Despite the difficulty of associating either of the nominal *Hellwigia* species with any other taxon, we assert that the very wide morphological separation between them are strong grounds for us to assign the nominal *Hellwigia obscura* to a different genus. It differs from the fossil *Protohellwigia obsoleta* in wing venation (figured by Brues (1910), although Townes (1966) states that the venation in the area of the pterostigma of *P. obsoleta* had been misinterpreted and is closer to that of the nominal *Hellwigia obscura*). In addition, many of the important characters of the nominal *Hellwigia obscura* (e.g. mandible, claws, hypostomal bridge) were simply not visible for assessment in the fossils. On balance it seems inappropriate to place the nominal *Hellwigia obscura* in *Protohellwigia* Brues even though Horstmann (1969, 1981) did so. An alternative and more clearly suitable generic name is already in existence: *Heinrichiella* Hedwig, 1949 (nec Tereshkin 2000) has its type species widely considered to be a subjective junior synonym of the nominal *Hellwigia obscura*, and it is logical therefore to resurrect as a valid genus *Heinrichiella* stat. rev. and transfer this species to become *Heinrichiella obscura* (Gravenhorst), comb. n.



Figure 13. *Hellwigia elegans*, hind claw (Israel).



Figure 14. *Heinrichiella obscura* comb. n., hind claw (Netherlands).



Figure 15. *Heinrichiella obscura* comb. n., part of fore wing with spurious vein (France).

Discussion

Biology

The way in which the adult *Heinrichiella obscura* comb. n. leaves its cocoon differs markedly from the emergence habits seen in European species of *Ophion* (a chewed hole involving the removal of many irregular bits) and *Enicospilus* (a neatly detached cap). Although not directly observed, the unusual means of eclosion of adult *Heinrichiella obscura* comb. n. must relate closely to the structure of its mandibles. In a few groups of Ichneumonidae (e.g. Diplazontinae, and the genus *Banchus* (Banchinae), cf. Broad et al. 2018) the upper tooth is similarly divided and the mandibles are used to

cut successive short strips from the cocoon (or host puparium in the case of Diplazoninae) as the adult emerges. In all 48 vacated cocoons of *Banchus* in the NMS collection, comprising four species, an oval emergence hole just below the cocoon apex had clearly been made by detaching successive short strips. Rotheray (1981) records and diagrammatically figures the cutting of a succession of discrete semi-circular strips of the syrphid host's puparium by the emerging adult diplazontine *Diplazon pectoratorius* (Thunberg), remarking that the outcome was similar in 12 other diplazontine species he had under less intensive observation. However, the cutting of a single continuous concentrically circular strip from the cocoon in the process of adult eclosion seen in *Heinrichiella obscura* comb. n. is, as far as we are aware, not recorded elsewhere in the Ichneumonidae. It seems probable that the divided lower tooth of *Heinrichiella obscura* comb. n., absent in both *Banchus* and Diplazoninae, may play an important part in this.

A series of female *Heinrichiella obscura* comb. n. in NMS collected by Malaise trap in France (Dordogne) by RR Askew in September (two in the period 1–21.ix.1999 and one 16–30.ix.2000), in conjunction with the present rearings in May, suggests that, like its *Horisme* hosts, *H. obscura* is at least bivoltine, and the late dates also indicate that it probably attacks final instar host larvae, as appears to be typical for European Ophioninae (cf. Broad et al. 2015).

Given the suggested basal position within Ophioninae of *Heinrichiella obscura* comb. n. (see below) it is of some significance that its host is a geometrid, a host group that may be ancestral for Ophioninae given also that it is used by a few species of apparently relatively basal *Ophion* in Europe (Schwarzfeld et al. 2015), although many species of both the putatively more derived *Ophion*- and *Enicospilus*-groups are, as far as is known, particularly associated with Noctuoidea (see also Rousse et al. 2016).

Commentary on the higher classification of *Hellwigia sensu* Gravenhorst

Although Townes (1970) continued his earlier (Townes et al. 1965) treatment of *Hellwigia* s. l. + *Skiapus* as an isolated tribe Hellwigiini within Campopleginae, Horstmann (1969) had recognised the distinctiveness of *Hellwigia sensu* Gravenhorst (1823) plus Brues' (1910) fossil taxon *Protohellwigia*, and proposed subfamily status for the group as Hellwigiinae (he did not consider *Skiapus*). More recent work, depending heavily on molecular genetics, but engaging also Miah's (1998) morphological study of Campopleginae s. l., has placed "*Hellwigia*" within the Ophioninae (Quicke et al. 2005; see also Belshaw and Quicke 2002) with the eventual conclusion that it represents a basal lineage of that subfamily, but without an identifiable tribal placement (Quicke et al. 2009, Rousse et al. 2016). However, the representative of "*Hellwigia*" on which these 21st century molecular genetic analyses were entirely based was not the type species *Hellwigia elegans* (Fig. 1) but rather the much more superficially and structurally ophionine-like *Heinrichiella obscura* comb. n. (Fig. 2), which also appears (Quicke et al. 2005, 2009) to be the sole "*Hellwigia*" in the morphological analysis. That, then,

is the putatively basal ophionine, leaving the interesting phylogenetic position of the more autapomorphic *Hellwigia elegans* open as, apart from considerable similarities in wing venation (Figs 5, 6, 15; but note the perhaps telling absence of the fore wing spurious vein in *H. elegans* and its lack of basal hamuli in the hind wing, as well as differences in vein 1cu-a), there seems little to strongly support their being very closely related—though future work may demonstrate that they are. For now, though, there is good reason to isolate the species believed to be a basal ophionine from the name *Hellwigia*.

It would, of course, be extremely interesting to discover the host of *Hellwigia elegans* (apart from capture data, nothing is known of its biology beyond its ovipositor structure (Fig. 1) suggesting that it should be a koinobiont endoparasitoid), but the probably easier exercise of investigating its phylogenetic position via molecular genetics will be more crucial for clarifying whether or not it, like *Heinrichiella obscura* comb. n., can be considered to be a basal ophionine.

It is relevant to point out that the caption for Fig. 14c in Quicke et al. (2009), showing the venom gland and reservoir intima, refers to *Hellwigia elegans*, but this is almost certainly a lapsus for *H. obscura*, because (i) the French female specimen (cited in appendices) loaned from the National Museums of Scotland (NMS) collection for DNA was returned with most of the metasoma snapped off, (ii) there is otherwise no mention of *H. elegans*, including in the lists of material examined, in the above interconnected series of 21st century papers, and (iii) the female specimens in the Natural History Museum, London, where the work was partly based, have intact metasomas.

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