



Research article

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The British species of *Enicospilus* (Hymenoptera: Ichneumonidae: Ophioninae)

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Abstract. The nine British and Irish species of *Enicospilus* are revised, mapped and an identification key provided. One species, *Enicospilus myricae* sp. nov., is described as new; *Enicospilus merdarius* (Gravenhorst, 1829) is a senior synonym of *E. tournieri* (Vollenhoven, 1879) syn. nov.; the only available name for *E. merdarius* auctt. is *Enicospilus adustus* (Haller, 1885) stat. rev., and a neotype is designated for *Ophion adustus* Haller, 1885. *Enicospilus cerebrator* Aubert, 1969 and *E. repentinus* (Holmgren, 1860) are newly recorded from Britain. Some host data are available for eight of the nine species.

Key words. Taxonomy, parasitoid, nocturnal, host, new species.

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Introduction

Enicospilus Stephens, 1835 is a distinctive genus of primarily nocturnal parasitoids of relatively large Lepidoptera larvae. The genus is immensely species-rich in the tropics (Gauld & Mitchell 1978, 1981; Gauld 1988) but only small numbers of species are found in north temperate regions. However, despite the small number of species in Britain (only five were listed by Fitton *et al.* 1978), there has been much confusion over the limits and identities of these species. Under the auspices of the first author's nocturnal Ichneumonoidea recording scheme (<http://nocturnalichs.myspecies.info/>), we have gathered host, distribution and phenology data on the British *Enicospilus* species and clarified some taxonomic issues. Considering the size of the fauna, now increased to nine species, the taxonomic problems were surprisingly extensive; these issues are summarised in the “Taxonomy of British *Enicospilus*” section below.

In Europe, *Enicospilus* species are easily recognised as the only Ophioninae with strongly narrowed mandibles, a large glabrous patch in the fore wing discosubmarginal cell (frequently with detached sclerites) and fore wing vein *Rs+2r* partly thickened (see Fig. 1). *Stauropoctonus bombycivorus*

(Gravenhorst, 1829), which might be confused with *Enicospilus* because they share twisted mandibles, lacks the occipital carina and has fore wing vein $Rs+2r$ abruptly angled near its origin on the pterostigma, in both respects unlike *Enicospilus*. Ophioninae can be recognised by the discosubmarginal cell extending beyond fore wing vein $2m-cu$ and the presence of a dark line (a “spurious vein”) ventrally in the fore wing anal cell (Fig. 1). In common with many other nocturnal ichneumonoids, they are large (or very large), almost always mostly testaceous, with large eyes and ocelli, and long antennae.

Hosts of the British *Enicospilus* fall into two categories: Lasiocampidae, in the case of the very large *E. inflexus* (Ratzeburg, 1844) and *E. undulatus* (Gravenhorst, 1829), and low-feeding noctuids for the remaining species (although *E. repentinus* (Holmgren, 1860) has not been reared). As with most Ophioninae that have been reared, the host is probably attacked as a late instar larva, and habitually killed as it prepares to pupate; however, few details of the biology of British *Enicospilus* have been studied. All but one British species seem to be univoltine, with rather narrow periods of flight activity. There are too few data to establish the limits of host ranges, but at least two species (*E. merdarius* (Gravenhorst, 1829) and *E. undulatus*) have very restricted host ranges that may reflect limited diversity of hosts in their particular habitats. Habitat specialisation may be important in limiting distribution, rather than absolute host taxon specificity. For example, *E. myricae* sp. nov. has only been collected in *Myrica* Linnaeus, 1753 bogs and wet woodland, where it has been reared from a common and widespread host caterpillar which is present in a range of habitats. Interestingly, females of all British species (at least, those with good sample sizes) far outnumber males in light trap samples, whereas both sexes are reared

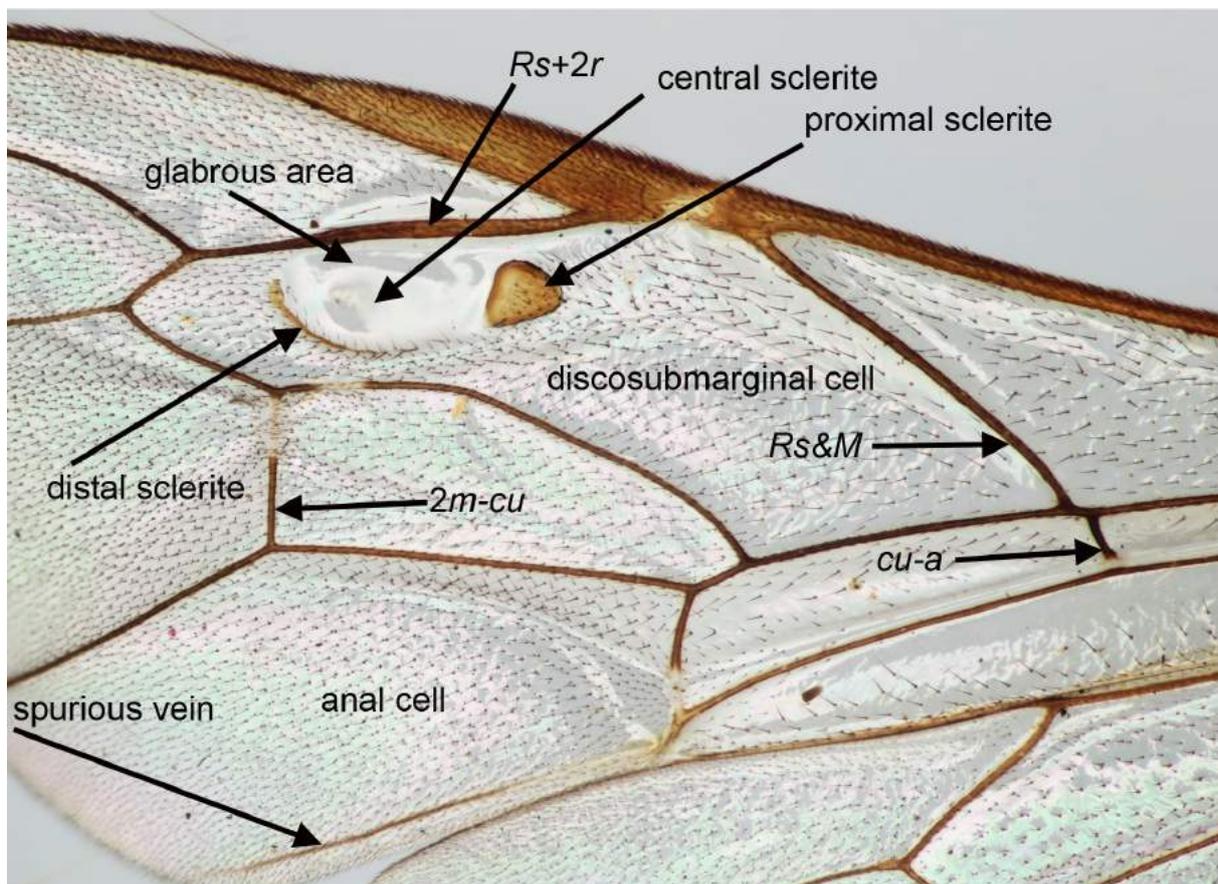


Fig. 1. Fore wing of *Enicospilus merdarius* (Gravenhorst, 1829) with sclerites, veins and cells referred to in the text labelled.

in approximately equal numbers. While this might largely reflect the difference in longevity between the sexes, males may also be rather less nocturnal, as is certainly the case with some other ophionines, such as *Eremotylus marginatus* (Jurine, 1807) and *Ophion ventricosus* (Gravenhorst, 1829), males of which can be collected flying around trees in the daytime, whereas females are more strictly nocturnal (pers. obs.), although in these two cases the species are partly patterned with black.

Material and methods

The distribution maps for Britain and Ireland are based on far more records than any preceding maps dealing with the British parasitoid fauna; nevertheless, the ranges shown are very incomplete and suffer from several sources of recording bias. Hopefully these maps, which illustrate broad patterns of distribution, will encourage entomologists to record *Enicospilus* species in the many blank areas, so that eventually it will be possible to map changes in distributions over time. Maps were plotted using DMAP, developed by Alan Morton (www.dmap.co.uk). The main sources of specimen data are the collections of the Natural History Museum, London (BMNH), and the National Museums of Scotland, Edinburgh (NMS). These collections have been considerably enriched in recent years by donations from many entomologists, particularly moth trappers who have kindly sent their ichneumonoid catches to us. For the geographic spread of their light trap network, the Rothamsted light trap survey (see Woiwod & Harrington 1994; Harrington & Woiwod 2007) was a particularly important source of specimens; we include records from Rothamsted light traps on the Channel Islands, although these are not faunistically a part of Britain. We have also seen specimens from several private collections as well as the collections of British Entomological and Natural History Society, World Museum Liverpool and Cambridge University Museum of Zoology. Following other papers cataloguing the collections of NMS (e.g. Schwarz & Shaw 1998, which explains the rationale), we give the numbers of specimens present in NMS (and BMNH in this case) and list the Vice Counties from which they have been recorded (from all data), as well as cataloguing non-British material in NMS. The full British dataset is available via the National Biodiversity Network Gateway (<https://data.nbn.org.uk/>), the full dataset via the Natural History Museum's Data Portal (<http://data.nhm.ac.uk/>) and in Supplementary File. "Unsexed" usually refers to specimens which now lack the metasoma.

Morphological terminology follows Gauld (1988, 1991). Sclerites and some wing veins and cells are labelled on Fig. 1; wing length is measured as the greatest distance from the apex of the tegula to the wing tip. Gauld & Mitchell (1978, 1981) and Gauld (1988) employ several wing venation indices but, as these are uninformative in distinguishing closely related British species, they are not detailed here. We include ranges of number of flagellar segments, based on British specimens, rather than the total antennal segments, i.e. we exclude the scape and pedicel from the counts. Photographs were taken using a Canon EOS 450D digital camera attached to a Leica MZ12, with images stacked using Helicon Focus. Whole insect photos were taken by Harry Taylor at the BMNH.

Collection abbreviations

- BENHS = British Entomological and Natural History Society, Dinton Pastures, Earley, UK (Peter Chandler)
 BMNH = Natural History Museum, London, UK
 ETHZ = Entomological Collection, Eidgenössische Technische Hochschule Zürich, Switzerland (Andreas Müller)
 MZLS = Musée de Zoologie, Lausanne, Switzerland (Anne Freitag)
 NMS = National Museums of Scotland, UK
 OUMNH = Oxford University Museum of Natural History, UK (James Hogan)
 WML = World Museum Liverpool, UK
 ZIN = Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia (Andrey Khalaim)

Results

Class Hexapoda Blainville, 1816
Order Hymenoptera Linnaeus, 1758
Superfamily Ichneumonoidea Latreille, 1802
Family Ichneumonidae Latreille, 1802
Subfamily Ophioninae Shuckard, 1840

Genus *Enicospilus* Stephens, 1835

Taxonomy of British *Enicospilus*

There have been no identification keys to British *Enicospilus* since Gauld's (1973) key and update (Gauld 1974). Unfortunately, these works contained significant misidentifications and lumped some species together. This is not surprising, as Gauld had access to rather small sample sizes and relied heavily on the number and shape of fore wing sclerites, which are of great use in *Enicospilus* taxonomy but are, unfortunately, almost identical in five of the British species. There has never been a thorough revision of European *Enicospilus* species, which is reflected in some frequent misunderstandings regarding species names and limits, although Viktorov's (1957) key is very useful. In Britain, *Enicospilus* can be divided into three species-groups, based on the sclerites in the fore wing discosubmarginal cell: *E. inflexus* and *E. undulatus* entirely lack sclerites (and have been referred to the genus *Allocamptus* Förster, 1869 by some authors); *E. merdarius* (= *Ophion tournieri* Vollenhoven, 1879) and *E. repentinus* have a well-defined proximal sclerite, with the central sclerite either absent or transparent; and the remaining five species (the *ramidulus* species-group) have both the proximal and central sclerites pigmented. There has been confusion in each of these species-groups, although it is within the *ramidulus* complex that species are most morphologically similar and hence have been persistently confused.

Gauld (1974) separated the very similar *E. inflexus* (Ratzeburg, 1844) and *E. undulatus* (Gravenhorst, 1829), that he had previously (Gauld 1973) confounded under the name *E. undulatus*; and Viktorov (1957) had already separated *E. repentinus* and *E. tournieri* (but see below), which Gauld (1973) had confused by identifying British specimens of *E. merdarius* (= *tourneri*) as *E. repentinus*, whereas the true *E. repentinus* had not been found in Britain at that time.

Most authors have recognised *E. merdarius* auctt. (but see below) as a separate species from *E. ramidulus* (Linnaeus, 1758). Although Gauld (1973) stated that there are specimens intermediate between *E. merdarius* auctt. and *E. ramidulus*, and treated them as synonymous, we have seen no such specimens, and Gauld & Mitchell (1981) subsequently recognised the two as separate species. Differences in opinion regarding the status of *E. merdarius* auctt. and *E. ramidulus* have arisen because, although *E. ramidulus* has a distinctive identifying feature in the black-tipped metasoma, *E. merdarius* auctt. has no distinctive features, which we now know is because it is in fact a complex of similar species. Aubert (1966) had already separated off *E. cerebrator* Aubert, 1966, a species subsequently recognised in several European countries but never sought in Britain. We have found *E. cerebrator* to be widespread in Britain and also discovered a third species in this complex, which had no name, described here as *E. myricae* sp. nov. The identity of *E. merdarius* has been ignored since Fitton (1984) designated a lectotype; both before and after Fitton's (1984) lectotype designation, the name *E. merdarius* has frequently been applied to any Palaearctic *Enicospilus* with two discrete fore wing sclerites and lacking either a dark tip to the metasoma or dark patches on the mesosoma (i.e., excluding *E. ramidulus* and *E. combustus* (Gravenhorst, 1829)). Unfortunately, the lectotype of *Ophion merdarius* Gravenhorst, 1829 is the species that has generally been called *E. tournieri*, with the result that literature citations for *E. merdarius* do not refer to the species properly called *E. merdarius* (quite apart from the many misidentifications). Remarkably, for such a widespread species, there is only one potential synonym of

E. merdarius auctt. (i.e., the larger species in the complex that includes *E. cerebrator* and *E. myricae* sp. nov.), namely *Ophion adustus* Haller, 1885, synonymised under *E. merdarius* by Horstmann (1997) on the basis of the brief original description, which could equally refer to *E. cerebrator* or *E. myricae* sp. nov. The type specimen(s) of *O. adustus* cannot be found so, to stabilise usage of the name, we designate a neotype for *O. adustus*, meaning that the widespread, large species, usually referred to as *Enicospilus merdarius*, should be called *Enicospilus adustus*. Allowing for his misconception of *E. merdarius*, this is in line with the synonymy proposed by Horstmann (1997).

Identification key to British and Irish species of *Enicospilus*

1. Fore wing lacking sclerites in glabrous area of discosubmarginal cell (Fig. 2A); large species, wing length *c.* 20 mm 2
 - Fore wing with at least one discrete sclerite in discosubmarginal cell (Fig. 2B–D); smaller species, wing length < 15 mm..... 3

2. Head posteriorly, in dorsal view, not expanded laterally beyond the eyes; ocelli touching or almost touching eye; antennal socket separated from inner margin of eye by not more than a third socket diameter (Fig. 3A) *Enicospilus inflexus* (Ratzeburg, 1844)
 - Head posteriorly, in dorsal view, expanded so that head is wider than its width at the eyes; ocelli distinctly separated from eye by about 0.2 × diameter of ocellus; antennal socket separated from inner margin of eye by about half socket diameter (Fig. 3B).....
 *Enicospilus undulatus* (Gravenhorst, 1829)

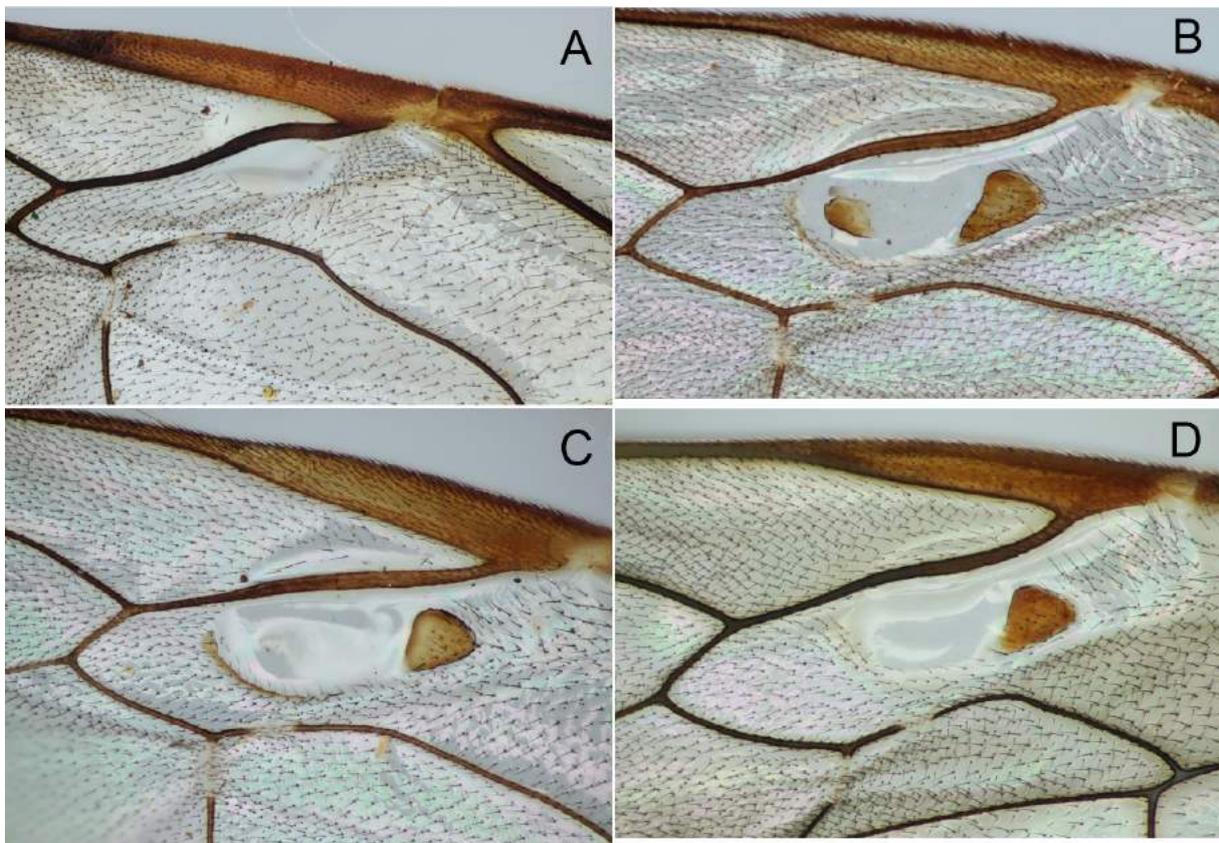


Fig. 2. Fore wing discosubmarginal cell. **A.** *Enicospilus undulatus* (Gravenhorst, 1829). **B.** *E. ramidulus* (Linnaeus, 1758). **C.** *E. merdarius* (Gravenhorst, 1829). **D.** *E. repentinus* (Holmgren, 1860).

3. Fore wing with distinct, pigmented proximal and central sclerites (Fig. 2B) 4
 - Fore wing with distinct, pigmented proximal sclerite: central sclerite may be present but translucent (Fig. 2C–D)..... 8
4. Pronotum, mesopleuron, mesoscutum and propodeum with dark patches (Fig. 14A).....
 - *Enicospilus combustus* (Gravenhorst, 1829)
 - Mesosoma lacking dark patches, uniformly testaceous..... 5
5. Metasoma abruptly tipped with black posteriorly, from 5th or 6th tergite (Fig. 14B).....
 - *Enicospilus ramidulus* (Linnaeus, 1758)
 - Metasoma not abruptly black-tipped (but may be diffusely infusate ventrally and apically)..... 6
6. Head with temples rounded, more buccate, and with distinct ocular-ocellar space (Fig. 4C); first metasomal tergite in lateral view with better-defined dorsal dip (Fig. 6C); male aedeagus apically paler, apex more rounded, protruding more dorsally and not reflexed ventrally (Fig. 9B).....
 - *Enicospilus myricae* sp. nov.
 - Head with temples narrowed, straighter, with ocelli adjacent to or only narrowly separated from eyes (Fig. 4A–B); first metasomal tergite with shallow dorsal dip (Fig. 6A–B); male aedeagus same colour throughout, apex more smoothly curved, not so protruding dorsally, reflexed ventrally (Fig. 9A).. 7

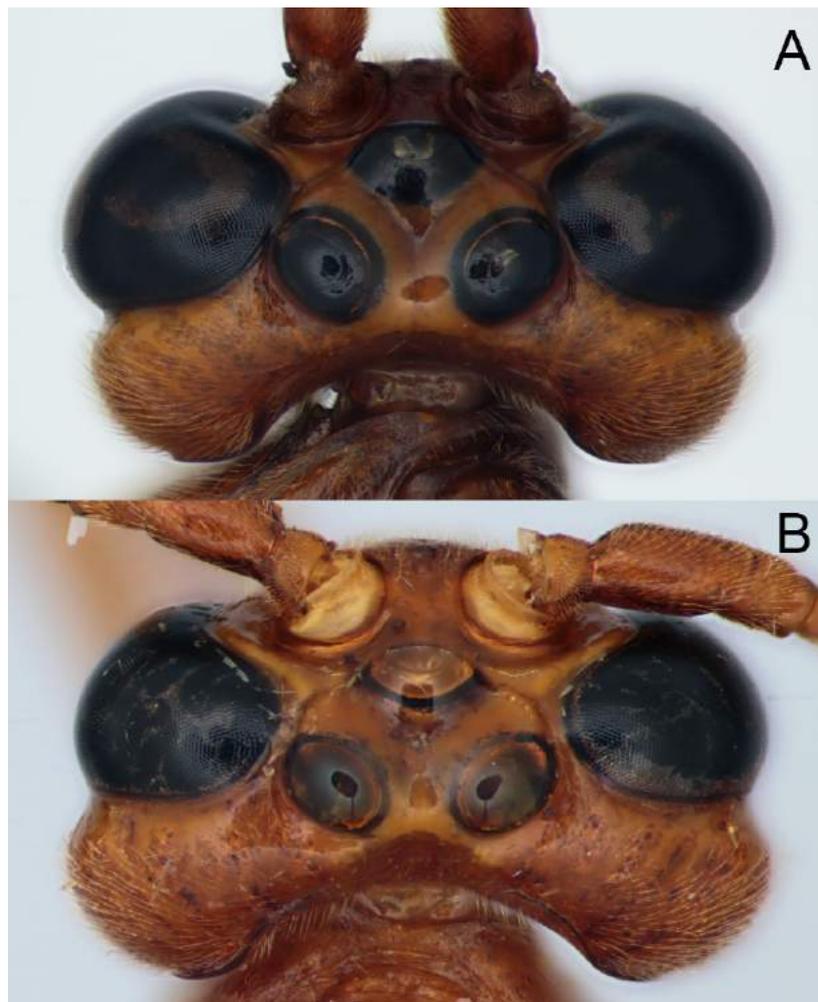


Fig. 3. Head, dorsal view. A. *Enicospilus inflexus* (Ratzeburg, 1844). B. *E. undulatus* (Gravenhorst, 1829).

7. Temples very strongly narrowed behind eyes (Fig. 4A); scutellum with sides more nearly parallel, heavily punctate and with slight posterior ridge (Fig. 5A); antenna with 51–56 flagellar segments, preapical flagellar segments stouter (Fig. 7B) *Enicospilus cerebrator* Aubert, 1966
- Temples less strongly narrowed posteriorly (Fig. 4B); scutellum with sides distinctly converging posteriorly, more sparsely punctate and smoothly curved posteriorly (Fig. 5B); antenna with 58–69 flagellar segments, preapical flagellar segments slender (Fig. 7A)
.....*Enicospilus adustus* (Haller, 1885) stat. rev.
8. Fore wing with small translucent central sclerite and narrow pigmented distal sclerite (Fig. 2C); fore wing vein *cu-a* distinctly proximal to *Rs&M* (Fig. 11A).....
.....*Enicospilus merdarius* (Gravenhorst, 1829)
- Fore wing lacking central sclerite and with very faint distal sclerite (Fig. 2D); fore wing vein *cu-a* opposite vein *Rs&M* (Fig. 11B).....*Enicospilus repentinus* (Holmgren, 1860)

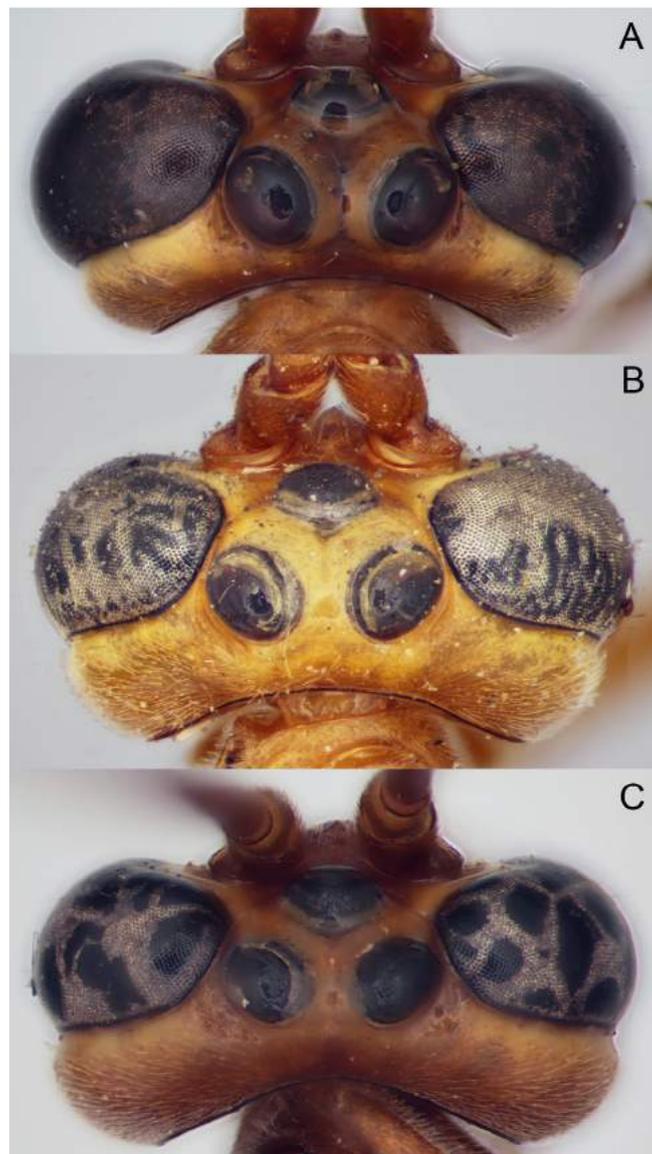


Fig. 4. Head, dorsal view. **A.** *Enicospilus cerebrator* Aubert, 1966. **B.** *E. adustus* (Haller, 1885). **C.** *E. myricae* sp. nov.

Enicospilus adustus (Haller, 1885) stat. rev.
Figs 4B, 5B, 6B, 7A, 8A, 9A, 15A, 17, 18A

Ophion adustus Haller, 1885: 200.

Enicospilus merdarius – auctt., misidentification (e.g., Gauld & Mitchell 1981; Horstmann 1997).

Status and taxonomy

As explained above, unfortunately the species generally known as *Enicospilus merdarius* (citations can be traced through Yu *et al.* 2012, including the inevitable gross misidentifications) is not conspecific with the lectotype, as designated by Fitton (1984). The next available name and, surprisingly, the only name currently placed in synonymy with *E. merdarius*, is *Ophion adustus* Haller, 1885 (Horstmann 1997). Unfortunately, the application of *E. adustus* is not straightforward either; there is no published type depository for *Ophion adustus* and it appears that nobody has ever referred to a type, if any existed, since Haller (1885) described the species. Haller's description is sufficient to identify his species as either *E. cerebrator* or *E. merdarius* in the sense of almost all subsequent authors (Haller describes the metasoma as being dark ventrally from the third tergite, which is a frequent discolouration in ophionines). Given that *E. merdarius* in the traditional sense is a widespread species in Europe we aim to preserve some nomenclatural stability by designating a neotype for *Enicospilus adustus*. Haller's types (he mentions two specimens) cannot be found (Horstmann 1997; H. Baur, A. Müller pers. comm., regarding Swiss collections) and are presumed lost or destroyed. We here designate a neotype, collected in Switzerland, as was Haller's specimen, and which is equivalent to the segregate after *E. cerebrator* and *E. myricae* sp. nov. have been separated. Neotype female: Switzerland, "dübdüf" [Dübendorf], "E. merdarius", "Ophion adustus Haller, 1885 neotype ♀ des. G. Broad 2013" (ETHZ). The fore wing sclerites and a dorsal view of the mesosoma are illustrated in Fig. 17. Across Europe, *E. merdarius* in the old sense is a variable taxon, which prompted Aubert (1966) to separate off *E. cerebrator*. What remains under the name *E. adustus* may still comprise more than one species, lacking the distinctive features of other species; however, British specimens are rather uniform and very similar to the neotype.

This is a fairly widespread but apparently uncommon species, reared from Noctuidae that feed on low vegetation. We have seen only one reared specimen, from an uncertain host.

Material

NMS: 15 ♀♀, 6 ♂♂; BMNH: 18 ♀♀, 11 ♂♂, 1 unsexed; material from other collections: 5 ♀♀.



Fig. 5. Scutellum. A. *Enicospilus cerebrator* Aubert, 1966. B. *E. adustus* (Haller, 1885). C. *E. myricae* sp. nov.

Distribution (Fig. 18A)

England: VCs 4, 15, 16, 17, 22, 24, 25, 26, 28, 29, 57; Scotland: VCs 75, 85, 86, 94, 96, 99, 110; Ireland: H16; Channel Islands: Jersey.

Additional material in NMS: Bulgaria: Aksakovo, Silistra region, Varna region; France: Côte-d'Or, Dordogne, Lot-et-Garonne; Hungary: Bugac; Italy: South Tyrol.

Flight time (non-reared material)

July–September, with one outlying November date, but 90% of specimens are concentrated in July–August.

Host

The only host record is of one specimen labelled as having been reared (M.R. Britton) from either *Blepharita adusta* (Esper) or *Lacanobia oleracea* (Linnaeus) (both Noctuidae) (NMS).

Despite the coincidence of the species name, Haller's specimens were not reared but were caught in the daytime, basking on vegetation (Haller 1885). There are no obvious habitat preferences discernible from the collection data.



Fig. 6. First metasomal segment (anterior to left). **A.** *Enicospilus cerebrator* Aubert, 1966. **B.** *E. adustus* (Haller, 1885). **C.** *E. myricae* sp. nov..

Remarks

Identification is relatively straightforward but not all material of “*E. merdarius*” from light traps was retained until it was realised that *E. cerebrator* had been overlooked in Britain. *Enicospilus adustus* is a large, testaceous species, lacking dark markings except, sometimes, for discolouration of the metasomal sternites and laterotergites. Morphologically it is very similar to *E. combustus* and *E. ramidulus*, which each have distinctive colour characters. The long antennae (58–69 flagellar segments in British specimens, usually in the range of 60–65, modal value 63; 62 flagellar segments in the neotype) with elongate preapical flagellar segments serve to distinguish *E. adustus* from *E. cerebrator*, together with the form of the scutellum and the slightly wider temples. *Enicospilus myricae* sp. nov. differs in several respects (see notes under that species) and the antenna is intermediate in length between *E. adustus* and *E. cerebrator*. Some European specimens of *E. adustus* are noticeably larger, with a more pronounced posterior ridge to the scutellum and there may be additional undescribed species in this complex. In both *E. adustus* and *E. cerebrator* the anterior transverse carina of the propodeum varies from complete to largely absent.



Fig. 7. Distal flagellar segments. **A.** *Enicospilus adustus* (Haller, 1885). **B.** *E. cerebrator* Aubert, 1966.

Enicospilus cerebrator Aubert, 1966
Figs 4A, 5A, 6A, 7B, 8B, 15B, 18B

Enicospilus cerebrator Aubert, 1966: 42; holotype ♂ examined (MZLS).

Status

New to Britain. Although widely recorded across the Western Palaearctic (e.g. Aubert 1966; Izquierdo 1984), British authors have overlooked *E. cerebrator*; however, this species turns out to be rather widespread in south-east England (one more northerly record, from Yorkshire) where it has been reared from several species of *Hadena* Schrank, 1802 and *Hecatera* Guenée, 1852 (Notuidae: Hadeninae)

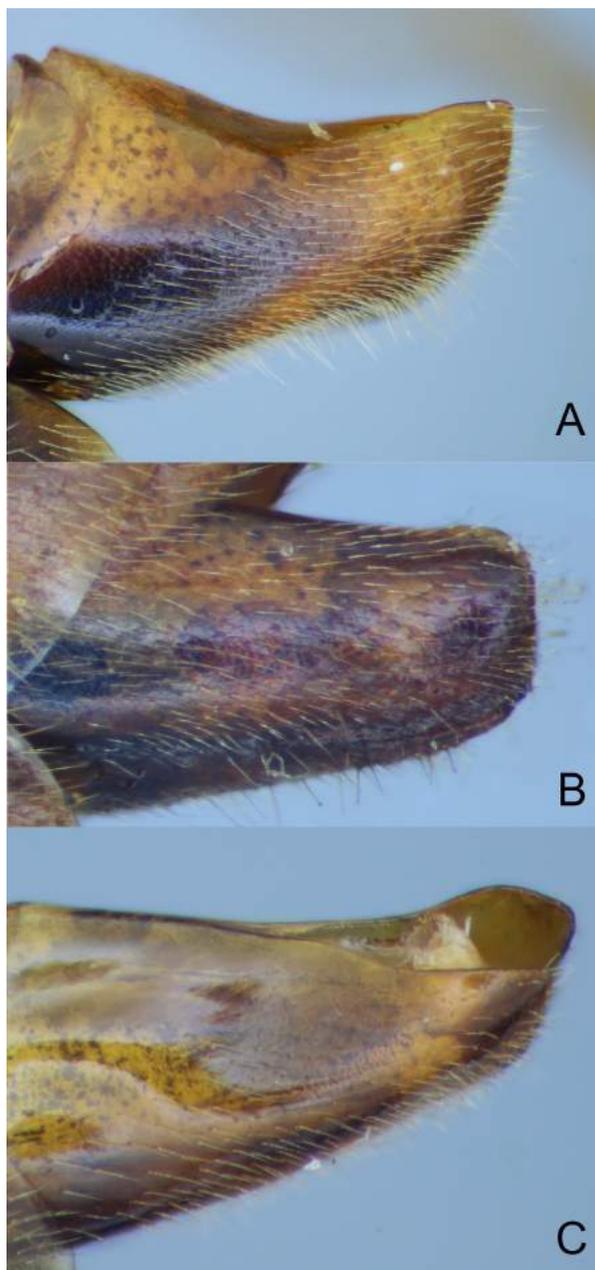


Fig. 8. Male parameres (claspers). **A.** *Enicospilus adustus* (Haller, 1885). **B.** *E. cerebrator* Aubert, 1966. **C.** *E. myricae* sp. nov.

whose larvae feed in seedheads or on flowers. There are three specimens reared from *Hecatera dysodea* (Denis & Schiffermüller, 1775), which has a restricted range in England and south Wales (Hill *et al.* 2010) and was extinct in Britain for many years; it is fairly frequently the case that there are good numbers of parasitoid rearings from rare hosts (e.g. *Enicospilus merdarius*), which are targeted by entomologists in preference to the more widespread host species (note the paucity of host records for *E. adustus* and *E. combustus*).

Material

British: NMS: 22 ♀♀, 10 ♂♂; BMNH: 25 ♀♀, 12 ♂♂, 6 unsexed; material from other collections: 11 ♀♀, 5 ♂♂, 1 unsexed.

Distribution (Fig. 18B)

England: VCs 1, 11, 15, 16, 17, 19, 20, 22, 24, 25, 26, 28, 30, 32, 62.

Additional material in NMS: Bulgaria: Aksakovo; France: Hérault, Lot-et-Garonne, Vaucluse; Hungary: Bugac; Italy: South Tyrol.



Fig. 9. Male aedeagus. A. *Enicospilus adustus* (Haller, 1885). B. *E. myricae* sp. nov.

Flight time (non-reared material)

May–August, with 51% having been collected in July; one specimen is labelled as “xi”. From a series in NMS collected at Dungeness (coll. C.W. Plant) from mid-May to late July, it seems that *E. cerebrator* is plurivoltine (at least bivoltine), in contrast to other British *Enicospilus*, although May specimens have not been seen from any other locality.

Hosts

Hadena albimacula (Borkhausen, 1792) (3) (G.T. Lyle, A. Wander; BMNH); *Hadena irregularis* (Hufnagel, 1766) (13, from one site and collector, C. Morley; BMNH); *Hecatera dysodea* (3) (R. Hayward, J. Platts, I. Sims; NMS); *Hecatera bicolorata* (Hufnagel, 1766) (4) (Harwood, C.G. Nurse; BMNH, WML) (all Noctuidae). Two specimens, seemingly from one collecting event, are labelled as having been reared from “*Anticlea sinuata*” (= *Catarhoe cuculata* (Hufnagel, 1767)) (Geometridae), which can be ruled out on size alone.

Remarks

Enicospilus cerebrator is a smaller species than *E. adustus*, with more strongly narrowed temples and a rather distinctive scutellum. The antennal flagellum is shorter than in *E. adustus* or *E. myricae* sp. nov. (51–56 flagellar segments, modal value 53), with stouter preapical flagellar segments than in *E. adustus*; the scutellum appears more parallel-sided, broader posteriorly, bordered posteriorly by a slightly raised ridge and with the sides more abruptly curved posteriorly than in similar species; the surface of the scutellum is more matt than in similar species; the male parameres are square-ended (Fig. 8B) compared to the more tapering parameres of *E. adustus* and *E. myricae* sp. nov.

Enicospilus combustus (Gravenhorst, 1829)

Figs 14A, 18C

Ophion combustus Gravenhorst, 1829: 701.

Status

A distinctive species of mainly southern distribution. It has not been found in Scotland. Reared from *Melanchra persicariae* (Linnaeus, 1761) (Noctuidae).

Material

NMS: 18 ♀♀, 2 ♂♂, 1 unsexed; BMNH: 41 ♀♀, 14 ♂♂; material from other collections: 19 ♀♀, 7 ♂♂, 3 unsexed.

Distribution (Fig. 18C)

England: VCs 1, 2, 3, 7, 11, 13, 15, 17, 20, 21, 22, 23, 24, 25, 26, 28, 29, 36, 58, 62, 64, 65; Wales: VC 41, 52; Channel Islands: Sark.

Flight time (non-reared material)

July–October, with the majority in August–September; is on the wing later in the year than *E. adustus*, *E. cerebrator* and *E. ramidulus*.

Hosts

Melanchra persicariae (1) (Noctuidae), reported via iSpot (www.ispot.org.uk), reared in Norfolk, released but identified from a photo. Additionally, there are two females in H. Schnee’s personal collection also reared, in Germany, from *M. persicariae* (Dübener, coll. ix.1985, em. v/vi.1986).

Remarks

Although very similar in general morphology to *E. adustus* and *E. ramidulus*, the colour pattern of *E. combustus* is distinctive, with the mesosoma extensively black, and the antennae have more flagellar segments (62–70 flagellar segments, modal number 65), especially compared to *E. ramidulus*, which shares a black-tipped metasoma. Other than colour pattern, though, there seem to be no reliable morphological distinctions from *E. adustus*, apart from a greater number of antennal segments (but with an overlapping range).

Enicospilus cruciator Viktorov, 1957

Enicospilus cruciator Viktorov, 1957: 205.

Material

Not British. NMS: FRANCE: 1 ♀, 2 ♂♂, Aude, 26–31 May 2012 (M.R. Shaw).

Remarks

This species is very similar to *E. merdarius* (see notes under *E. merdarius*) and it is possible that some other continental specimens identified as *E. merdarius* (or *E. tournieri*) in BMNH and NMS in fact belong to this species.

Enicospilus inflexus (Ratzeburg, 1844) Figs 3A, 12, 20A

Ophion inflexus Ratzeburg, 1844: 102.

Status

A relatively widespread parasitoid of *Lasiocampa*, and possibly other Lasiocampidae, particularly on heaths and moorland.



Fig. 10. Fore wing sclerites of *Enicospilus myricae* sp. nov.

Material

NMS: 16 ♀♀, 7 ♂♂, 1 unsexed; BMNH: 12 ♀♀, 8 ♂♂, 1 unsexed; material from other collections: 17 ♀♀, 3 ♂♂, 1 unsexed.

Distribution (Fig. 20A)

England: VCs 1, 2, 3, 5, 9, 10, 11, 13, 15, 17, 28, 31, 39, 50, 57, 64, 67, 69; Scotland: VCs 72, 87, 89, 95, 97, 98, 99, 102, 104, 105, 110; Wales: VC 49.

Flight time (non-reared material)

June–September, with the majority in August.

Hosts

Lasiocampa quercus (Linnaeus, 1758) (including f. *callunae* Palmer, 1847) (10) (Lasiocampidae) (T.H. Ford, J.L. Gregory, Harwood, A. Kennedy, D.K. Kevan, M. R. Shaw, C.H.S. Vimter, L. Wakely, P. Yarlett) (BMNH, NMS); one specimen in BMNH labelled as reared from *Euthrix potatoria* (Linnaeus, 1758) (Lasiocampidae) (R. South), and another labelled as ex *Cerura vinula* (Linnaeus, 1758) (Notodontidae) (A.H. Sperring), which seems very improbable.

Remarks

Along with *E. undulatus*, with which it has frequently been confused, *E. inflexus* belongs to a distinctive group of species (in older literature sometimes referred to as the genus *Allocamptus*) that lack fore wing sclerites, are very large and have a strongly sinuous fore wing vein $Rs+2r$. Compared to *E. undulatus*, *E. inflexus* has more narrowed temples, giving it a less buccate head, but it is otherwise very similar.

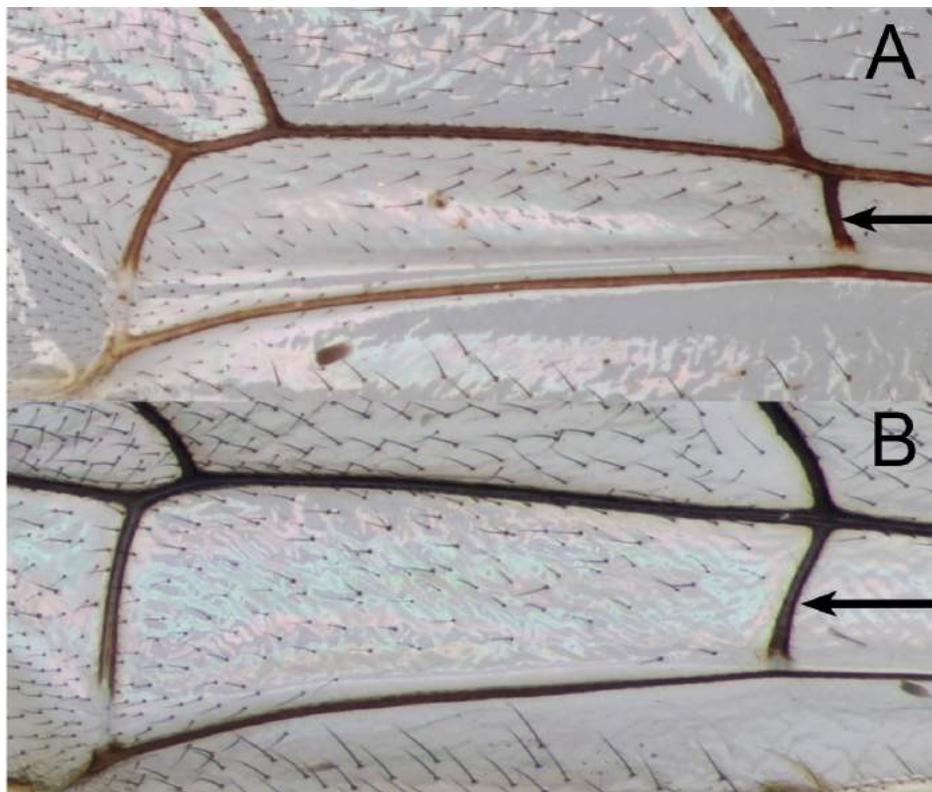


Fig. 11. Fore wing (distal to left), vein *cu-a* arrowed. **A.** *Encospilus merdarius* (Gravenhorst, 1829). **B.** *E. repentinus* (Holmgren, 1860).

Enicospilus merdarius (Gravenhorst, 1829)

Figs 1, 2C, 11A, 13A, 19A

Ophion merdarius Gravenhorst, 1829: 698; lectotype ♂, OUMNH, examined.

Ophion tournieri Vollenhoven, 1879: 61, pl. 39; syn. nov.

Henicospilus rossicus Kokujev, 1907: 170; lectotype ♂, ZIN, photos examined; syn. nov.

Enicospilus contributus Shestakov, 1926: 256; syn. nov.

Enicospilus repentinus – misidentification (Gauld 1973).

Status

As described in the “Taxonomy of British *Enicospilus*” section above, the lectotype male of *Ophion merdarius* is a specimen of the species usually called *E. tournieri*. The (probably non-British) female paralectotype is a specimen of *Enicospilus adustus* (i.e., the usual interpretation of the name), so the choice of lectotype was unfortunate. We have not examined type material of *Ophion tournieri* or *Enicospilus contributus* as these types cannot be located; instead we have followed the synonymies (under *tournieri*) of Aubert (1962, 1964) and Viktorov (1957). The type of *E. contributus* should be in ZIN but could not be located (A. Khalaim, pers. comm.). The whereabouts of the type male of *O. tournieri* is a mystery; Townes *et al.* (1965) report the type depository as the Muséum national d’Histoire naturelle, Paris, but it cannot be found there (A. Touret-Alby, pers. comm.) and it seems unlikely when most of the Vollenhoven’s types were deposited in Dutch collections. There is also no trace of a type in Naturalis, Leiden (F. Bakker, pers. comm.), which includes the former Amsterdam collections. The type locality of Switzerland makes it likely that *O. tournieri* is a synonym of *E. merdarius* rather than *E. cruciator*, described from Turkmenistan and apparently more of a species of hot, dry climates (judging by published records and the collections of BMNH).

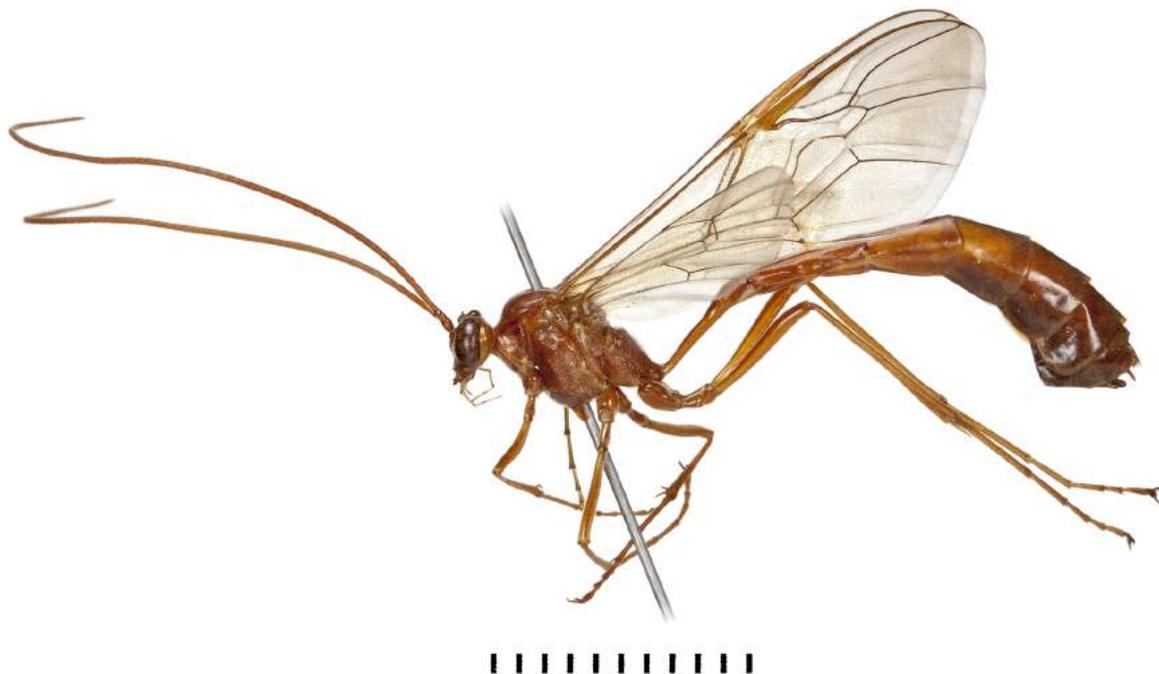


Fig. 12. *Enicospilus inflexus* (Ratzeburg, 1844), ♀, Tredinnick Stack, England, BMNH(E) 962205, habitus. Scale bar = 10 mm.

Restricted to a few coastal sites in England and Scotland. Only reared from *Agrotis ripae* (Hübner, 1823) (Noctuidae) (7 rearings), which inhabits the strandlines of sandy beaches and is very localised. The apparent host specificity of *E. merdarius* may be a result of the restricted noctuid fauna in its habitat. Gauld (1973) recorded *E. repentinus* as a British species but, based on his description of the species as being coastal, and the lack of true *E. repentinus* in the BMNH collections until recently, it seems he was describing *E. merdarius*; in fact, Sperring (1952) had already published on *E. tournieri* as a British species, with a host record (specimens in BMNH and BENHS).

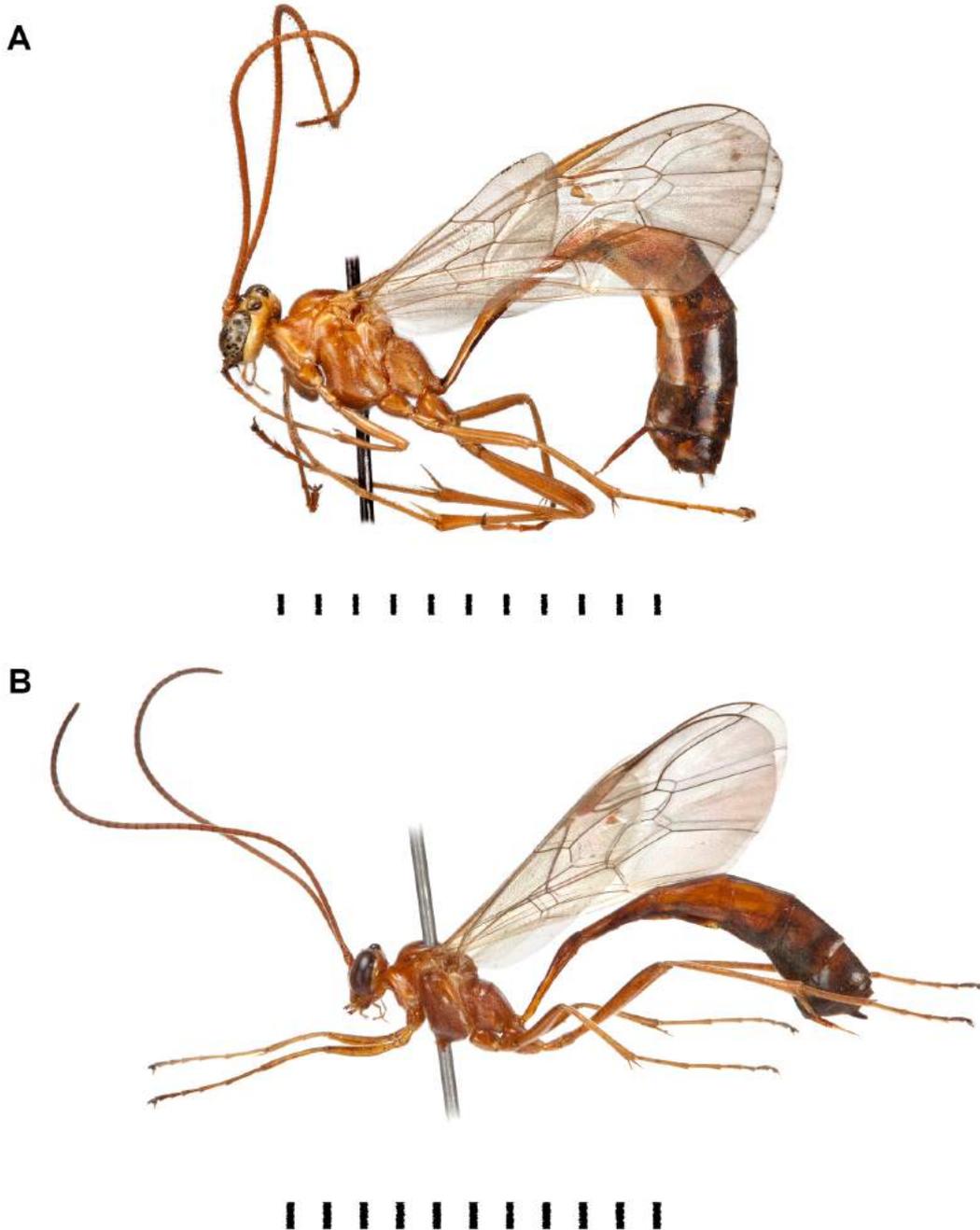


Fig. 13. Habitus. **A.** *Encospilus merdarius* (Gravenhorst, 1829), ♀, Eastbourne, England, BMNH(E) 1022376. **B.** *E. repentinus* (Holmgren, 1860), ♀, Aldbury, England, BMNH(E) 962208. Scale bars = 10 mm.

Material examined

ENGLAND: 1 ♀, Dawlish Warren (VC 3), 14 Aug. 1977 (A.A. Allen) (NMS); 1 ♂, Winterton (VC 27), ex *Agrotis ripae* coll. as larva 7 Sep. 1988, em. spring 1989 (J.M. Chalmers-Hunt) (NMS); 1 ♀, 1 ♂, Hayling Island (VC 11), ex *A. ripae* coll. as larvae, em.[dates presumed to be emergence dates] 28 Jul., 17 Aug. 1951 (A.H. Sperring); 1 unsexed (VC 11), ex *A. ripae* coll. as larva, Aug. 1931 (A.H. Sperring); 1 ♂, East/West Wittering (VC 13), ex *A. ripae* coll. as larva 4 Aug. 1932 (A.J. Wightman); 1 ♀, Eastbourne (VC 14), Aug. 1900 (C.G. Nurse); 1 ♀, Clacton (VC 19), Aug. 1926 (Harwood); 1 ♂,



Fig. 14. Habitus. **A.** *Enicospilus combustus* (Gravenhorst, 1829), ♀, Bath, England, BMNH(E) 962204. **B.** *E. ramidulus* (Linnaeus, 1758), ♀, Cornwall, England, BMNH(E) 962207. Scale bars = 10 mm.



Fig. 15. Habitus. **A.** *Encospilus adustus* (Haller, 1885), ♀, Tentsmuir, Scotland, BMNH(E) 962202. **B.** *E. cerebrator* Aubert, 1966, ♀, Calshot, England, BMNH(E) 962203. Scale bars = 10 mm.

Freshwater Bay [there are Freshwater Bays in Dorset and on the Isle of Wight], <1904 (T.E. Marshall) (all BMNH); 1 ♂, Hayling Island (VC 11), ex *A. ripae* coll. as larva, em.[?] 5 Aug. 1951 (A.H. Sperring) (BENHS).

SCOTLAND: 1 ♂, St Cyrus NNR (VC 91), ex *A. ripae* em. Jul. 1993 (A.J. Halstead) (NMS).

Additional material in NMS

BULGARIA: 6 ♀♀, 1 ♂, Aksakovo (C.W. Plant) (NMS).

The lectotype ♂ was supposedly collected in Netley, Shropshire (Fitton 1984), but this locality has been ascribed to most of the British material sent by F.W. Hope to J.L.C. Gravenhorst and seems very unlikely to be the actual collection locality for this sand dune inhabitant: entomologists of that period seemed often to name their home town, presumably to identify specimens as theirs, on what might otherwise be taken as data labels (which were, to say the least, unfashionable at the time).

Remarks

Most similar in the British fauna to *E. repentinus* but larger (52–58 flagellar segments, $n = 10$, modal value 52) and with distinct differences in fore wing sclerites and venation; also the propodeum has rather different sculpture, with the rugosity more raised and thus making it less shiny than in *E. repentinus*. Unlike in *E. repentinus*, there are some rather vaguely defined pale yellow patches on the mesosoma (Fig. 13A). The non-British *Enicospilus cruciator* is similar and the two species may well be confused in collections. Judging by Viktorov's (1957) key and photographs of a female and male of the type series, *E. cruciator* differs from *E. merdarius* in the longer, less narrowed temples (in dorsal view of the head) and the larger ocellar-ocular gap.

Enicospilus myricae sp. nov.

urn:lsid:zoobank.org:act:31771CB3-729B-4157-A201-B6736BBB2800

Figs 4C, 5C, 6C, 8C, 9B, 10, 16, 18D

Diagnosis

Separated from *E. adustus* and *E. cerebrator* by the more rounded temples, wider ocellar-ocular space (especially compared to *E. cerebrator*), more obvious dorsal “dip” on the first tergite and by the distinctly different aedeagus of the male.

Etymology

Named after the association with the distinctive habitat of *Myrica gale*-dominated bog, from which this species was reared.

Material examined

Holotype

SCOTLAND: ♀: “[Scotland] Resipole, Argylls. NM 723645. *Orthosia gracilis*, *Myrica gale* coll. 4.7.92, PLE [parasitoid larva erupted] 7.92 em. 7.1993 M.R. Shaw” (NMS).

Paratypes

SCOTLAND: 2 ♀♀, same data as holotype (NMS); 1 ♂, Resipole, Argyllshire, coll. 4 Jul. 1992 (M.R. Shaw) (NMS); 1 ♀, 5 ♂♂, Loch Arkaig, Invernesshire NN0291, Malaise trap in native pinewood, Jun. 1992 (I. MacGowan) (NMS).

WALES: 1 ♀, Glamorgan, Kenfig, 30 Jun. 1963 (R.B. Benson) (BMNH).

ENGLAND: 1 ♀, Huntingdonshire, Monks Wood NNR, 17–29 Jul. 1978 (M.G. Fitton & J.S. Noyes) (BMNH).

AUSTRIA: 1 ♀, Burgenland, Leitha Gebirge, 10–23 Jun. 1956 (E.W. & I.D. Classey) (BMNH).

Description

Female

There is very little variation between specimens; variation is covered in the description. Fore wing length 11–13.5 mm. Antenna with 57–59 flagellar segments ($n = 6$) (57 in holotype). 1st flagellomere about 5× as long as apically wide, preapical flagellomere 1.5× as long as wide. Head (Fig. 4C) with distinct gap between lateral edge of stemmaticum and edge of eye, lateral ocellus separated from eye by 0.25× maximum length of ocellus; temples in dorsal view curved, rounded immediately behind eye, then more linearly narrowed, measured in straight line from eye margin to lateral margin of occipital carina, $c.$ 0.8× length of greatest eye width; in lateral view, at level of antennal sockets, gena 0.8× width of eye. Mandible strongly bent, slightly twisted, with curved groove containing long setae, from



Fig. 16. *Enicospilus myricae* sp. nov., habitus, paratype, ♀, Monks Wood, England, BMNH(E) 962209. Scale bar = 10 mm.

dorsal proximal corner to base of teeth, as in other members of *E. ramidulus* group; lower tooth about 0.5× length of upper. Clypeus apically truncate with wide, thin flange, very sparsely punctate. Eyes ventrally slightly convergent, face at mid-height 1.6× as wide as high, evenly, fairly closely punctate. Mesopleuron entirely, closely punctate, with faint transverse striae across dorsal portion below subalar prominence and more prominently in narrow band along dorsal 0.5 of posterior edge (deflected anteriorly by unsculptured speculum) and across wide area medio-ventrally on mesopleuron; Austrian paratype with striation reduced, only noticeable on medio-ventral area of mesopleuron. Epicnemial carina almost complete, fading out dorsally just before reaching anterior edge of mesopleuron. Mesoscutum with notauli faintly indicated anteriorly, entirely closely punctate (punctures small, closer than puncture



Fig. 17. *Enicospilus adustus* (Haller, 1885) neotype ♀. Dorsal view of head and mesosoma, fore wing discosubmarginal cell and, inset, original locality label.

diameter), shiny. Scutellum (Fig. 5C) shiny, regularly punctate, punctures larger than on mesoscutum and further apart (larger and closer anteriorly); lateral carinae complete to near posterior end of scutellum, indicated around posterior end of scutellum as rugosity/carinae. Fore wing (Fig. 10) as in other species of *E. ramidulus* group; glabrous area (fenestra) of discosubmarginal cell extending from proximal sclerite to posterior 0.3 of $Rs+2r$ (along thickened area of vein); proximal sclerite entirely pigmented, approximately triangular with rounded anterior angle, more elongate on distal corner; central sclerite roughly "D"-shaped, pigmented distally, fading to unpigmented, transparent proximally; distal sclerite represented by faintly pigmented line along distal-ventral margin of fenestra; fore wing vein $Rs+2r$ sinuous, uniformly widened along anterior 0.7; $3rs-m$ 0.45× section of M between $1m-cu$ and $3rs-m$; $cu-a$ slightly to distinctly proximal to $Rs&M$. Metapleuron shiny, closely punctate. Propodeum with weakly defined central section of anterior transverse carina, anterior of this shiny and superficially punctate, posterior to this entirely reticulate-rugose or sculpture much reduced dorso-laterally. First metasomal tergite (Fig. 6C) with shallow dorsal concavity at anterior 0.45. Second metasomal segment with laterotergite narrow, folded under; third tergite with laterotergite not demarked.

Colour

Uniformly testaceous (Fig. 16), varying from dull orange to a darker, reddish-orange (although probably dependent on preservation), except for black mandibular teeth and varying amounts of dark brown infuscation on the venter of the metasoma from 4th tergite onwards, and apical tergites at most weakly infuscate. Antenna darker apically. Generally slightly darker than *E. adustus*.

Male

As in female but with more antennal segments (61–64 flagellar segments; $n = 4$) and striation on mesopleuron much feebler, basically absent medio-ventrally. Paramere (Fig. 8C) rather strongly narrowed posteriorly, smoothly angled into apical edge; aedeagus (Fig. 9B) with dorsal, apical area concave and laterally carinate, more rounded apically than in *E. adustus* (Fig. 9A) or *E. cerebrator*, in which apex of aedeagus less protruding dorsally and more strongly reflexed ventrally.

Distribution

Austria, England, Scotland, Wales, as detailed in the list of type material (British distribution in Fig. 18D).

Flight time (non-reared material)

June-July.

Hosts

Orthosia gracilis (Denis & Schiffermüller, 1775) (3 specimens, from one collecting event) (Noctuidae: Hadeninae).

The majority of the few known specimens were collected in Scotland but it is a much more widespread species and it may be that it prefers boggy habitats in which few people collect ichneumonids. One paratype was collected in Monks Wood NNR, an ancient deciduous woodland with a rather rich fauna of fen or bog-associated noctuids. Unlike other British *Enicospilus* there is a distinct sexual dimorphism in antenna length, as males have more flagellar segments, with no overlap in the small sample size available.

Enicospilus ramidulus (Linnaeus, 1758)

Figs 2B, 11B, 18E

Ichneumon ramidulus Linnaeus, 1758: 566.

Sphex truncatus Poda, 1761: 107.

Henicospilus instabilis Kokujev, 1907: 174.

Status

A common and widespread species, regular in light traps and rather frequently reared from Noctuidae, particularly of the subfamily Hadeninae.

Material

NMS: 53 ♀♀, 20 ♂♂, 9 unsexed; BMNH: 80 ♀♀, 31 ♂♂, 3 unsexed; material from other collections: 60 ♀♀, 23 ♂♂, 14 unsexed.

Distribution (Fig. 18E)

England: VCs 1, 2, 3, 4, 5, 6, 9, 10, 11, 13, 14, 15, 16, 17, 19, 20, 21, 22, 24, 25, 26, 27, 28, 29, 31, 36, 39, 40, 54, 55, 56, 57, 58, 59, 61, 62, 63, 65; Scotland: VCs 75, 84, 86, 87, 89, 90, 96, 97, 98, 99, 101, 105, 106, 110; Wales: VC 41, 45, 48, 50, 52; Ireland: H5; Channel Islands: Jersey.

Flight time (non-reared material)

June–September, with the majority in July.

Hosts

Actebia praecox (Linnaeus, 1758) (Noctuidae: Noctuinae) (1) (no collector specified; BMNH); ?*Anarta myrtilli* (Linnaeus, 1761) (1) (T.H. Ford) (NMS); *Lacanobia oleracea* (Linnaeus, 1758) (3) (P. Baker, M.R. Shaw) (NMS); *Melanchra pisi* (Linnaeus, 1758) (28) (P. Baker, A.E. Cockayne, A. Lord, G.T. Lyle, M.R. Shaw) (BMNH, NMS); *Phlogophora meticulosa* (Linnaeus, 1758) (1) (P. Baker) (NMS) (all Noctuidae, mostly Hadeninae).

Additional material in NMS: Bulgaria: Kavarna; Finland: Houtskär; France: Alpes-Maritimes, Côte-d'Or, Dordogne, 1 ex *Panolis flammea* (Denis & Schiffermüller, 1775) (M.R. Shaw); Spain: Zaragoza, 1 ex *Lacanobia oleracea* (G.E. King).

Remarks

Amongst the British *Enicospilus* species with two discrete, pigmented fore wing sclerites, *E. ramidulus* is distinctive in that the mesosoma is entirely testaceous and the metasoma apically sharply black, from the 5th or 6th tergite onwards. Structurally very similar to *E. adustus* and *E. combustus*, but *E. ramidulus* has shorter antennae (54–60 flagellar segments, modal value 56) and colour patterns are invariable. According to published records this is a very widely distributed species; however, there are other, similar species in various parts of the world that have been misidentified as *E. ramidulus*.

Enicospilus repentinus (Holmgren, 1860)

Figs 2D, 11B, 13B, 19B

Ophion repentinus Holmgren, 1860: 11.

Status

New to Britain. Found in a few localities in southern England, particularly along the eastern end of the Chilterns; all specimens have been collected in the past 30 years, all but one at light. Previous records of *E. repentinus* in Britain (e.g., Gauld 1973) refer to *E. merdarius* (= *turnieri*). We know of no reliable host records.

Material examined

ENGLAND: 1 ♂, Horse Down (VC 8), 30 Jun 1984 (G.R. Else); 2 ♀♀, Tilshead (VC 8), 13 Jul. 2013 (P. Sharpe) (T. Newton coll.); 1 ♀, Newlands Corner (VC 17), 4 Jul. 2010 (P. Wheeler); 8 ♀♀, 1 ♂,

Aldbury (VC 20), 2, 15 Jul. 2008, 8, 20, 21 Jul. 2010, 23, 25 Jul. 2012, 1 ♂, 7 Jul 2013 (G.R. Broad); 1 ♀, 1 ♂, College Lake (VC 20), 15 Jul. 2006 (M. Albertini); 1 ♀, Ellesborough (VC 24), 21 Jul. 2006 (M. Albertini); 1 ♀, Incombe Hole (VC 24), 22 Jul. 2005 (M. Albertini) (all BMNH); 1 ♀, Incombe Hole (VC 24), 22 Jul. 2005 (M. Albertini) (NMS); 1 ♀, Ivinghoe Hills (VC 24), 31 Jul. 2011 (S.N. Fletcher) (S.N. Fletcher coll.); 1 ♀, Radnage (VC 24), 18 Jul. 2010 (A.M. George) (A.M. George coll.); 1 ♀, Rushbeds Wood (VC 24), 12 Jul. 2007 (M. Albertini) (M. Albertini coll.); 2 ♀♀, Pitsford Water Nature Reserve (VC 32), Aug. 2012, 13 Jul. 2013 (M. Furfaro) (M. Furfaro, T. Newton colls).

Additional material in NMS

FRANCE: 1 ♀, Hautes-Alpes, Briançon 22 Jul. 2005 (M.R. Shaw); 1 ♂, Hautes-Alpes, Col du Lautaret 6-9 Jul. 2005 (M.R. Shaw).

TURKEY: 1 ♂, Ankara, Beynam 15 Jul. 1999 (M.R. Shaw).

The flight time is basically limited to July, other than one specimen collected at the very end of June and one in August.

Remarks

Smaller than *E. merdarius* (46–49 flagellar segments, modal value 47 in *repentinus*), with which it has been confused, lacking both the transparent central sclerite in the discosubmarginal cell and the elongate pigmented strip (distal sclerite) along the distal edge of the glabrous patch in the discosubmarginal cell. There are also subtle differences in the propodeal sculpture, which is less raised and shinier in *E. repentinus*. The two species are found in very different habitats: mainly calcareous grassland or woodland edges in the case of *E. repentinus*, sandy coasts in *E. merdarius*.

Enicospilus undulatus (Gravenhorst, 1829)

Figs 2A, 3B, 20B

Ophion undulatus Gravenhorst, 1829: 697.

Ophion arcuatus Brullé, 1846: 146.

Status

A very rarely collected species, found on southern coastal heaths where it has been reared from *Lasiocampa trifolii* (Denis & Schiffermüller, 1775) (Lasiocampidae). The host is now very local and *E. undulatus* has not been found in Britain since 1971.

Material examined

ENGLAND: 1 ♀, 1 ♂, Dungeness (VC 15), ex *Lasiocampa trifolii* coll. as larva 6 Jun. 1945 (G.V. Bull) (BMNH); 1 ♀, 1 ♂, Ilfracombe (VC 4), Jul. 1971 (I.D. Gauld); 1 ♀, Lowestoft (VC 25), Jul. 1971 (I.D. Gauld) (latter two records taken from Gauld, 1974; specimens not in BMNH).

Additional material in NMS

SPAIN: 1 ♀, Zaragoza, Montes de Torrero, 230 m, 24 May 1998 (G.E. King).

Remarks

Enicospilus inflexus has been separated from *E. undulatus* on the basis of differences in head shape (Gauld 1974) which seem to be consistent, based on the limited material in BMNH. Although there may be a difference in host use, this is based on only two rearings of *E. undulatus*, from one place and date; although *Lasiocampa trifolii* is rather smaller than *L. quercus*, *E. inflexus* and *E. undulatus* do not differ significantly in size.



Fig. 18. Distribution maps. **A.** *Enicospilus adustus* (Haller, 1885). **B.** *E. cerebrator* Aubert, 1966. **C.** *E. combustus* (Gravenhorst, 1829). **D.** *E. myricae* sp. nov. **E.** *E. ramidulus* (Linnaeus, 1758).

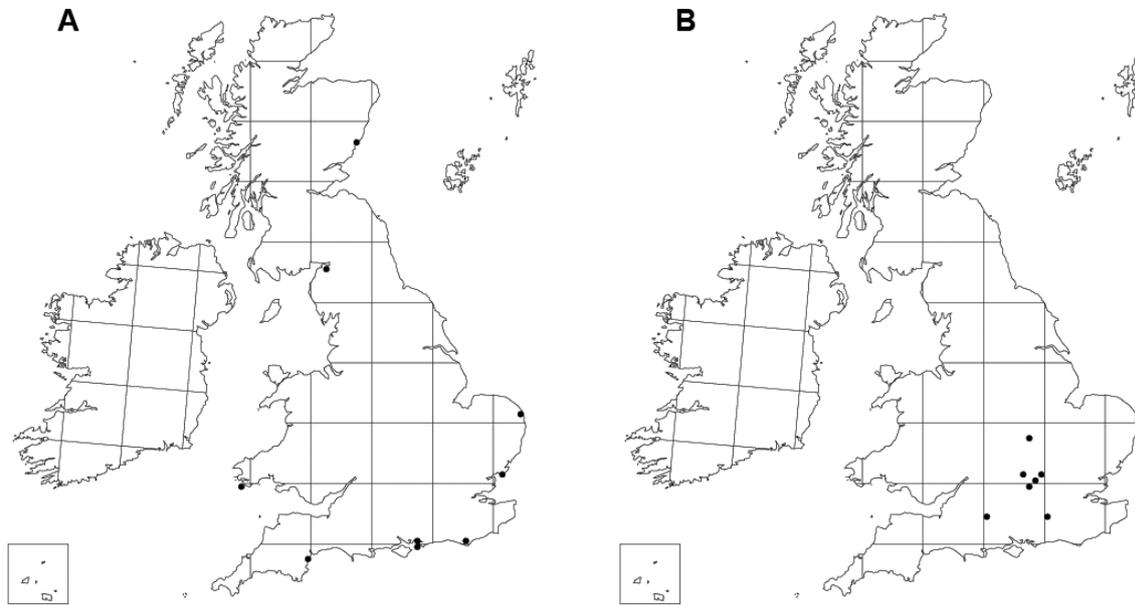


Fig. 19. Distribution maps. A. *Enicospilus merdarius* (Gravenhorst, 1829). B. *E. repentinus* (Holmgren, 1860).

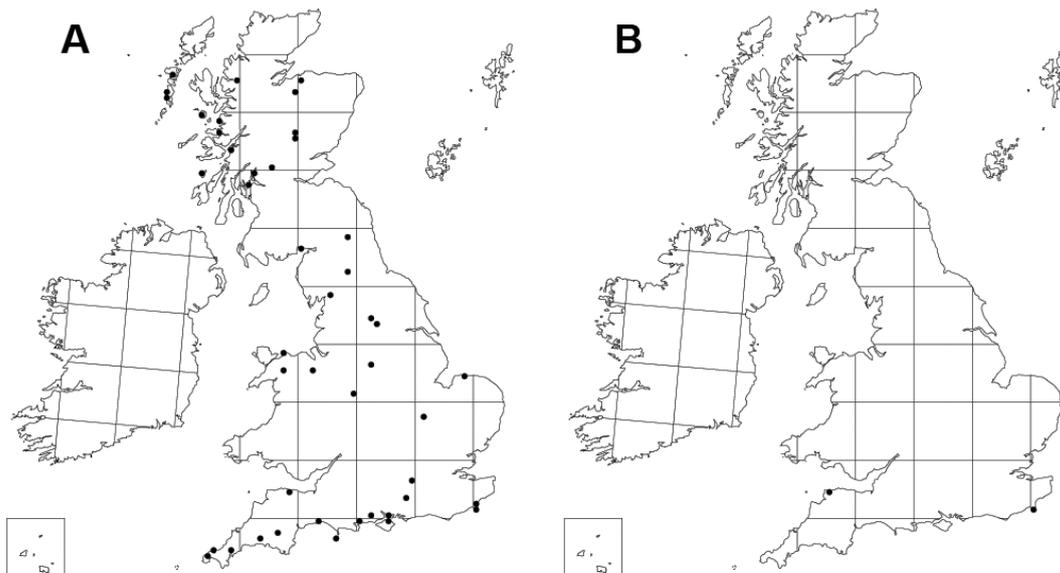


Fig. 20. Distribution maps. A. *Enicospilus inflexus* (Ratzeburg, 1844). B. *E. undulatus* (Gravenhorst, 1829).

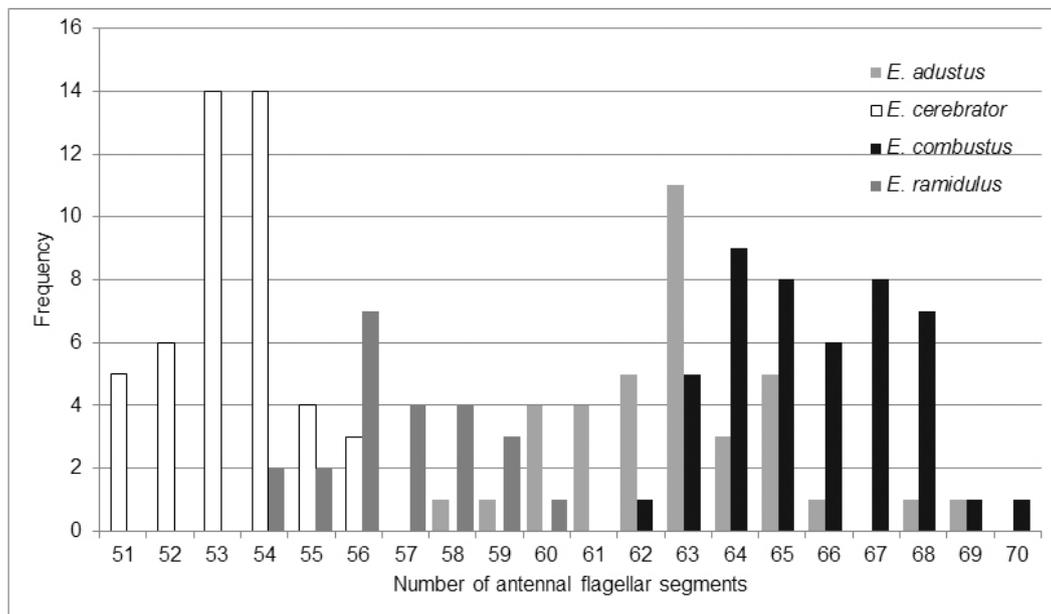


Fig. 21. Frequency distribution of number of antennal flagellar segments in four species of the *Enicospilus ramidulus* species-group.

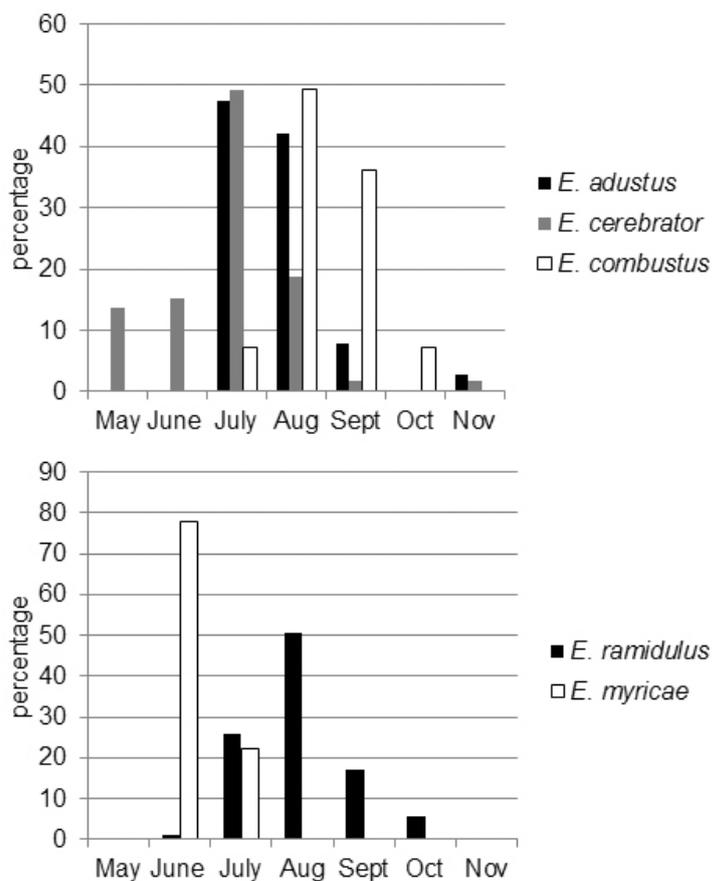


Fig. 22. Phenology of the five British species of the *Enicospilus ramidulus* species-group, expressed as proportions of the total, excluding reared specimens.

Discussion

There are now five known species in Britain that are very close morphologically, which we refer to as the *ramidulus* complex (this is a widespread species complex with many more extralimital species, e.g., Gauld 1988). Within the *ramidulus* complex in Britain there is evidence of two species-pairs: *E. cerebrator* and *E. ramidulus* are smaller, with shorter antennae, fly slightly earlier in the year and have both been reared regularly from several species of Hadeninae (Noctuidae) that feed moderately high up on field layer plants; *E. adustus* and *E. combustus* are larger, with longer antennae, fly later in the season and have both been reared only very infrequently, from noctuid larvae that feed exposed, low in the vegetation; *Enicospilus myricae* sp. nov. may be closer to *E. cerebrator* and *E. ramidulus*, and has been reared from noctuid larvae that feed more or less exposed on more bushy vegetation. The frequency of flagellomere numbers and dates of capture (of non-reared specimens) are plotted in Figs 21 and 22. There are distinct discontinuities in flagellar segment number and no specimens with intermediate colour patterns. *Enicospilus adustus* and *E. cerebrator* have been confounded, as they both lack any distinctive markings, although they are structurally distinct. It would be very interesting to obtain DNA sequence data for these species and test our conclusions on relationships with molecular data; however, at the moment there is a distinct shortage of recently collected specimens of some species.

Acknowledgements

Anne Freitag (MZLS), James Hogan (OUMNH), Andrey Khalaim (ZIN) and Andreas Müller (ETHZ) kindly lent type material or photos of types and Andreas Müller interpreted the handwritten locality label of the *E. adustus* neotype. Numerous entomologists have sent specimens, mainly from their light traps, and Phil Gould (formerly of Rothamsted Research) went to great efforts to extract Ichneumonoidea from Rothamsted light trap catches. We are grateful to those who have passed on reared material. Bill Ely forwarded numerous records of *Enicospilus* and other nocturnal ichneumonoids from Yorkshire. William Foster (Cambridge University), Peter Chandler (BENHS), Guy Knight and Tony Hunter (WML) lent specimens and provided access to their collections. Heinz Schnee sent several German *Enicospilus*, including some rare rearing records.

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