

Western Palaearctic Meteorinae (Hymenoptera: Braconidae) in the National Museums of Scotland, with rearing, phenological and distributional data, including six species new to Britain, and a discussion of a potential route to speciation

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Synopsis

Distributional, phenological and in many cases rearing data are given for 44 species of western Palaearctic Meteorinae in the genera *Meteorus* and *Zelee*, from the nearly 2,500 specimens of the group present in the collection of the National Museums of Scotland, Edinburgh. Six species are newly recorded from Britain. Patterns in the breadth of host ranges are discussed in relation to a reiterated speciation hypothesis and a recently published molecular phylogeny.

Key words: Braconidae, Meteorinae, parasitoids, *Meteorus*, *Zelee*, phenology, distribution, hosts, Lepidoptera, Coleoptera, host range, speciation, British Isles.

Introduction

The cosmopolitan subfamily Meteorinae includes about 60 western Palaearctic species currently classified in the two genera *Meteorus* Haliday, parasitizing the larvae of Coleoptera and Lepidoptera, and *Zelee* Curtis, which are confined to Lepidoptera. Recently the group has variously been regarded as a tribe Meteorini of the subfamily Euphorinae (Muesebeck, 1923; Maeto, 1986; van Achterberg, 1979; 1984; 1993; Tobias, 1986; Li *et al.*, 2003; Stigenberg & Ronquist, 2011) or as a subfamily in its own right (Foerster, 1862; Shaw, 1985; Maeto, 1990; Shaw & Huddleston, 1991; Zitani, 2003; Boring, 2010). Here we treat it as a subfamily. Although debate on this point continues (e.g. Pitz *et al.*, 2007; Sharanowski, Dowling & Sharkey, 2011), there is wide agreement (but see van Achterberg *et al.*, 2000) that Meteorinae (or Meteorini) is a monophyletic group; however, *Meteorus* as currently understood is probably paraphyletic with respect to *Zelee* (Stigenberg & Ronquist, 2011).

Some, but not all, of the species of *Meteorus* that parasitize exposed Lepidoptera larvae kill the host before it reaches full growth and construct their cocoon at the end of a thread, from which it hangs clear of the substrate. This habit gives the genus its name (from the Greek meteōros, = raised from the ground, hanging, lofty). Other species, especially those parasitizing more concealed hosts, spin less specialized, non-pendulous cocoons in a concealed situation. This is the case for all *Zelee* species, which normally kill their hosts in their pupation retreats. As these habits are of some phylogenetic interest we

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include an indication (when known) in the schematic cladogram illustrated in Figure 1, which is a simplified derivation of the molecular phylogeny published by Stigenberg & Ronquist (2011). Some tropical gregarious *Meteorus* species produce amazing cocoon arrangements (Zitani & Shaw, 2002; Zitani, 2003; Barrantes *et al.*, 2011), but in Europe such extreme specializations are not known and the gregarious species (*M. acerbiavorus*, *M. heliophilus* and *M. rubens*) form their cocoons in the host's pupation site. We also indicate in Figure 1 which species are known to parasitize Coleoptera and which Lepidoptera (there are no species unequivocally known to use both host groups; the literature citations suggesting that some do are almost certainly based on erroneous assumptions resulting from poorly controlled substrate rearings).

Meteorinae are largely haemolymph feeders and the hosts of *Meteorus* in particular often persist in a more or less active state for a varying period after the host larva erupts, often wandering far from the scene. The host never resumes development, however, although the tortricid hosts of *Meteorus ictericus* often (perhaps usually) resume feeding, as was noted by Shaw (1981a). Further information is given in the entry for that species. As far as we are aware, resuming feeding by Lepidoptera larvae after parasitoid eruption has not been noted for hosts of other *Meteorus* species (nor indeed for other endoparasitoid ichneumonoids), but conceivably it might occur.

The National Museums of Scotland (NMS) has a large collection of western Palaearctic Ichneumonoidea that is mostly of fairly recent origin (since about 1970), and is particularly rich in reared material, thanks to many entomologists who have generously donated specimens as well as the prolonged rearing efforts of the second author. The collection has also been immensely enriched by donations of the unmounted ichneumonoid fractions resulting from surveys using Malaise traps (see Schwarz & Shaw (1998) for details). Almost 2500 specimens of Meteorinae are present, comprising 40 species of *Meteorus* and four of *Zelee*, of which all but five species of *Meteorus* are represented by British specimens. Six species (*M. alborossicus*, *M. eklundi*, *M. limbatus*, *M. longipilosus*, *M. oculatus*, *M. sibyllae*) are here recorded as new to Britain, of which three (*M. eklundi*, *M. longipilosus*, *M. sibyllae*) belong to new species recently described elsewhere on the basis of material from other collections as well (Stigenberg & Ronquist, 2011). Most of the material is British (in the sense of the British Isles – i.e. with the inclusion of Ireland), though with considerable inputs from southern France. Other parts of the western Palaearctic are less well represented. A synonymic check-list of British Braconidae is available on the web – <http://www.nhm.ac.uk/resources-rx/files/braconidae-checklist-for-web-34139.pdf> – and outline biological information on Meteorinae is given by Shaw & Huddleston (1991).

The main purposes of this paper are several: to give an outline of the holding of this group in NMS; to present distributional data and rearing records therefrom; and to provide realistic summaries of host-range and flight times for as many species as the data allow. Additionally, host ranges are discussed in the light of a speciation hypothesis (Shaw, 1994; 2003) and a recently published molecular phylogeny.

Methods

The basis for determination of *Meteorus* species includes Huddleston (1980), but further work by van Achterberg (unpublished) and the first author has led to

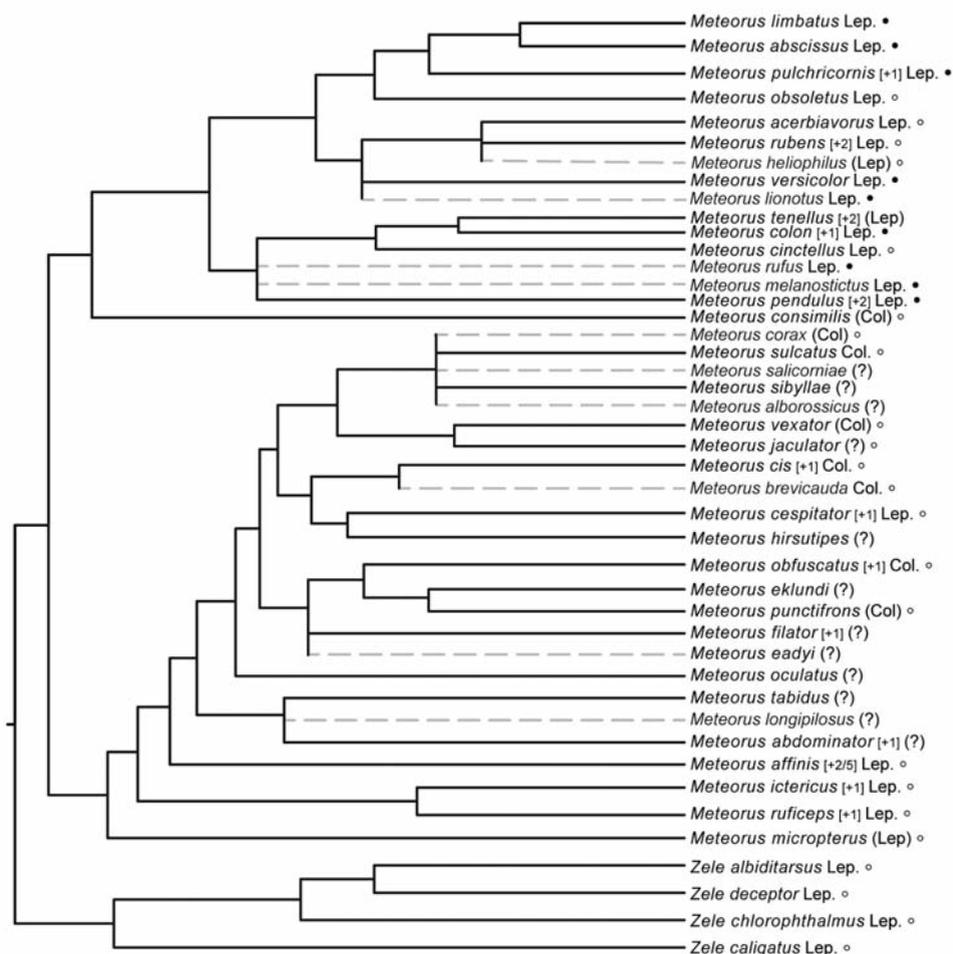


Fig. 1. Schematic indication of relationships of the species of Meteorinae treated in this paper, adapted from the molecular phylogeny of Stigenberg & Ronquist (2011). Dashed lines are best-guess placements of species for which gene sequences are unavailable. The lengths of lines shown are arbitrary (they do not correspond to branch lengths). Additional cryptic species present within some morphospecies are indicated by [+1] (etc.) after the name. The host order used is indicated Lep = Lepidoptera or Col = Coleoptera; brackets are used when the evidence stems from sources other than our data (for example, Huddleston (1980) or original descriptions), and ? signifies that (although there may be published records) we have not traced detailed evidence. A filled (black) circle indicates that the cocoon is pendulous and an open circle that it is not; neither is given in cases that are unclear to us.

a new key to the western Palaearctic fauna, with the recognition of several additional species (Stigenberg & Ronquist, 2011). *Zelee* species are determined largely on the basis of van Achterberg's (1979; 1984) keys. Stigenberg & Ronquist (2011) published molecular phylogenies based on the mitochondrial gene marker CO1 and the nuclear gene marker 28S, revealing that several of the morpho-

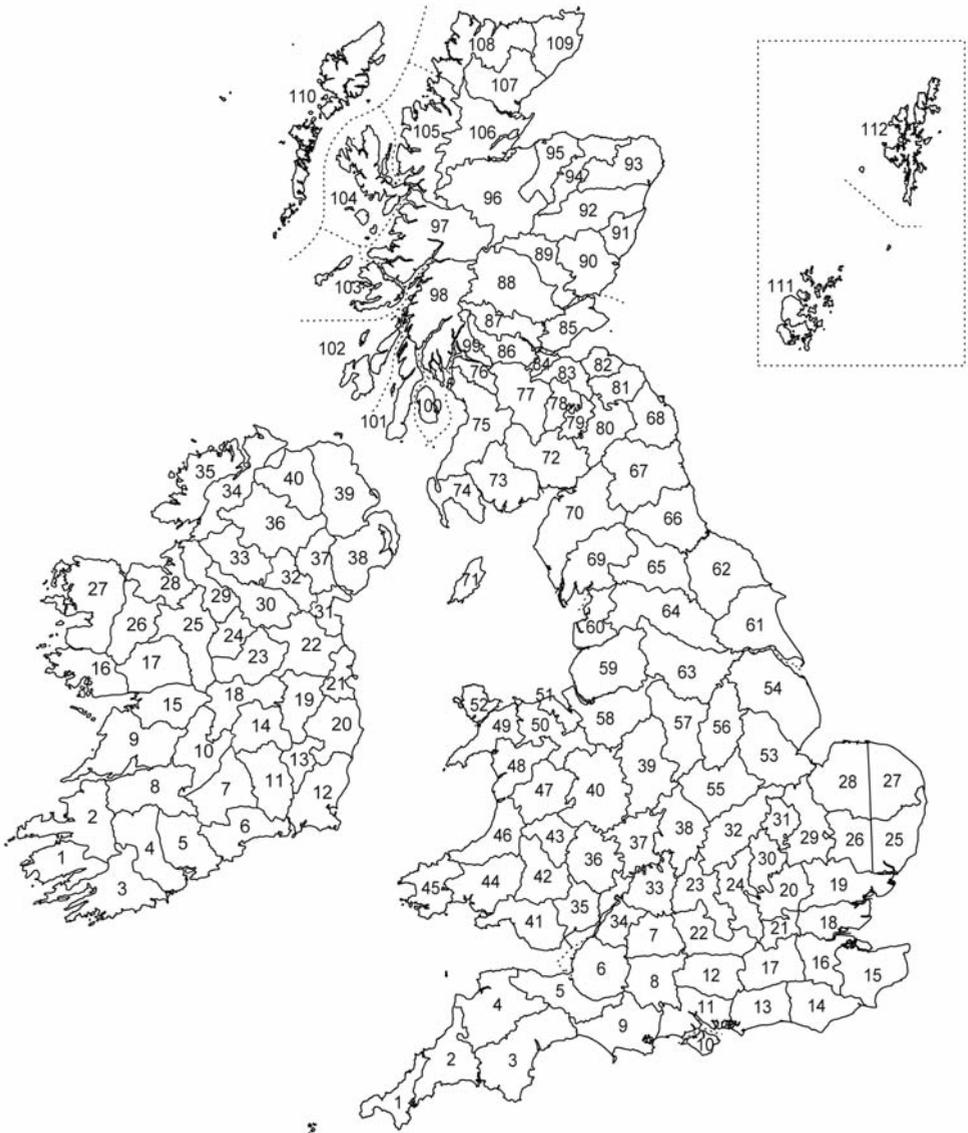


Fig. 2. Vice counties of Great Britain and of Ireland. The Irish series is prefixed 'H' when referred to in the text.

species are in fact aggregates of two or more cryptic species (i.e. for which morphological distinguishing characters have not so far been found). This is commented upon in the text under the relevant species, but we also give a simple schematic representation of their cladogram (Fig. 1) indicating for which species these aggregates are known.

Distributional data are given on a vice county basis for British and Irish material (cf. Fig. 2); the Irish (= whole island) series of vice counties is prefixed 'H'. The number of specimens is condensed to 'several' (4–10 specimens), 'many' (11–25) or 'numerous' (more than 25). More exact data are given when specimens from fewer than five British localities are present.

The date ranges given for flight times exclude data from reared specimens, because the husbandry conditions behind much of the reared material donated to MRS (ultimately deposited in NMS) do not necessarily constitute a good reflection of nature. However, it can often be deduced whether or not a species is univoltine from the rearing data, and when possible we note that. The term 'plurivoltine' is used to signify more than one annual generation: in such cases often there will be only two, but 'bivoltine' is too restrictive a term for species that pass a generation without obligatory diapause, as under favourable conditions some species in that category undoubtedly have three or possibly even more generations in a year.

Rearing records are given quantitatively (in host mortalities in the case of the few gregarious species). In his revision of western Palaearctic *Meteorus*, Huddleston (1980) had included some host records from the NMS collection (at that time, and so called by him, the M. R. Shaw collection, Reading). As our account covers all the material in the NMS collection, it is important to recognize when we are not necessarily giving new, independent citations. Therefore in these cases the host names given here are marked with an asterisk (*) to avoid undue reinforcement. Unless otherwise indicated (for the species that use Coleoptera), the hosts recorded are Lepidoptera. When a host association is given solely on the basis of non-British material, the country is indicated: otherwise host records are (at least in part) British. We have attempted to update host names according to current nomenclature, rather than transcribe often obsolete or misspelled names from data labels.

Material in MNS and taxonomic notes

Meteorus abominator (Nees, 1811)

Numerous specimens. **England:** V.C.s 7, 11, 22, 23, 28, 29, 64. **Wales:** V.C.s 42, 52. **Scotland:** V.C.s 87, 88, 92, 96, 99, 103, 105. **Ireland:** V.C. H30. **France:** Jura. **Germany:** Baden-Württemberg. Specimens collected from v–ix.

Molecular evidence (CO1) suggests that an additional, cryptic species is present in Europe (Stigenberg & Ronquist, 2011), but it is unknown whether or not it occurs in Britain, nor have hosts been assigned to the segregates.

Meteorus abscissus Thomson, 1895

England: 1 ♂, Berkshire, Ascot, Silwood Park (V.C.s 22), ex *Operophtera brumata* (Linnaeus) (Geometridae) on *Betula*, coll. 12.vi.1994, coc. 20.vi.1994, em. 6.vii.1994 (*M. R. Shaw*). **Scotland:** 2 ♀, Sutherland, Migdale Wood, NH 6590, 26.vi.1999 (1 ♀) and 31.v.2002 (1 ♀) (*P. J. Chandler*). **France:** 3 ♀, Vendée, Vienne, Hautes-Alpes.

Two of the French specimens are reared from unidentified Arctiidae (*V. Cameron-Curry*; *J. E. Pateman*). Although having the morphological characters of *M. abscissus* well developed, the reared English male must be considered doubtfully determined, as *M. abscissus* is otherwise certainly known only from Arctiidae, and the close relative *M. pulchrichornis* (Wesmael) has a broad host range likely to encompass *O. brumata*.

Meteorus acerbiavorus Belokobylskij, Stigenberg & Vikberg, 2011

Finland: 1 ♀, 767:325, Enontekiö Lapland, Jehkats, ex cocoon *Acerbia alpina* (Quensel) (Arctiidae), vi.2009 (*H. Lonka*); 1 ♀, same data, but 7679:3245, coll. 2006 (*M. Mutanen*); 1

♂, 769:326, Enontekiö Lapland, Loussujärvi, ex cocoon *A. alpina* coll. 2.vi.1992 (J. Kytömaa). These are all paratypes, from different gregarious broods. **Sweden:** Torne Lappmark, Abisko, Nissuntjärro, 1050 m. 2 broods (20 ♀, 35 ♂ and 3 ♀, 39 ♂) ex cocoons *A. alpina* coll. 29.vi.2012, em. respectively 11.vii.2012 and 9.vii.2012 (*A. Amandusson*). It is interesting that both broods are male-dominated, the second one extremely so. The tough parasitoid cocoons are entirely constrained within that of the host, and are loosely associated via short threads at their caudal ends (i.e. the cocoons are broadly of the pendulous type, without actually being pendulous).

As this species has not been recorded in Sweden previously, despite many collections of the host cocoons from this area in the past (Claes Eliasson, pers. comm.), 2 ♀, 2 ♂ from the first and 4 ♂ from the second brood have been transferred to the Swedish Museum of Natural History, Stockholm; a pair from the first brood has similarly been donated to the Natural History Museum (BMNH), London. The CO1 sequences of Finnish and Swedish specimens are identical.

Meteorus affinis (Wesmael, 1835) aggregate

Numerous specimens. **England:** V.C.s 2, 3, 6, 7, 8, 11, 14, 15, 17, 22, 23, 28, 29, 34, 58. **Wales:** V.C. 49. **Scotland:** V.C.s 83, 87, 88, 92, 93, 101, 105, 106, 110. **Ireland:** V.C. H30. **Sweden:** Västerbotten, Skåne. **Finland:** North Karelia. **Netherlands:** Gelderland, North Brabant. **France:** Seine-et-Marne. **Switzerland:** Grisons, Solothurn, Zürich. **Spain:** Madrid. **Madeira.** Specimens collected from v-x. Reared from Psychidae: *Bruandia comitella* (Bruand) (3, Switzerland) (*S. E. Whitebread*), *Dahlica inconspicua* (Stainton) (1) (*J. M. Chalmers-Hunt*), *Dahlica lichenella* (Linnaeus) (6, Sweden, Switzerland, Netherlands) (*N. Ryrholm*, *J. Voogd*, *S. E. Whitebread*), *Narycia duplicella* (Goeze) (3) (*E. S. Bradford*, *J. Voogd*, *M. R. Young*), ?*N. duplicella* (1) (*M. R. Young*), *Psyche casta* (Pallas) (2) (*J. P. Brock*), *Solenobia* sp. (1, Switzerland) (*S. E. Whitebread*); Tineidae: *Infurcitinea argentimaculella* (Stainton)* (35) (*E. S. Bradford*, *M. F. V. Corley*, *R. J. Heckford*), ?*Monopis laevigella* ([Denis & Schiffermüller]) (1) (*K. P. Bland*); Oecophoridae: *Aplota palpella* (Haworth) (2) (*M. F. V. Corley*, *J. R. Langmaid*), *Crassa unitella* (Hübner) (1) (*R. J. Heckford*), *Denisia albimaculea* (Haworth) (1, Netherlands) (*R. J. Heckford*), ?*Endrosia sarcitrella* (Linnaeus) (1) (*K. P. Bland*), *Esperia sulphurella* (Fabricius) (1) (*R. J. Heckford*), *Metalampra italica* Baldizzone (1) (*R. J. Heckford*); Gelechiidae: *Bryotropha senectella* (Zeller) (1) (*R. J. Heckford*); Pyralidae: *Dipleurina lacustrata* (Panzer) (5) (*M. R. Shaw*, *P. A. Sokoloff*), *Eudonia angustea* (Curtis) (3) (*E. S. Bradford*), ?*E. angustea* (2) (*E. S. Bradford*, *R. J. Heckford*), *Eudonia mercuriella* (Linnaeus) (1) (*J. R. Gregory*), *Eudonia murana* (Curtis) (1) (*K. P. Bland*), *Eudonia truncicolella* (Stainton) (1) (*R. J. Heckford*), *Scoparia ambigualis* (Treitschke) (1) (*R. J. Heckford*), *Scoparia basistrigalis* Knaggs (2) (*R. J. Heckford*); Geometridae: *Xanthorhoe fluctuata* (Linnaeus) (1) (*G. E. King*). The last record is not supported by the presence of host remains and is regarded as suspect; in any case, it is clearly outside any reasonable definition of host range (cf. Shaw, 1994).

The molecular phylogeny undertaken by Stigenberg & Ronquist (2011) demonstrates the existence of either two additional cryptic species (on the basis of both CO1 and 28S) or an extra five (from CO1 only). So far it has not been possible to assign many hosts to these segregates, but it has been found that at least two of the cryptic species occur in Britain, one associated with *Metalampra italica* and one with *Eudonia murana*. It seems likely, but by no means certain, that the other segregates will be found to be associated with other host families, probably including those listed above. For the moment, however, there is no sensible alternative than to list all the NMS material under one (aggregate) name.

Meteorus alborossicus Lobodenko, 2000

New to Britain. **England:** 5 ♀, Cambridgeshire, Chippenham Fen, TL 650693 (V.C. 29), 25.vi-8.vii.1983 (1 ♀) and 25.vi-9.vii.1985 (4 ♀) (*J. Field*); 2 ♀, Norfolk, Santon Downham, TL 818883 (V.C. 28), 6-20.vii.1985 (1 ♀) and 20-30.vii.1985 (1 ♀) (*J. Field*). United Kingdom was mentioned in the list of countries given for this species by Stigenberg & Ronquist (2011) on the basis of these specimens.

Meteorus brevicauda Thomson, 1895

England: 1 ♀ Cheshire, Lindow Common (V.C. 58), ex *Zeugophora subspinosa* (Fabricius) (Coleoptera: Chrysomelidae) mining *Populus tremulus*, coll. 12.x.1979, erupted ex prepupa in

soil, em. 15.vi.1980 (*M. R. Shaw*); unsexed fragment, Lancashire, Ainsdale Dunes (V.C. 59) ex *Z. subspinosa* mining *Populus alba* + *P. canescens*, coll. 26.vii.1989, em. 1990 (*M. R. Shaw*). See Shaw (1988).

Meteorus cespitator (Thunberg, 1824)

Numerous specimens. **England:** V.C.s 4, 7, 22, 23, 29, 33, 58. **Wales:** V.C. 52. **Scotland:** V.C.s 77, 81, 83, 99. **Corsica.** Specimens collected from vi–ix and in x/xi. Reared from the tineids *Monopis laevigella* ([Denis & Schiffermüller])* (8) (*S. D. Beavan, K. P. Bland, M. R. Shaw*), *Tinea trinotella* Thunberg (2) (*R. P. Knill-Jones*), *Tineola bisselliella* (Hummel) (37) (*G. Salt*).

Additionally, there are several specimens reared from bird nests, owl pellets, old blankets etc. harbouring the above and other tineids (sometimes along with oecophorids from which, however, we have no certain rearing). Emergence from such substrates has sometimes been in vi of the year following autumn collection, but it is not clear at what stage (e.g. larva in host larva, cocooned prepupa, etc.) the winter is passed. This species is evidently at least largely thelytokous (males occur, but they are scarce; in NMS are 77 females, and only 2 males), and it is clear from the rearing and capture data that it is plurivoltine.

From molecular evidence Stigenberg & Ronquist (2011) inferred the presence of an additional European species within this morpho-species, but its host relations are unknown and there is no evidence that it occurs in Britain.

Meteorus cinctellus (Spinola, 1808)

Numerous specimens. **England:** V.C.s 3, 6, 12, 16, 22, 23, 28, 29, 58. **Wales:** V.C. 46. **Scotland:** V.C.s 75, 83, 92, 97, 108. **France:** Dordogne. Specimens collected in iv/v, from vi–viii(?ix) and in ix/x. Reared from the pyralids *Crambus uliginosellus* Zeller (1) (*R. J. Heckford*), ?*Eudonia angustea* (Curtis) (1) (*R. J. Heckford*), *Nomophila noctuella* ([Denis & Schiffermüller]) (3) (*S. D. Beavan, R. J. Heckford*), *Pyrausta purpuralis* (Linnaeus) (10) (*S. D. Beavan, R. J. Heckford*), *Scoparia ambigualis* (Treitschke) (4) (*R. J. Heckford*), *S. ambigualis* or *Eudonia truncicolella* (Stainton) (1) (*R. J. Heckford*).

All reared specimens have emerged in the year of host collection, the dates ranging from iii–x, which suggest that it is plurivoltine but leaves its means of overwintering unclear. Although males have occasionally been seen, all 67 specimens in NMS are female and it is clear that this species is thelytokous. The specimen from *Crambus uliginosus*, which is British, has an anomalous CO1 sequence, but it is unclear how to interpret this.

Meteorus cis (Bouché, 1834)

Numerous specimens. **England:** V.C.s 22, 58. **Wales:** V.C.s 41, 42. **Scotland:** V.C.s 81, 110. Specimens collected in viii(?ix). Reared from *Cis boleti* Scopoli (Coleoptera: Ciidae) in *Trametes gibbosa* (20 on one occasion) (*I. Sims*), *Trametes versicolor* (Linnaeus) (2) (*G. Orledge*) and *Coriolus* sp. (1) (*G. Orledge*).

In some cases the parasitoids emerged in early summer from fungus collected the previous autumn, but from late summer collections emergence was in vii and ix. Although the exact way of overwintering is unclear, the species is evidently plurivoltine. It reproduces thelytokously and males are virtually unknown.

The molecular phylogeny (CO1 and 28S) published by Stigenberg & Ronquist (2011) demonstrated that there is an additional European species within the morpho-species, but neither its host relations nor whether it occurs in Britain are known.

Meteorus colon (Haliday, 1835)

Numerous specimens. **England:** V.C.s 3, 11, 12, 14, 17, 22, 23, 27, 28, 29, 33, 36, 62, 63, 69. **Wales:** V.C.s 48, 52. **Scotland:** V.C.s 77, 82, 88, 95, 96, 97, 99, 103, 105, 106, 108. **France:** Haute-Marne, Puy-de-Dôme. **Hungary:** Barsod-Abaúj-Zemplén. Specimens collected from v–x. Reared from Nymphalidae: *Limenitis camilla* (Linnaeus)* (5) (*J. E. Pateman, P. W. Cribb*); Geometridae: *Anticollix sparsata* (Treitschke)* (1) (*J. R. Langmaid*), *Hydriomena furcata* (Thunberg) (1) (*T. H. Ford*), *Xanthorhoe biriviata* (Borkhausen) (1, France) (*M. R. Shaw*), indet. Geometridae (6); Noctuidae: *Diarsia brunnea* ([Denis & Schiffermüller]) (1) (*R. I. Lorimer*), *Orthosia cerasi* (Fabricius) (2) (*M. R. Shaw*), *Orthosia gothica* (Linnaeus) or *Antitype chi* (Linnaeus) (1) (*T. H. Ford*), *Pseudoips prasinana* (Linnaeus) (1, France) (*M. R. Shaw*), ?*Xestia agathina* (13) (*T. H. Ford*), indet. Noctuidae (1).

The broad host range represented by the reared material is to some extent paralleled by considerable variation in *M. colon*, with apparent host fidelity in some cases; for example, specimens from *L. camilla* are invariably pale. Taken as a whole, *M. colon* is clearly plurivoltine; the rearing data accompanying some of the above clearly indicate that it overwinters as a young larva in *L. camilla* (of which it is an especially common parasitoid (Shaw, 1981b)), *Diarisia brunnea* and *Xestia agathina*. Two male specimens reared from arctiids in England: Cornwall (V.C. 1, *Arctia villica* (Linnaeus), G. E. King; V.C. 2, *Spilosoma lutea* (Hufnagel), J. L. Gregory) do not quite fit the morphological limits of *M. colon* and may belong to an undescribed species. Another specimen, a female from Scotland: Orkney (V.C. 111) from the geometrid *Thera* sp. on *Juniperus* (*R. I. Lorimer*), is also outside the normal limits, but it is apparently not conspecific with the males from arctiids.

From a molecular phylogeny based only on the mitochondrial CO1 gene, Stigenberg & Ronquist (2011) found that *M. colon* as presently understood is probably an aggregate of two recently diverged species, but as yet host data have not been associated with either segregate. It is also unclear whether or not both occur in Britain.

Meteorus consimilis (Nees, 1834)

England: 1 ♀, 1 ♂, Norfolk, Catfield, TG379201 (V.C. 27), 25.ix–24.x.1983 (1 ♀) and 17–29.viii.1983 (1 ♂) (*R. T. J. Jarvis*); 2 ♀, 1 ♂, Norfolk, Santon Downham, TL818883 (V.C. 28), 15–27.viii.1984 (1 ♀), 5.ix–12.x.1985 (1 ♀) and 22.viii–5.ix.1985 (1 ♂) (*J. Field*); 1 ♀, Yorkshire, Askham Bog (V.C. 64), viii.1999 (*P. J. Mayhew*). **France:** 2 ♀, 1 ♂, Lot-et-Garonne, Bernac, 11–31.vi.1992 (1 ♀), 3–21.viii.1987 (1 ♀) and 25.vii–2.viii.1993 (1 ♂) (*R. Askevo*).

This appears to be a univoltine species that flies mainly in late summer and autumn, although the data for one of the French specimens might suggest that it is plurivoltine.

Meteorus corax Marshall, 1898

Finland: 1 ♀, Northern Savonia, Kangaslampi, 10.vii.1998 (*N. Laurence*).

Meteorus eadyi Huddleston, 1980

England: 2 ♀, Oxfordshire, Taynton Fen, SP233248 (V.C. 23), 16.vi–17.vii.1989 (1 ♀) and 7–28.vii.1989 (1 ♀), (*K. Porter/NCC*); 2 ♀, Norfolk, Santon Downham, TL818883 (V.C. 28), 25.vi–6.viii.1985 (*J. Field*); 6 ♀, Cambridgeshire, Chippenham Fen, TL650693 (V.C. 29), 16–24.vi.1983 (1 ♀), 8–21.viii.1983 (1 ♀), 22.viii–27.ix.1984 (1 ♀), 25.vi–5.vii.1985 (1 ♀) and uncertain dates (2 ♀) (*J. Field*).

Meteorus eklundi Stigenberg, 2011

New to Britain. **England:** 2 ♀, Cambridgeshire, Chippenham Fen, TL650693 (V.C. 29), 9–20.vii.1984 (1 ♀) and 25.vi–9.vii.1985 (1 ♀) (*J. Field*). **Sweden:** 1 ♀, Västerbotten, Romelsön, RN7208/1759, 21.vi–29.viii.2003 (*R. Petterson*). These three specimens are all cited paratypes and the two English specimens are the basis for the mention of United Kingdom in the distribution given by Stigenberg Ronquist (2011).

Meteorus filator (Haliday, 1835)

Numerous specimens. **England:** V.C.s 3, 16, 17, 19, 22, 23, 24, 27, 28, 29, 36, 39, 58, 63, 64, 69. **Scotland:** V.C.s 76, 84, 96, 99, 101. **France:** Seine-et-Marne. Specimens collected from vi–xi, particularly in late summer and autumn.

This is another species for which the CO1 and 28S molecular evidence (Stigenberg & Ronquist, 2011) demonstrates the existence of a further European species within the morpho-species, but no hosts are assigned to either segregate and it is unclear whether or not both occur in Britain.

Meteorus heliophilus Fisher, 1970

France: 1 ♀, Côte-d'Or, Léry, 15.vii.2003 (*M. R. Shaw*); 1 ♂, Côte-d'Or, Val Suzon, 13–14.vii.2003 (*M. R. Shaw*).

Meteorus hirsutipes (Huddleston, 1980)

England: 4 ♀, Buckinghamshire, Burnham Beeches, SU943848 (V.C. 24), 5–31.viii.1996 (2 ♀) and 13–26.x.1996 (2 ♀) (*J. W. Ismay*); 1 ♀, 1 ♂, Hampshire, Leckford Estate (V.C. 12), 25.vii.1998 (*P. J. Chandler*); 1 ♀, Wiltshire, Savernake Forest, SV214671 (V.C. 7), 26.ix–

17.x.1990 (*K. Porter/NCC*); 1 ♂, Surrey, West End Common, TQ1262 (V.C. 17), 17.vii.2002 (*P. J. Chandler*). An Irish paratype was included by Huddleston (1980) in his description of this species, but the above appear to be the first records for the British mainland.

Meteorus ictericus (Nees, 1811)

Numerous specimens. **England:** V.C.s 1, 2, 3, 4, 7, 8, 11, 13, 14, 15, 16, 17, 18, 21, 22, 23, 27, 28, 29, 33, 34, 58, 59, 61, 63, 67, 69. **Isle of Man:** V.C. 71. **Wales:** V.C. 45. **Scotland:** V.C.s 72, 77, 83, 84, 89, 92, 95, 96, 101, 103, 104. **Ireland:** V.C. H17. **France:** Haute-Marne, Côte-d'Or, Dordogne, Var, Vaucluse. Specimens collected from (?v)vi–x. Reared from Gracillariidae: *Caloptilia syringella* (Fabricius) (1) (*K. P. Bland*), *Povolnya leucapennella* (Stephens) (1) (*R. J. Heckford*); Ypsolophidae: ?*Ypsolopha parenthesesella* (Linnaeus) (1) (*J. N. Greatorex-Davies*); Tortricidae: *Acleris ferrugana* ([Denis & Schiffermüller]) (1) (*E. C. Pelham-Clinton*), *Acleris hastiana* (Linnaeus) (2) (*E. C. Pelham-Clinton*, *P. A. Sokoloff*), *Acleris rufana* ([Denis & Schiffermüller]) (1) (*R. J. Heckford*), *Acleris unbrana* (Hübner) (1) (*R. J. Heckford*), ?*Acleris variegana* ([Denis & Schiffermüller]) (4) (*J. L. Gregory*, *R. J. Heckford*, *M. R. Shaw*), ?*Ancylis upupana* (Treitschke) (1) (*E. C. Pelham-Clinton*), *Ancylis xylosteana* (Linnaeus) (10) (*G. E. King*, *M. R. Shaw*), *Archips podana* (Scopoli) (5) (*K. P. Bland*, *B. Fox*), ?*A. podana* (1) (*J. L. Gregory*), *Archips rosana* (Linnaeus) (1) (*M. R. Shaw*), *Cacoecimorpha pronubana* (Hübner) (2) (*F. D. Bennett*, *G. A. T. Jeffs*), *Croesia forsskaleana* (Linnaeus) (1) (*R. J. Heckford*), *Ephiphyas postvittana* (Walker)* (18) (*F. D. Bennett*, *J. M. Chalmers-Hunt*, *R. Craske*, *J. L. Gregory*, *R. J. Heckford*, *M. R. Shaw*), ?*E. postvittana* (2) (*R. J. Heckford*, *G. E. King*).

In addition there are large numbers of rearings from unidentified tortricids feeding on a wide range of trees and bushes, and it is clear that *M. ictericus* is (largely) specialized to that family. Emergence has always taken place from the cocoon without a true winter diapause, indeed sometimes in the depths of winter, and the species seems to be not only plurivoltine but also practically continuously brooded. It has been noted (Shaw, 1981a) that the host is often left able to resume feeding after the parasitoid has erupted, although never to develop further. This has been observed many times subsequently in several tortricid species, and in one closely observed case an unidentified tortricid larva resumed feeding (on *Arbutus unedo*) and produced 35 fecal pellets before eventually dying (*M. R. Shaw*, unpublished). Males are rare and *M. ictericus* is clearly at least largely thelytokous. However, a series of nine specimens reared in France (Var) from *Ancylis xylosteana* (Linnaeus) (*M. R. Shaw*) included three males.

From the CO1 molecular phylogeny produced by Stigenberg & Ronquist (2011) it appears that *M. ictericus*, as currently understood, is an aggregate of two morphologically indistinguishable species whose host associations remain unresolved. It is not clear whether or not both occur in Britain.

Meteorus jaculator (Haliday, 1835)

Numerous specimens. **England:** V.C.s 7, 22, 23, 28, 29, 37, 58. **Wales:** V.C. 52. **Scotland:** V.C.s 95, 96, 99, 105, 106. Specimens collected from viii–x(?xi). Reared in vi or later from standing dead wood collected in iv on three occasions; once with the tineid *Nemapogon cloacella* (Haworth) (*A. N. B. Simpson*) (though it is possible that this was not the host) and once each from *Alnus glutinosa* and *Sorbus aucuparia* (both *M. R. Shaw*) with no indication of a possible host.

Meteorus limbatus Maeto, 1989

New to Britain. Many specimens. **England:** V.C.s 29, 69. **Scotland:** V.C.s 72, 84, 86, 96, 107, 108. **France:** Dordogne. **Italy:** South Tyrol. **Sweden:** Västerbotten. Specimens collected from (?vi)vii–viii(?ix). Reared from the noctuids *Hypena proboscidalis* (Linnaeus) (8) (*J. Connell*, *B. C. Grobler*, *M. R. Shaw*) and *Hypena rostralis* (Linnaeus) (2, Sweden) (*C. U. Eliasson*). This seems to be a highly specialized parasitoid of *Hypena*. The specimens in NMS, and also one in BMNH, are the basis for the inclusion of United Kingdom in the distribution given by Stigenberg & Ronquist (2011).

Meteorus lionotus Thomson, 1895

Numerous specimens. **England:** V.C.s 9, 11, 15, 21, 22, 28, 34, 58, 59, 69. **Scotland:** V.C. 86. All the specimens in the collection are reared, with emergence in ca v–vi and viii–x. It

is clearly plurivoltine and the winter is passed within the host larva. Reared from the geometrids *Thera obeliscata* (Hübner)* (15) (M. R. Britton, J. M. Chalmers-Hunt, J. L. Gregory, G. M. Haggett, M. R. Shaw), *Thera britannica* (Turner) (7) (G. M. Haggett, P. E. Hatcher), *Eupithecia indigata* (Hübner) (1) (R. P. Knill-Jones), *Eupithecia tantillaria* Boisduval (1) (P. E. Hatcher) and incompletely identified geometrids on *Pinus* (2). All of the foregoing feed on conifers, with rearings from *Abies*, *Pinus*, *Pseudotsuga* and *Tsuga*.

Meteorus longipilosus Stigenberg, 2011

New to Britain. Many specimens. **England:** V.C.s 22, 23, 24, 28, 29. **Wales:** V.C. 46. **France:** Dordogne, Lot-et-Garonne. Specimens collected in (?v)vi and from (?vii)viii–ix(?x).

Meteorus melanostictus Capron, 1887

England: 1 ♀, 2 ♂, Wiltshire, Bentley Wood, SU2530 (V.C. 8) reared from the geometrid *Apeira syringaria* (Linnaeus) feeding on *Lonicera*, coll. iii–iv, em. iv–v in 1993–1994 (B. Fox), in which it had presumably overwintered. Huddleston (1980) cites many rearings from this host (G. T. Lyle), and also (although on what basis is unclear) gives the related species *Ennomos quercinaria* (Hufnagel), which feeds a little later in the year having over-wintered as an egg. This indicates that *M. melanostictus* is plurivoltine and probably specialized to a very narrow group of related hosts.

Meteorus micropterus (Haliday, 1835)

Numerous specimens. **England:** V.C.s 7, 29, 58, 62. **Wales:** V.C.s 42, 46, 49, 52. **Scotland:** V.C.s 92, 95, 99, 101, 105, 106, 108. Most of the sites are more or less boggy, and some are acidic. Specimens collected from v–x, especially in late summer. Although none of the specimens in NMS is reared, Huddleston (1980) had seen material reared from two species of Hepialidae.

Meteorus obfuscatus (Nees, 1811)

Numerous specimens. **England:** V.C.s 17, 20, 24, 29. Specimens collected from vii–x. Reared on three occasions, from the melandryid beetles *Orchesia micans* (Panzer) in *Fistulina hepatica* (10) (I. Sims) and in bracket fungus on *Quercus* (21) (J. A. Owen), and *Orchesia minor* (Walker) in a hard fungus on *Fraxinus* (9) (J. A. Owen). In two cases the fungus was collected during the winter and the adults emerged in spring, but the precise stage in which the parasitoid over-wintered is not clear. In the third case the fungus was collected in v, and the parasitoids emerged in vii, possibly representing a second generation.

On the basis of CO1 and 28S molecular data Stigenberg & Ronquist (2011) showed that two European species are present in this morpho-species, but it is unclear how many occur in Britain and host records remain un-apportioned.

Meteorus obsoletus (Wesmael, 1835)

Several specimens. **England:** V.C.s 17, 28. **Scotland:** V.C.s 88, 91, 98, 110. Specimens collected in vi and viii. Reared from the tortricids *Rhopobota ustomaculana* (Curtis) (3) (K. P. Bland) and *Epinotia cruciana* (Linnaeus) (1) (R. J. Heckford), as well as incompletely identified 'Microlepidoptera' (2).

Meteorus oculatus Ruthe, 1862

New to Britain. **Scotland:** 3 ♀, Perthshire, Rannoch, NN5655 (V.C. 88), vii.1990 (2 ♀) and viii.1990 (1 ♀) (I. MacGowan). The site is a native pine wood.

Meteorus pendulus (Müller, 1776) aggregate

Numerous specimens. **England:** V.C.s 3, 5, 7, 9, 10, 11, 12, 13, 16, 17, 18, 19, 20, 21, 22, 23, 25, 27, 28, 29, 33, 36, 38, 57, 59, 61, 63, 65, 66, 67, 69. **Wales:** V.C.s 35, 41, 45, 48, 52. **Scotland:** V.C.s 76, 77, 83, 84, 85, 86, 88, 89, 91, 96, 97, 99, 101, 102, 105, 106. **Ireland:** V.C.s H2, H3. **France:** Calvados, Seine-et-Marne. **Austria:** Lower Austria, Vienna. **Spain:** Madrid. Specimens collected from v–xi, females quite frequently in x and xi when the main hosts of the overwintering generation, such as *Mythimna*, *Noctua* and *Xestia* species, are plentiful as early instar larvae in grassland. Reared from the noctuids ?*Apamea unaminis* (Hübner) (1) (M. R. Shaw), *Agrochola lota* (Clerck)* (10) (M. R. Shaw), *Brachylochia viminalis* (Fabricius)* (1) (M. R. Shaw), *Ceramica pisi* (Linnaeus) (2) (P. Baker), *Cerapteryx graminis*

(Linnaeus) (3, Netherlands) (*K. Carl*), *Conistra vaccinii* (Linnaeus) (2, Austria) (*J. Connell*), *Cosmia trapezina* (Linnaeus)* (10) (*H. Abbasipour, J. P. Brock, T. H. Ford, J. L. Gregory, M. R. Shaw*), *Dryobotodes eremita* (Fabricius) (2) (*G. E. King, M. R. Shaw*), *Eremobia ochroleuca* ([Denis & Schiffermüller]) (1) (*M. R. Shaw*), *Euplexia lucipara* (Linnaeus)* (11) (*P. Baker, M. R. Shaw*), *Eupsilia transversa* (Hufnagel) (1) (*J. P. Brock*), *Lacanobia oleracea* (Linnaeus)* (4) (*P. Baker, T. H. Ford, M. R. Shaw*), *Mythimna conigera* ([Denis & Schiffermüller]) (2) (*J. Connell*), *M. ?conigera* (1) (*G. M. Haggett*), *Mythimna ferrago* (Fabricius) (1) (*G. M. Haggett*), *Mythimna impura* (Hübner) (1) (*G. M. Haggett*), *M. ?impura* (2) (*R. Leverton*), *Mythimna* sp.* (4) (*R. A. Softly, M. R. Shaw*), *Noctua orbona* (Hufnagel) (2) (*G. M. Haggett*), *Noctua fimbriata* (Schreber) (1) (*D. Howdon*), *Orthosia gracilis* ([Denis & Schiffermüller]) (4) (*M. F. V. Corley, M. R. Shaw*), *Phlogophora meticulosa* (Linnaeus) (7) (*P. Baker, T. H. Ford, J. L. Yela*), *Thalpophila matura* (Hufnagel)* (2) (*G. M. Haggett, R. A. Softly*), *Xestia xanthographa* ([Denis & Schiffermüller])* (2) (*M. R. Britton, M. R. Shaw*), *?X. xanthographa* (3) (*T. H. Ford*); also several specimens from incompletely identified noctuid larvae. There is also a single specimen (unfortunately lacking host remains) from the geometrid *Eupithecia venosata* (Fabricius) (1) (*J. M. Chalmers-Hunt*), but this is unlikely to be a regular association in the light of its evidently strong fidelity for noctuid hosts. A further specimen labelled as reared from the tenthredinid sawfly *Strongylogaster* also lacks host remains; the host record seems doubtful, and in any case this is unlikely to be part of any reasonable definition of the host range of *M. pendulus* (cf. Shaw, 1994).

The rearing data clearly show that this is a plurivoltine parasitoid that overwinters in larvae of grassland noctuids, emerging in spring early enough to take advantage of noctuid hosts feeding on the 'spring flush' of trees. Subsequently it becomes common on noctuids feeding on low plants in the middle and late part of the summer, emerging in early autumn to seek its overwintering hosts. There are probably three generations in many areas, though this could easily reduce to two. There are also two males in NMS reared from the lasiocampid *Malacosoma castrensis* (Linnaeus) (Turkey, Sivas) (*M. R. Shaw*) which come very close to *M. pendulus* but probably represent a different, perhaps undescribed, species.

According to the molecular phylogeny (CO1+28S) published by Stigenberg & Ronquist (2011), there are two additional cryptic species within the *M. pendulus* morpho-species in Europe. Few reared specimens have been sequenced, but one of those listed above, from *Noctua fimbriata*, belongs to one segregate, and those from *Euplexia lucipara*, *Mythimna conigera* and *Orthosia gracilis* to another. Both of these segregates are known in Britain but, apart from the above, hosts have not been apportioned and the affinity of the vast majority of specimens is unknown. Therefore, for now, there is no practical alternative but to list all NMS specimens under one (aggregate) name.

***Meteorus pulchricornis* (Wesmael, 1835)**

Numerous specimens. **England:** V.C.s 3, 9, 11, 13, 22, 69. **Wales:** V.C. 52. **Scotland:** V.C.s 83, 92, 94, 95, 97, 98, 99, 101, 104, 105, 106. **France:** Hérault, Var, Vaucluse. **Corsica. Spain:** Barcelona. Zaragoza. **Portugal:** Algarve. **Hungary:** Veszprém. Specimens collected from vi–viii(?ix). Reared from Choreutidae: *Anthophila fabriciana* (Linnaeus) (1, France) (*M. R. Shaw*); Gelechiidae: *Hyatima rhomboidella* (Linnaeus) (3) (*M. R. Shaw*); Pyralidae: *Uresiphita gilvata* (Fabricius) (3, Spain, Portugal) (*M. F. V. Corley, G. E. King*); Pterophoridae: *Amblyptilia acanthadactyla* (Hübner) (1) (*M. R. Shaw*); Nymphalidae: *Charaxes jasius* (Linnaeus) (1, Spain) (*G. Stefanescu*); Lasiocampidae: *Lasiocampa trifolii* ([Denis & Schiffermüller]) (1, Portugal) (*G. E. King*); Geometridae: *Agriopsis aurantiaria* (Hübner)* (2) (*M. R. Shaw*), *Cyclophora* sp. on *Quercus* (3, Hungary) (*M. R. Shaw*), *Eupithecia* sp. on *Juniperus* (1) (*R. Leverton*), *Operophtera brumata* (Linnaeus) (4) (*A. Page, M. R. Shaw*), *Operophtera fagata* (Scharfenberg) (2) (*M. R. Shaw*); Noctuidae: *Anata myrtilli* (Linnaeus) (2) (*R. Leverton*), *Eupsilia transversa* (Hufnagel)* (1) (*M. R. Shaw*), *Lycophotia porphyrea* ([Denis & Schiffermüller])* (6) (*M. Brooks, M. R. Shaw*), *Orthosia cruda* ([Denis & Schiffermüller]) (1) (*E. C. Pelham-Clinton*). The rearing data clearly demonstrate that this species is plurivoltine; *Lycophotia porphyrea* seems to be an important host, at least where it occurs, of the overwintering generation in Britain. There is also a female specimen from Turkey: Kahraman Maraş, Göksün (E.), Findik (1–2 km W), 1400 m, reared from the zygænid *Zygaena vicia*

([Denis & Schiffermüller]), coll. vi.1999, em. 14.vi.1999 (*W. G. Tremewan*), that is close to the *M. pulchrichornis*/*M. abscessus*/*M. limbatus* group, but on the basis of DNA appears to belong to a distinct and probably undescribed species.

The overall host range is evidently extremely wide. Molecular data suggest that a second European species is present in the *M. pulchrichornis* morpho-species, but so far it has not been detected in Britain and hosts have not been apportioned.

Meteorus punctifrons Thomson, 1895

France: 1 ♀, Gard, Camprieu, 1400m, on dead *Pinus sylvestris* with xylophagous beetles, 1.vii.1989 (*G. Delvare*).

Meteorus rubens (Nees, 1811)

Numerous specimens. **England:** V.C.s 3, 23, 28, 31, 34. **Wales:** V.C. 52. **Isle of Man:** V.C. 71. **Scotland:** V.C.s 72, 84, 88, 89, 92, 96, 97, 99, 103, 105. **France:** Alpes-de-Haute-Provence, Côte-d'Or, Dordogne, Indre-et-Loire, Lot, Vaucluse, Vienne. **Faeroe Islands.** **Corsica.** **Spain:** Zaragoza. **Turkey:** Ankara, Bolu. **Russia:** Primorski Krai. Specimens collected from v–x. Reared gregariously from the noctuid *Noctua pronuba* (Linnaeus) (2) (*S. Jancek*, *P. Waring*) and an unidentified noctuid (*F. D. Bennett*). Brood sizes were 22 in one case (*N. pronuba*) and uncounted but at least eight in the other two. There is an additional Scottish specimen labelled as reared from an unidentified geometrid on *Vaccinium myrtillus*, with no indication that it was gregarious. The identity of the specimen is not in doubt, but as the specimen lacks both its cocoon and host remains we regard the host data as suspect.

The molecular phylogeny (CO1 + 28S) published by Stigenberg & Ronquist (2011) revealed the presence of two additional cryptic species within the morpho-species in Europe. No hosts have been assigned to any of these three species and it is not known how many occur in Britain.

Meteorus ruficeps (Nees, 1834)

Several specimens. **England:** V.C.s 22, 27. **Isle of Man:** V.C. 71. **Scotland:** V.C.s 82, 84. Specimens collected in v and from viii–xi; probably plurivoltine. Reared from the tortricids *Epiblema cynosbatella* (Linnaeus) (1) (*K. P. Bland*), *Epiblema roborana* ([Denis & Schiffermüller]) (1) (*K. P. Bland*) and *Epiblema uddmanniana* (Linnaeus) (1) (*I. Sims*). It may be significant not only that these spring-feeding hosts are congeneric, but also that they feed on *Rosa* and *Rubus*. A further female was collected as an adult in v on *Rosa pimpinellifolia* (*F. D. Bennett*).

Stigenberg & Ronquist (2011) in their molecular phylogeny (CO1 + 28S) demonstrated the presence of an additional European species in the morpho-species, but it is not known whether both occur in Britain, and hosts are not assigned to either.

Meteorus rufus (De Geer, 1773)

Numerous specimens. **England:** V.C.s 15, 22. **France:** Dordogne, Loire-Atlantique, Morbihan. **Germany:** Baden-Württemberg. **Turkey:** Ankara, Kars, Nevşehir. Almost all the material is reared from Zygaenidae; in Britain from *Zygaena lonicerae* (Scheven) (10) from various more or less connected sites adjoining the M4 motorway where this moth colonized and became abundant on the pioneer growth of *Trifolium pratense* along the new embankments in 1982–1988, and subsequently could be found with this parasitoid in nearby sites at least until about 1995 (all *B. T. Parsons*); in France from *Zygaena trifolii* (Esper) (10) at four sites (*J. M. Desse*, *A. Rouch*); in Turkey at three sites from *Zygaena carniolica* (Scopoli) (18) (all *W. G. Tremewan*); and in Germany from an unknown number of sites from *Zygaena* sp. (5) (*J. Hermann*).

This is evidently a specialized and local species, far from ever-present in colonies of its *Zygaena* hosts, and perhaps prone to being out-competed by other parasitoids. Some of the material was collected early enough in the year for it to be reasonably certain that it would have over-wintered in the host larva, and adult emergence around or a little after midsummer suggests that it is univoltine.

Meteorus salicorniae Schmiedeknecht, 1897

Corsica: 1 ♀, Corte, Val de Restonica, 500m, 29.vii–3.viii.2001 (*M. R. Shaw*).

Meteorus sibyllae Stigenberg, 2011

New to Britain. **England:** 1 ♀, Oxfordshire, Taynton Fen, SP233148 (V.C. 22), 16.viii–8.ix.1989 (*K. Porter/NCC*); 2 ♀, Cambridgeshire, Chippenham Fen, TL650693 (V.C. 29), 25.vi–5.vii.1985 (*J. Field*); 1 ♀, Cheshire, Abbots Moss, SJ5868 (V.C. 58), 25.viii–21.ix.1986 (*R. R. Askew*). **Scotland:** 1 ♀, Dumbartonshire, Caldarvan, NS450836 (V.C. 99), 21.viii–19.ix.1999 (*I. C. Christie*); 1 ♀, Inverness-shire, Loch Garten (V.C. 95), ix.1981 (*J. A. Owen*).

Meteorus sulcatus Szépligeti, 1896

Numerous specimens. **England:** V.C. 22. **Poland:** Masovian, Maciej Zywno. Reared in England (Berkshire, Silwood Park) from 1–2 cm diameter twigs of a fallen, slowly dying *Quercus* with the cerambycid *Phymatodes alni* (Linnaeus) and infrequent *Agrilus* sp. (Buprestidae) (3) (*M. R. Shaw*); and in Poland from *Quercus* twigs with *P. alni* and Anthribidae (9) (*J. Hilszczanski*), from *Quercus* with the cerambycid *Pogonocherus hispidulus* (Piller & Mitterpacher) and the bostrichid *Xyloperla retusa* (Olivier) (16) (*J. Hilszczanski*), from *Quercus* with *Phymatodes alni* (Linnaeus) (4) (*J. Hilszczanski*, *M. Milkowski*), and from *Acer campestre* with the cerambycid *Molorchus umbellatarum* (Schreber) (1) (*J. Hilszczanski*). All 36 specimens are female, and it is clear that this species is thelytokous. It seems probable that various small Cerambycidae can serve as hosts, *Phymatodes alni* especially often. The dead wood substrate was generally collected very early in spring, and emergence took place within a month of its being brought indoors; from this it seems probable that the parasitoid is cocooned through the winter.

Meteorus tabidus, (Wesmael, 1835)

Scotland: 1 ♂, Inverness-shire, Insh Marshes (V.C. 96), 23.vi.2006 (*M. R. Shaw*)
Switzerland: 1 ♀, Graubünden, Albula Pass, 2300m, at *Saxifraga aizoides* flowers, 15.viii.1999 (*C. U. Eliasson*).

Meteorus tenellus Marshall, 1887

Confirmed as British (or perhaps new to Britain, as Marshall gave no locality and his material therefore may not have been British). Reinstated as a valid species from the synonymy of *M. cincitellus* by Stigenberg & Ronquist (2011). **Scotland:** 1 ♀, Aberdeenshire, Glen Tanar, NO4892 (V.C. 92), vi.1990 (*I. MacGowan*).

In the molecular phylogeny, based on both CO1 and 28S, constructed by Stigenberg & Ronquist (2011), two additional European species within the *M. tenellus* morpho-species are revealed, but neither has been detected in Britain, nor are host records apportioned.

Meteorus versicolor (Wesmael, 1835)

Numerous specimens: **England:** V.C.s 3, 11, 13, 17, 18, 26, 28, 37, 57, 59, 63. **Wales:** V.C.s 46, 47. **Scotland:** V.C.s 73, 79, 80, 83, 88, 89, 92, 95, 96, 97, 104, 105, 106, 108, 111. **France:** Ardèche, Lot-et-Garonne, Var, Vaucluse, Vendée. **Belgium:** Antwerp. **Spain:** Zaragoza. **Switzerland:** Bernese Oberland, **Madeira.** Specimens collected from vi–x. Reared from Gelechiidae: *Dichomeris ustalella* (Fabricius) (2) (*A. N. B. Simpson*, *J. M. Chalmers-Hunt*); Lycaenidae: *Callophrys rubi* (Linnaeus) (1) (*M. R. Shaw*); Lasiocampidae: *Macrothylacia rubi* (Linnaeus) (1) (*J. Mackay*); Geometridae: *Agriopsis aurantiaria* (Hübner) (1) (*M. R. Shaw*), *Agriopsis marginaria* (Fabricius) (1) (*M. R. Shaw*), *Apocheima pilosaria* ([Denis & Schiffermüller]) (1) (*M. R. Shaw*), *Ematurga atomaria* (Linnaeus) (7) (*M. R. Shaw*), *Epirrita* sp. (1) (*M. R. Shaw*), *Eulithis testata* (Linnaeus)* (1) (*M. R. Shaw*), *Hydriomena ruberata* (Freyer) (1) (*R. I. Lorimer*), *Pachycnemia hippocastanaria* (Hübner) (1, France) (*T. H. Ford*), *Thera juniperata* (Linnaeus) (4, France) (*M. R. Shaw*); Thaumetopoeidae: *Thaumetopoea pityocampa* (Linnaeus) (4, Spain) (*G. E. King*); Noctuidae: *Agrochola haematidea* (Duponchel) (1) (*G. M. Haggert*), *Anarta myrtilli* (Linnaeus)* (3) (*A. A. Allen*, *T. H. Ford*), *Lycophotia porphyrea* ([Denis & Schiffermüller])* (4) (*M. R. Shaw*), *Orthosia miniosa* ([Denis & Schiffermüller]) (5, France) (*M. R. Shaw*), *Nycteola revayana* (Scopoli) (1, France) (*T. H. Ford*); Lymantridae: *Orgyia antiquoides* (Hübner) (1, Belgium) (*K. Janssens*), *Orgyia dubia* (1, Spain) (*G. E. King*), *Euproctis chrysorrhoea* (Linnaeus) (4) (*P. H. Sterling*, *A. J. Halstead*), *Calliteara pudibunda* (Linnaeus)* (2, France, Switzerland) (*M. R. Shaw*, *S. E. Whitebread*) – as well as many from incompletely or doubtfully determined geometrids and noctuids.

Although *M. versicolor* is essentially restricted to 'Macrolepidoptera' feeding in an exposed situation, this is an extremely wide host range, encompassing species that feed on trees and bushes as well as many on heath and moorland vegetation. As *Calluna* heath can be regarded as canopy in a local sense, the searching niche becomes clearer as comprising more or less woody plants in open canopy. The rearing data make it clear that this is a plurivoltine species; hosts of the overwintering generation include *Euproctis chrysorrhoea* and *Lycophotia porphyrea*. *Meteorus versicolor* has been imported into North America for the biological control of *E. chrysorrhoea*. Typically the hosts of *M. versicolor* are relatively large species, the host is then killed before it is fully grown, and a stout dark brown, shortly pendulous cocoon is constructed. In the cases of small hosts, such as *Dichomeris ustalella* and *Nycteola revayana*, the host may become prepupal before the parasitoid erupts, in which case the cocoon is less stout, not pendulous, and constructed in the host's pupation site. The three females we have seen from these two hosts are morphologically typical specimens and it seems improbable that they belong to a different species.

Stigenberg & Ronquist (2011) published a molecular phylogeny that appeared, from limited DNA gene sequence data, to suggest the presence of a cryptic species within the *M. versicolor* morpho-species in Europe, but this was based on a misreading of part of the sequence and no such segregate really exists. We take this opportunity to rectify the error.

Meteorus vexator (Haliday, 1935)

Numerous specimens. **England:** V.C.s 7, 11, 12, 15, 17, 19, 22, 23, 24, 25, 27, 28, 29, 38, 58. **Scotland:** V.C. 96. **France:** Lot-et-Garonne. **Corsica.** **Hungary:** Veszprém. **Russia:** Primorski Krai. Specimens collected from v–x.

Reared several times from bracket fungi (and often collected around such fungi, even on living trees) and more especially dead wood harbouring various small Coleoptera, but as far as we are aware there are no unequivocal host records for this species. One of the above specimens, reared from a very soft, rotten, dead *Quercus* twig collected from the living tree (*M. R. Shaw*), had a cocoon to which beetle host larval remains, with prominent curved caudal processes, adhered. These were sent to a respected retired coleopterist with a developed interest in larvae, and who had agreed to examine them, but he has failed to respond to many requests over an 18-month period for either a determination or the return of the material. From the rearing data it is clear that this is a plurivoltine species that is present in the substrate through the winter, probably as a cocooned stage. Although they do occur (7 out of 219 specimens in NMS), males are rare and *M. vexator* is clearly thelytokous.

Zele albiditarsus Curtis, 1832

Numerous specimens. **England:** V.C.s 3, 12, 15, 16, 17, 21, 22, 23, 28, 29, 60, 63. **Scotland:** V.C.s 72, 76, 79, 83, 85, 92, 94, 95, 96, 97, 101, 104, 105, 107, 111. **Bulgaria:** Silistra, Varna. **Poland:** Masovian. **Hungary:** Vas. Specimens collected from v–viii. Reared from the noctuid *Panolis flammea* ([Denis & Schiffermüller]) (29, mostly from extensive surveys of this host) (*B. Hicks*, *S. R. Leather*, *R. I. Lorimer*), and ostensibly from the geometrids *Epirrita dilutata* ([Denis & Schiffermüller]), (2) (*M. R. Shaw*) and *Erannis defoliaria* (Clerck) (1) (*W. A. Watson*). Also reared several times from unidentified noctuids.

When parasitizing noctuids it appears to be univoltine, overwintering in its cocoon, with the adult emerging in around v/vi. It seems to be only infrequently reared from (moderately large) Geometridae and in fact the ones recorded here from *Epirrita* seem to be phenologically at odds with those ex noctuids, because the adult parasitoids emerged from their cocoons in the same year. Although these two specimens (both males) conform to van Achterberg's (1979; 1984) diagnosis of *Z. albiditarsus*, it seems possible that they may in fact be large dark specimens of *Z. deceptor*, illustrating the difficulties in the separation of some specimens of the two species. The specimen from *Erannis*, which spent about ten months in its cocoon, is much easier to accept as *Z. albiditarsus*. However, Gavin Broad (pers. comm.) has noted 'a diminishing trickle' of *Z. albiditarsus* in late summer through to October received from correspondants operating light traps, which may represent second generation specimens.

Zele caligatus (Haliday, 1835)

Many specimens. **England:** V.C.s 16, 56, 57, 63. **Scotland:** V.C.s 96, 111. **France:** Côte-d'Or. Specimens collected in vii. Reared from *Eupithecia* (Geometridae) species feeding on

moorland and prominent field layer plants as follows: *E. absinthiata* (Clerck) (2) (*T. H. Ford*), *E. assimolata* Doubleday (1) (*R. I. Lorimer*), *E. ?expallidata* Doubleday (1) (*J. Bowman*), *E. goossensiata* Mabille (3) (*T. H. Ford*), *E. goossensiata* or *E. nanata* (Hübner) (3) (*T. H. Ford*), *E. simpliciatata* (Haworth) (1) (*M. R. Shaw*), *E. subfuscata* (Haworth) (1) (*T. H. Ford*), *E. vigaureata* Doubleday (2) (*T. H. Ford*, *J. L. Gregory*).

This is a rather local, univoltine species, specializing on *Eupithecia*. All but one of the specimens are reared, emerging in about vii–viii from hosts collected in viii–x of the previous year, having passed the winter in the cocoon.

Zelee chlorophthalmus (Spinola, 1808)

Numerous specimens. **England:** V.C.s 2, 3, 7, 10, 11, 12, 15, 16, 17, 18, 21, 22, 23, 25, 27, 29, 33, 63, 64, 65, 69. **Scotland:** V.C.s 77, 83, 96. **France:** Côte-d'Or, Dordogne, Lot, Lot-et-Garonne. **Poland:** Mazowsze, Silesia. **Sweden:** Gotland. Specimens collected from iv–ix(x). Reared from the pyralids *Eurrhynpara hortulata* (Linnaeus) (2) (*J. L. Gregory*, *D. Hackett*), *Trachycera advenella* (Zinken) (6) (*M. R. Shaw*), *Algedonia terrealis* (Treitschke) (2) (*L. T. Ford*), and many times from cocoons found in winter under bark, in soft rotten wood, etc. that are compatible with *E. hortulata*.

Rearing and capture data show that this is a plurivoltine species, which appears to be specialized to Pyralidae. In Britain it can overwinter after using the common and widespread *E. hortulata*, and another common host, *T. advenella*, is available in early summer.

Zelee deceptor (Wesmael, 1835)

Numerous specimens. **England:** V.C.s 3, 7, 9, 11, 12, 13, 16, 17, 22, 23, 24, 27, 28, 29, 31, 36, 56, 57, 58, 59, 62, 63, 64, 69. **Wales:** V.C.s 45, 52. **Scotland:** V.C.s 73, 77, 81, 82, 83, 84, 86, 88, 89, 90, 92, 93, 95, 96, 97, 99, 101, 105, 106, 108. **Ireland:** V.C.s H5, H20, H29. **France:** Côte-d'Or, Puy-de-Dôme. **Sweden:** Västerbotten. **Switzerland:** Jura. Specimens collected from iv–x. This is a plurivoltine species, reared from Ethmiidae: *Ethmia dodocea* (Haworth) (1, Switzerland) (*S. E. Whitebread*); Geometridae: *Agriopsis leucophaearia* ([Denis & Schiffermüller]) (1) (*G. M. Haggert*), *Alcis repandata* (Linnaeus) (*M. R. Shaw*), *Anticlea badiata* (2) ([Denis & Schiffermüller]) (*T. H. Ford*), *Campaea margaritata* (Linnaeus) (1) (*M. R. Shaw*), *Catarhoe cuculata* (Hufnagel) (1) (*J. M. Chalmers-Hunt*), *Ematurga atomaria* (Linnaeus) (1) (*M. R. Shaw*), *Entephria flavicinctata* (Hübner) (2) (*I. C. Christie*), *Epirrhoe galiata* ([Denis & Schiffermüller]) (1) (*M. R. Shaw*), *Epirrita autumnata* (Borkhausen) (1) (*T. H. Ford*), *Epirrita dilutata* ([Denis & Schiffermüller]) (4) (*M. R. Shaw*), *Epirrita* sp. (2) (*M. R. Shaw*), *Eupithecia nanata* (Hübner) (3) (*T. H. Ford*, *M. R. Shaw*), *Eupithecia pygmeata* (Hübner) (1) (*G. M. Haggert*), *Eupithecia simpliciatata* (Haworth) (1) (*M. R. Shaw*), *Eupithecia tantillaria* Boisduval (1) (*P. E. Hatcher*), *Eupithecia* sp. (*R. P. Knull-Jones*, *M. R. Shaw*), *Macaria liturata* (Clerck) (1) (*P. E. Hatcher*), *Odontoptera bidentata* (Clerck) (1) (*M. Immes*); Noctuidae: *Anarta myrtilli* (Linnaeus) (11) (*A. A. Allen*, *K. P. Bland*, *T. H. Ford*, *M. R. Shaw*) – as well as many rearings from unidentified Geometridae.

This is predominantly a parasitoid of geometrids, although it is also a frequent parasitoid of the small noctuid *Anarta myrtilli*, which (like several of its geometrid hosts) feeds on *Calluna*. The rearing data show that *Z. deceptor* is a plurivoltine species that can overwinter in its cocoon; although some of its hosts overwinter as partly grown larvae, it is not clear in these cases whether they are parasitized before or after the winter. From *A. myrtilli*, both cocoons that overwinter as well as those from which adult emergence occurs in the year of their formation have arisen under (essentially) outdoor rearing conditions (*M. R. Shaw*).

Discussion

The rearing data presented above show that both *Meteorus* and *Zelee* contain a mixture of species having quite broad host ranges (in some cases disjunct, or discontinuous; cf. Shaw, 2003), and species that appear to be narrow taxon specialists with all their hosts being closely related. This pattern is found in many koinobiont (cf. Askew & Shaw, 1986) ichneumonoid genera (e.g. Shaw & Horstmann, 1997; Shaw, 2003), and conforms to the hypothesis (Shaw, 1994;

2003) firstly that some (not all) koinobionts over time recruit species to their widening host ranges piecemeal from the potential hosts encountered regularly in their searching environment, and secondly that such host ranges, especially if disjunct, can be a platform from which sympatric speciation occurs, the nascent/daughter species arising as a specialist on just part of the ancestral/parental host range. In essence, the trigger for both recruitment and subsequent specialization might be simple: just that, through some sort of environmental change or under extreme local circumstances, a particular potential host becomes sufficiently frequently encountered for the inherent disadvantage of adapting to it to be offset by the ease of finding it. Various mechanisms (including temporal displacement) can be envisaged to result in the next essential, of progeny arising through parasitism of the particular host then disproportionately encountering (or preferring) each other as mates. Also, whether or not the relative generalist will retain the host (or hosts) of the nascent specialist in its host range, or be competitively excluded from it (or them), is likely to depend on several factors, one of which might be how long ago the speciation event took place. The hypothesis is not, however, that all specialists have arisen recently, as there are also mechanisms whereby species can remain being taxon-specialists through evolutionary time without recruiting new disjunct hosts; these species then tending to become well isolated (i.e. lacking close relatives because none has arisen through relatively recent speciation). In order to test the speciation hypothesis adequately, rather than just to observe that the pattern of host range variation occurs in many parasitoid genera (and in particular koinobiont species whose development in concert with the living host tends to restrict host ranges, for example on grounds of physiological compatibility; cf. Askew & Shaw, 1986), an independent and robust phylogeny for species in the parasitoid genus is required, such as one based on gene sequence data. Indeed, there is some support for the hypothesis in the braconid subfamily Rogadinae from this quarter (Zaldivar-Riveron *et al.*, 2008).

The molecular phylogeny of European *Meteorus* and *Zele* species produced by Stigenberg & Ronquist (2011) in concert with the host range indications for the species associated with Lepidoptera (data on species parasitizing Coleoptera are clearly insufficient by far) given above might seem to provide an opportunity to test these ideas. The hypothesis suggests that there should be closely related species pairs (or groups) in which one relative generalist and one or more specialists are present (but it does not demand that for every specialist there should be a proximal generalist, nor indeed that speciation from every generalist will have occurred). In Figure 1 (a schematic representation of the molecular phylogeny) it is seen that there is at least weak support for the hypothesis. Firstly, the pattern is as predicted: species with on the one hand broad, and on the other hand narrow, host ranges are both distributed widely across the tree; secondly, in *Zele deceptor* (generalist) and *Z. caligatus* (specialist), and also in the *M. pulchricornis* (generalist) and *M. limbatus* and *M. abscissus* (both specialists) clade, the predicted relationships are present; and finally, some of the most isolated species in the phylogeny proposed by Stigenberg & Ronquist (2011) appear to be taxon specialists, for example *Meteorus micropterus*, *M. ruficeps* and perhaps less clearly *M. ictericus*. Unfortunately, however, the strongest conclusion is that available knowledge is too incomplete to test these ideas with any rigour. Partly

this is because sequence data for some of the known specialists are lacking, but also – more importantly – the great majority of the segregates (i.e. presumed good biological species) that have been detected within many morpho-species completely lack host information; and it is especially in these presumably recently nascent, morphologically as yet undifferentiated, species that the hypothesis predicts narrow host ranges.

We therefore urge that further research on Meteorinae, in rearing from wild-collected hosts and in sequencing as well as preserving in research collections the resulting parasitoid adults, is undertaken in what is now a reasonably accessible and interesting group of parasitoids. Unfortunately, most of the reared material detailed in this paper is too old (or has not been appropriately preserved) for DNA still to be extractable.

It is worth adding that many Meteorinae (especially species of *Zele*) are frequent visitors to light traps and, given that the key to European meteorines provided by Stigenberg & Ronquist (2011) is an open access publication available to anyone with an internet connection, the group is now ripe for inclusion, and indeed welcomed, in the British nocturnal ichneumonoid distribution mapping scheme organised by Gavin Broad (<http://www.nhm.ac.uk/research-curation/staff-directory/entomology/g-broad/index.html>).

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References

- Achterberg, C. van** 1979. A revision of the subfamily Zelinae auct. (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* **122**: 241–479.
- 1984. Addition to the revision of the genus *Zele* Curtis (Hymenoptera: Braconidae). *Entomologische Berichten* **44**: 110–112.
- 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandlungen* **283**: 1–189.
- Achterberg, C. van, Kenis, M. & Sileshi, G.** 2000. *Perilitus (Microctonus) larvicida* spec. nov. (Hymenoptera: Braconidae: Euphorinae) from Zambia. *Zoologische Mededelingen* **74**: 57–62.
- Askew, R. R. & Shaw, M. R.** 1986. Parasitoid communities, their size, structure and development, pp. 225–264. In Waage J. & Greathead D. (Eds), *Insect parasitoids*. London.
- Barrantes, G., Triana, E., Shaw, S. & Jones, G.** 2011. Characteristics of the cocoon and natural history of the gregarious *Meteorus restionis* sp. n. (Hymenoptera, Braconidae, Meteorinae). *Journal of Hymenoptera Research* **20**: 9–21.
- Boring, C. A.** 2010. *Morphology and Systematics of braconid Wasps* 123 pp Ph.D. Dissertation, University of Kentucky.
- Broad, G. R., Shaw, M. R. & Godfray, H. C. J.** Checklist of British and Irish Braconidae (Hymenoptera) <http://www.nhm.ac.uk/research-rx/files/braconidae-checklist-for-web-34139.pdf>
- Foerster, A.** 1862. Synopsis der Familien und Gattungen der Braconiden. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens* **19**: 225–288.
- Huddleston, T.** 1980. A revision of the western Palaearctic species of the genus *Meteorus* (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)*, (Entomology) **41**: 1–58.
- Li, F. F., Chen, X. X., Oaio, M. H., He, J. H. & Ma, Y.** 2003. Phylogenetic relationships of the Euphorinae (Hymenoptera: Braconidae) based on the D2 variable region of 28S ribosomal RNA. *Entomotaxonomia* **25**: 217–225.

- Maetô, K.** 1986. Systematic studies on the tribe Meteorini from Japan (Hymenoptera, Braconidae). I, the genus *Zele* Curtis. *Kontyû*, Tokyo **54**: 246–256.
- 1990. Phylogenetic relationships and host associations of the subfamily Meteorinae Cresson (Hymenoptera: Braconidae). *Japanese Journal of Entomology* **58**: 383–396.
- Muesebeck, C. F. W.** 1923. A revision of the North American species of ichneumon-flies belonging to the genus *Meteorus* Haliday. *Proceedings of the U.S. National Museum* **63**:1–44.
- Pitz, K. M., Dowling, A. P. G., Sharanowski, B. J., Boring, C. A., Seltmann, K. C. & Sharkey, M. J.** 2007. Phylogenetic relationships among the Braconidae (Hymenoptera: Ichneumonoidea): a reassessment of Shi *et al.* (2005). *Molecular Phylogenetics and Evolution* **43**: 338–343.
- Schwarz, M. & Shaw, M. R.** 1998. Western Palaearctic Cryptinae (Hymenoptera, Ichneumonidae) in the National Museums of Scotland, with nomenclatural changes, taxonomic notes, rearing records and special reference to the British check list. Part 1. Tribe Cryptini. *Entomologist's Gazette* **49**: 101–127.
- Sharanowski, B. J., Dowling, A. P. G. & Sharkey, M. J.** 2011. Molecular phylogenetics of Braconidae (Hymenoptera: Ichneumonoidea), based on multiple nuclear genes, and implications for classification. *Systematic Entomology* **26**: 549–572.
- Shaw, M. R.** 1981a. Some parasites of *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in Cornwall. *Entomologist's Gazette* **32**:36–38.
- 1981b. Parasitism by Hymenoptera of larvae of the white admiral butterfly, *Ladoga camilla* (L.) in England. *Ecological Entomology* **6**: 333–335.
- 1988. *Meteorus brevicauda* Thomson (Hymenoptera: Braconidae) reared from larvae of *Zeugophora subspinosa* (Fabricius) (Coleoptera: Chrysomelidae). *Entomologist's Gazette* **39**: 205–206.
- 1994. Parasitoid host ranges, pp. 111–144. In Hawkins, B. A. & Sheehan, W. (Eds), *Parasitoid community Ecology*. Oxford.
- 2003. Host ranges of *Aleiodes* species (Hymenoptera: Braconidae), and an evolutionary hypothesis, pp. 321–327. In Melika, G. & Thurczy, C. (Eds), *Parasitic Wasps: evolution, systematics, biodiversity and biological control*. Budapest.
- Shaw, M. R. & Horstmann, K.** 1997. An analysis of host range in the *Diadegma nanus* group of parasitoids in western Europe, with a key to species (Hymenoptera: Ichneumonidae: Campopleginae). *Journal of Hymenoptera Research* **6**: 273–296.
- Shaw, M. R. & Huddleston, T.** 1991. Classification and biology of braconid wasps (Hymenoptera: Braconidae). *Handbooks for Identification of British Insects* **7** (11): 1–126.
- Shaw, S. R.** 1985. A phylogenic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). *Entomography* **3**: 277–370.
- Stigenberg, J. & Ronquist, F.** 2011. Revision of the western Palearctic Meteorini (Hymenoptera, Braconidae), with a molecular characterization of hidden Fennoscandian species diversity. *Zootaxa* no. 3084: 1–95.
- Tobias, V. I.** 1986. Subfamily Euphorinae, pp. 181–250. In Tobias, V. I. (Ed.), *Keys to the Insects of the European part of the USSR* **3**. Hymenoptera. Part 4. Leningrad. [In Russian. English translation 1995, pp. 317–437. Science Publishers.]
- Zaldivar-Riveron, A., Shaw, M. R., Saez, A. G., Mori, M., Belokobilskiy, S. A., Shaw, S. R. & Quicke, D. L. J.** 2008. Evolution of the parasitic wasp family Rogadinae (Braconidae): phylogeny and evolution of lepidopteran host ranges and mummy characteristics. *BMC Evolutionary Biology* **8**: 329.
- Zitani, N. M.** 2003. *The evolution and adaptive significance of silk use in the Meteorinae (Hymenoptera, Braconidae)* 126 pp. Ph.D. Dissertation, University of Wyoming.
- Zitani, N. M. & Shaw, S. R.** 2002. From meteors to death stars: variations on a silk thread (Hymenoptera: Braconidae: Meteorinae). *American Entomologist* **48**: 228–225.