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To cite this article: Mark R. Shaw (2017): Anatomy, reach and classification of the parasitoid complex of a common British moth, *Anthophila fabriciana* (L.) (Choreutidae), *Journal of Natural History*, DOI: [10.1080/00222933.2017.1315837](https://doi.org/10.1080/00222933.2017.1315837)

To link to this article: <http://dx.doi.org/10.1080/00222933.2017.1315837>



Published online: 27 Apr 2017.



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Anatomy, reach and classification of the parasitoid complex of a common British moth, *Anthophila fabriciana* (L.) (Choreutidae)

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ABSTRACT

The small plurivoltine moth *Anthophila fabriciana* is widespread and often abundant in Britain wherever its main larval foodplant, stinging nettle, occurs. It overwinters as a larva (first generation) then has one or more partly overlapping summer broods (notionally second generation). A total of 5017 larvae were collected and reared from widely distributed populations in Britain, and the resulting 2167 host mortalities due to parasitoids were assessed. Small collections of pupae were also made. Altogether 25 parasitoid species, including secondary parasitoids, were found. Larval parasitism was heaviest in the second generation. In each generation there was a dominant parasitoid that was absent from the other. Summary information on the developmental biology and host range (expressed quantitatively and resulting from very broad rearing programmes) for each parasitoid is given. They are classed as 'absolute specialists', 'taxon oligospecialists', 'niche oligospecialists', 'niche generalists', 'casuals' and 'strays'. Both kinds of oligospecialists can be 'paraspecialists' if only one potential host occurs locally. Although constructing a quantitative food web is not appropriate, providing both source web and sink web data in quantitative form enables the parasitoid complex to be understood in the wider context of the ecosystem, necessary for both biodiversity and nature conservation interests. In Appendix 1, parasitoids reared from other European Choreutidae are listed quantitatively.

ARTICLE HISTORY

Received 12 January 2017

Accepted 31 March 2017

KEYWORDS

Specialisation categories; generation differences; Ichneumonoidea; Eulophidae; *Urtica dioica*

Introduction

Few terrestrial holometabolous insect species escape attack from parasitoids and, for many, parasitoidism (hereinafter 'parasitism') constitutes a major source of mortality. The parasitoid species that can be reared from a given host species are collectively termed its parasitoid complex. This will normally include both primary and secondary parasitism (hyperparasitism), and consideration of a parasitoid complex should carefully distinguish between these trophic levels. A further distinction is needed between true hyperparasitoids, that parasitise the primary parasitoid as it continues its own feeding development, and pseudohyperparasitoids that attack the primary parasitoid (typically in its cocoon) only after

its association with its host is over (Shaw and Askew 1976). Another important distinction concerns the way in which the parasitoid interacts with and develops in (or on) the host: as an idiobiont, by arresting the host practically at the time of attack; or as a koinobiont, allowing the host to continue its life for a time after the egg is laid (Askew and Shaw 1986). The species in a parasitoid complex may be quite numerous, and may include both frequent parasitoids of that host and ones that use it only rarely in relation to their more regular hosts. In the former category, there may be species whose host range is centred on the host in question – even to the point of absolute monophagy – and others which also regularly parasitise other hosts, typically either close relatives or unrelated taxa that share physical or ecological properties. Even among the most specialised, there may be parasitoids that are inherently rare or restricted to particular kinds of habitat, such that they may not be present in all or even most colonies of the host. Among those which habitually also use one or more different hosts there might be situations in which, as a result of the local absence of these alternative hosts, at a population level the parasitoid is essentially monophagous. A parasitoid's participation in the parasitoid complex of a particular host may also be seasonally variable, to a greater or lesser extent.

Both qualitative and quantitative aspects of a host's parasitoid complex are important components of its autecology, but for non-pest species little detailed knowledge exists even for extremely well-studied taxa such as species of British Lepidoptera (the few exceptions are mainly leaf-miners), or European butterflies (Shaw et al. 2009). Further, parasitoids are among the largest and least understood groups of insects in most faunas – in Britain, parasitic wasps constitute around a quarter of all insect species, and our biological knowledge of most of them is either non-existent or rudimentary. Gaps in autecological knowledge need to be filled in order to understand and monitor the wider ecosystem well enough to ensure its conservation. For specialised parasitoids, occupying narrow niches at high trophic levels, the extent of lacunae in autecological knowledge is in itself a serious conservation issue (Shaw and Hochberg 2001). Detailed analysis of a parasitoid complex, including consideration of the developmental biology and host ranges of the component species, is a useful approach that can provide a wealth of species-level information, and additionally leads to more general understandings of parasitoids and their reach within ecosystems. It might be argued that 'biodiversity' should always imply a consideration of complexity at least down to this level.

This paper analyses the results of an extensive survey of parasitism of the choreutid moth *Anthophila fabriciana* (L.) in England, Wales and Scotland, based largely on its larval stage with a little additional data on prepupal/pupal parasitism, examining in particular the consistency and constancy of the parasitoid complex. Samples of larvae were collected at various times and locations from 1976 to 2011 and totaled 5017 host individuals, from which 2167 mortalities due to parasitism resulted.

In a subsequent section, information on the developmental biology and host range of the 25 parasitoid species reared from *A. fabriciana* during the study are presented, from which the anatomy of the parasitoid complex, and the reach of the parasitoids that comprise it, can be more fully understood. Their taxonomy (with authorship) is also recorded in that section. Appendix 1 itemises quantitatively the parasitoids reared from other Choreutidae in Britain and Europe during more limited but concurrent investigations.

Materials and methods

The host

Anthophila fabriciana (adult wing span 11–15 mm) is widespread in Britain (Pelham-Clinton 1985) and usually at least moderately common wherever there are stands of its main foodplant, *Urtica dioica* (stinging nettle), a very widespread and frequently abundant prominent non-woody perennial. Eggs are laid singly on the foodplant and hatch within a few days. There are four larval instars (confirmed in this study). Throughout its larval life the host lives solitarily beneath a rather conspicuous web on its foodplant, either spun over the upper surface of a single leaf, whose edges are thereby somewhat drawn inwards to partially enclose the larva, or encompassing much of a terminal shoot. The webbed leaf is fed upon and, during its lifetime, the larva typically uses a succession of about three leaves. Because these are generally in the uppermost, exposed parts of the plant, the host larvae are easily found and sampled – probably with very little bias. Pupation occurs in a distinctive dense cocoon, usually made under a looser shelter within a folded leaf either low down on the foodplant or in litter below: for this reason it is much more difficult to sample cocoons, and especially to do so without bias.

In all but the most extreme environments there are several, partially overlapping, generations in the year. The winter is spent as early instar larvae, as was confirmed for both first and second instars entering diapause in autumn; in contrast, late-autumn larvae in their third and fourth instars have always continued to feed until pupation, with subsequent adult emergence without diapause. It has not been possible to overwinter adult moths under captive conditions that were highly successful for the choreutids *Choreutis pariana* (Clerck) and *Choreutis nemorana* (Hübner), and it seems certain that the only regular way that *A. fabriciana* has to survive the British winter is as early instar larvae. Post-diapause larvae recommence feeding on fresh nettle growth as it becomes available during mild periods in late winter, and in early spring (from late February or early March through May) there is a strong larval population that appears to have entirely originated during the previous autumn. This overwintered population, which is referred to as the ‘first generation’ or ‘Generation 1’, is more uniform in its developmental phenology than the subsequent generations, and in most localities and seasons pupation occurs mostly in April–May (with stragglers into June), with adults usually present by mid May. In this way it is effectively isolated from the subsequent summer population (‘second generation’ or ‘Generation 2’), whose larvae first appear from about June, but do not attain full growth until about July. That is to say, at any locality, usually commencing around early June, there will be a time when, if larvae are present at all, there is not a continuity of sizes: any late fourth-instar stragglers from the first generation will be readily separable from the earliest of the first and second instars of the next generation. Thus, from a sampling stance, there is no confusion between the two ‘generations’. Owing to both rapid larval development and adult longevity, by about August and September the summer population becomes an intractable mix of second-, third- and perhaps even fourth-generation individuals, and it is all treated here as ‘Generation 2’.

Sampling and rearing

Sampling was undertaken in small areas (‘sites’), typically only a few tens of metres in extent, and all individuals found were collected until sampling was stopped; ideally not until at least

50 larvae had been collected, but sooner if time was limited or the host was scarce. A wide range of semi-natural and spontaneous habitats in which stinging nettles tend to be abundant were sampled, though isolated patches in towns or surrounded by arable land were avoided. As far as possible, the full range of conditions (e.g. sun/shade, wind shelter/exposure, plant patch size) present at a site was sampled. Collections were only made when it was judged that at least half of the larvae present were in the third or fourth (final) instar. Some sites were revisited for different generations, and a few over successive years, but otherwise different sites (at least a kilometre distant) were sampled when dates ran close. Each larva was removed from its feeding web, and the counted cohort comprising a sample (= site + date) were reared together in closed plastic sandwich boxes (usually $17 \times 11 \times 6$ cm, but for small samples sometimes $13 \times 8 \times 6$ cm) bottom-lined with copious absorbent tissue (lavatory roll) on fresh, intact and carefully searched *Urtica dioica* leaves. The boxes were kept under outdoor conditions in a well-ventilated and fully shaded detached wooden shed, and were turned out for tissues and food to be replenished at less than weekly intervals: on these occasions parasitoid cocoons, matching host remains, and host cocoons were removed and scored, making a careful effort to find and account for all of the hosts supposed to be present. Parasitoid cocoons were kept individually in large (7.5×2.5 cm) corked glass tubes to await adult emergence; cocooned host pupae were kept in similar tubes but in batches according to recovery date and collection data. General details of rearing and accounting protocols are given by Shaw (1997). During rearing, small numbers of larval hosts died from causes unrelated to parasitism, including both viral and protozoan diseases and predation from overlooked anthocorid bug nymphs and cecidomyiid midge larvae. This combined mortality amounted to around 1% overall, but the loss was far from uniform across samples, and also afflicted the second generation disproportionately. In all cases the sample score was simply reduced accordingly. When (very rarely) loss through disease exceeded about 20% the sample was discounted, but usually the presence of serious disease could be detected at the time of collection, in which case a sample was not taken. Mortality at the pupal stage was sometimes heavier, but any pupa that had clearly progressed towards a pharate adult state was scored as unparasitised and in practice it was very seldom necessary to reduce sample sizes, and even then only marginally. Although it was clear that host population density varied greatly between years at several sites, it was not possible to monitor that nor to elucidate the causes.

The host pupates away from its feeding site, often off the plant, and consequently sampling the cocooned stages is difficult, and moreover particularly unlikely to accurately reflect the levels of parasitism or even the species of parasitoids that use those stages. No serious attempt was made to investigate this further, but the few host pupae and parasitoid cocoons casually encountered in the field were also collected, and kept individually in corked glass tubes. Because pupation occurs in a different area from larval feeding, these samples are not combined with the larval samples. No effort was made to assess egg parasitism. The host also feeds on the perennial herb *Parietaria judaica* (pellitory of the wall) but sampling from that plant was not extensive, and insufficient to compare with samples from *Urtica dioica*, so only samples from the latter plant are included here. No sign of *A. fabriciana* was seen during limited but significant time spent searching *Urtica urens* (small nettle), a sporadic annual, and it was concluded that the moth seldom, if ever, uses that plant. More extensive searching of that plant in S. Wales led to a similar conclusion (A. Davies, pers. comm.).

Data organisation and analysis

Apart from the gregarious koinobiont ectoparasitoids *Elachertus anthophilae* and *Stenomesus rufescens*, all the larval parasitoid species reared are solitary koinobiont endoparasitoids. The numbers given for each species refer to host mortalities: this is straightforward except for *Clinocentrus cunctator* (= *gracilipes*), in which about 12% of hosts envenomed by this species escape oviposition but, after initially recovering feeding activity, are arrested and die at the end of the instar (Shaw 1981, 1983). The arrested hosts are characteristic and, although no parasitoid develops, they are accounted as host mortalities due to *C. cunctator* rather than being deducted from the sample score.

The first- and second-generation samples were summed separately, and compared by the percentage similarity of primary parasitoid species' representation. This is calculated simply as the sums of the lower percentage representations within the parasitoid complex of shared parasitoids. To assess relative abundance of a parasitoid species in the two generations, only the number of that species and the numbers of unparasitised hosts were taken into account. An informal assessment of the number of parasitoid species present vs sample size suggested that samples of 35 were likely to contain practically as many species of parasitoids as samples of 70; accordingly, samples of 35 and more were used to assess the constancy of given parasitoid species in the complex (measured simply as the proportion of the samples of that size and above in which it occurred). The absolute number of samples (a sample being anything from one upwards at a discrete location and time) in which a given parasitoid species occurred was also recorded. Fisher's exact test (two-tailed) was used for 2×2 contingency comparisons (GraphPad.com QuickCalcs used 19 April 2016).

Some of the primary parasitoid species present in the host larvae collected had been attacked by true hyperparasitoids (cf. Table 1) – that is, secondary parasitoids that develop as koinobiont parasitoids of the primary parasitoid while the latter is itself developing in the host. This is presented and analysed in a separate section.

In the final section, concepts of host range are based strongly on the collection in the National Museums of Scotland (NMS), which is uniquely rich in Ichneumonoidea reared from Lepidoptera that have been determined (both hosts and parasitoids) by specialists. Reared material in most of the relevant groups has been catalogued and published quantitatively: see Shaw (1994) for a rationale of this approach towards understanding host ranges as opposed to unquantitative literature abstraction. In addition, particular account is taken of smaller scale investigation of parasitism of other Choreutidae carried out for comparative purposes (M.R. Shaw, unpublished including donated material; and Shaw 1984), as detailed in Appendix 1.

Results

Composition and seasonality

Table 1 records the summed rearings from first- and second-generation collections separately. For each parasitoid species the absolute number of samples (ranging from a single larva to over 100) in which it occurred, as well as its constancy (the proportion of samples of 35+ in which it occurred), in each of the two generations is also given. Figure 1 shows the most significant collecting locations in England, Scotland and Wales, and Table 2 presents the full data numerically according to six main areas.

Table 1. Adult moth and primary parasitoid outcomes from summed larval collections of *Anthophila fabriciana*, indicating also hyperparasitism by *Mesochorus* spp.

	Generation 1 N = 2650			Generation 2 N = 2367				
	Number/of which hyperparasitised	% sample/% parasitoids	Number of samples	Proportion of large samples	Number/of which hyperparasitised	% sample/% parasitoids	Number of samples	Proportion of large samples
Moths	1620	61.13			1230	51.96		
Diptera: Tachinidae								
<i>Actia pilipennis</i>	17/0	0.64/1.65	3	3/34 = 0.09	1/0	0.04/0.09	1	1/30 = 0.03
<i>Nemorilla floralis</i>	2/0	0.08/0.19	1	1/34 = 0.03	0/0			
Hymenoptera: Ichneumonidae								
<i>Lissonota stigmator</i>	527/53	19.89/50.73	36	30/34 = 0.88	0/0			15/30 = 0.50
<i>Triclistus anthophilae</i>	70/0	2.64/6.80	8	8/34 = 0.24	92/3	3.87/8.09	22	29/30 = 0.97
<i>Diadegma fabricianae</i>	92/7	3.47/8.93	26	20/34 = 0.61	292/84	12.34/25.68	49	
<i>Campoplex pyraustae</i>	0/0				4/0	0.17/0.35	3	2/30 = 0.07
<i>Campoplex tumidulus</i>	0/0				2/0	0.08/0.18	2	1/30 = 0.03
<i>Campoplex lyratus</i>	0/0				2/0	0.08/0.18	2	1/30 = 0.03
<i>Tranosemella citrofrontalis</i>	0/0				9/1	0.38/0.79	5	3/30 = 0.1
<i>Tranosemella praerogator</i>	0/0				1/0	0.04/0.09	1	1/30 = 0.03
Hymenoptera: Braconidae								
<i>Clino-centrus cunctator</i> ^a	3(3)/0	0.11/0.29	2	2/34 = 0.06	455(399)/0	19.22/40.00	46	27/30 = 0.90
<i>Microgaster nixalebion</i>	0 ^b /0				31/9	1.31/2.73	16	7/30 = 0.23
<i>Glyptapanteles lateralis</i> ^c	301/13	7.74/19.90	30	26/34 = 0.76	183/39	7.73/16.01	39	24/30 = 0.80
<i>Glyptapanteles fausta</i> ^c	14/2	0.53/1.35	9	7/34 = 0.21	43/13	1.82/3.78	17	11/30 = 0.37
<i>Chelonus contractus</i>	0/0				3/0	0.13/0.26	1	1/30 = 0.03
<i>Charmon cruentatus</i>	0/0				2/0	0.08/0.18	1	1/30 = 0.03
Hymenoptera: Eulophidae								
<i>Elachertus anthophilae</i>	1/0	0.38/0.97	1	0/34 = 0	13/0	0.55/1.14	5	4/30 = 0.13
<i>Stenomeseius rufescens</i>	0/0				1/0	0.04/0.09	1	1/30 = 0.03
Nematoda: Mermithidae								
Gen. sp. indet.	3/0	0.11/0.29	2	2/34 = 0.06	3/0	0.13/0.26	1	1/30 = 0.13

^a Hosts stung by *C. cunctator* do not always receive an egg, but die anyway. The total mortality caused is the first figure in columns 1 and 5, with the number of parasitoids actually developing in brackets. The first figure is used in the measure of total parasitism; thus, percentage of the total parasitism achieved by other species is scored fractionally lower than the percentage of parasitoids reared.

^b Although *Microgaster nixalebion* did not appear in these first-generation samples, specimens have been reared from the first generation of *A. fabriciana* in Britain (S. Wales) by A. Davies (pers. comm.).

^c Cocoon of the two *Glyptapanteles* species could not be separated; therefore, cocoons that failed to produce an adult *Glyptapanteles* (e.g. because hyperparasitised, or through unexplained mortality) were apportioned in line with abundance in the sample.

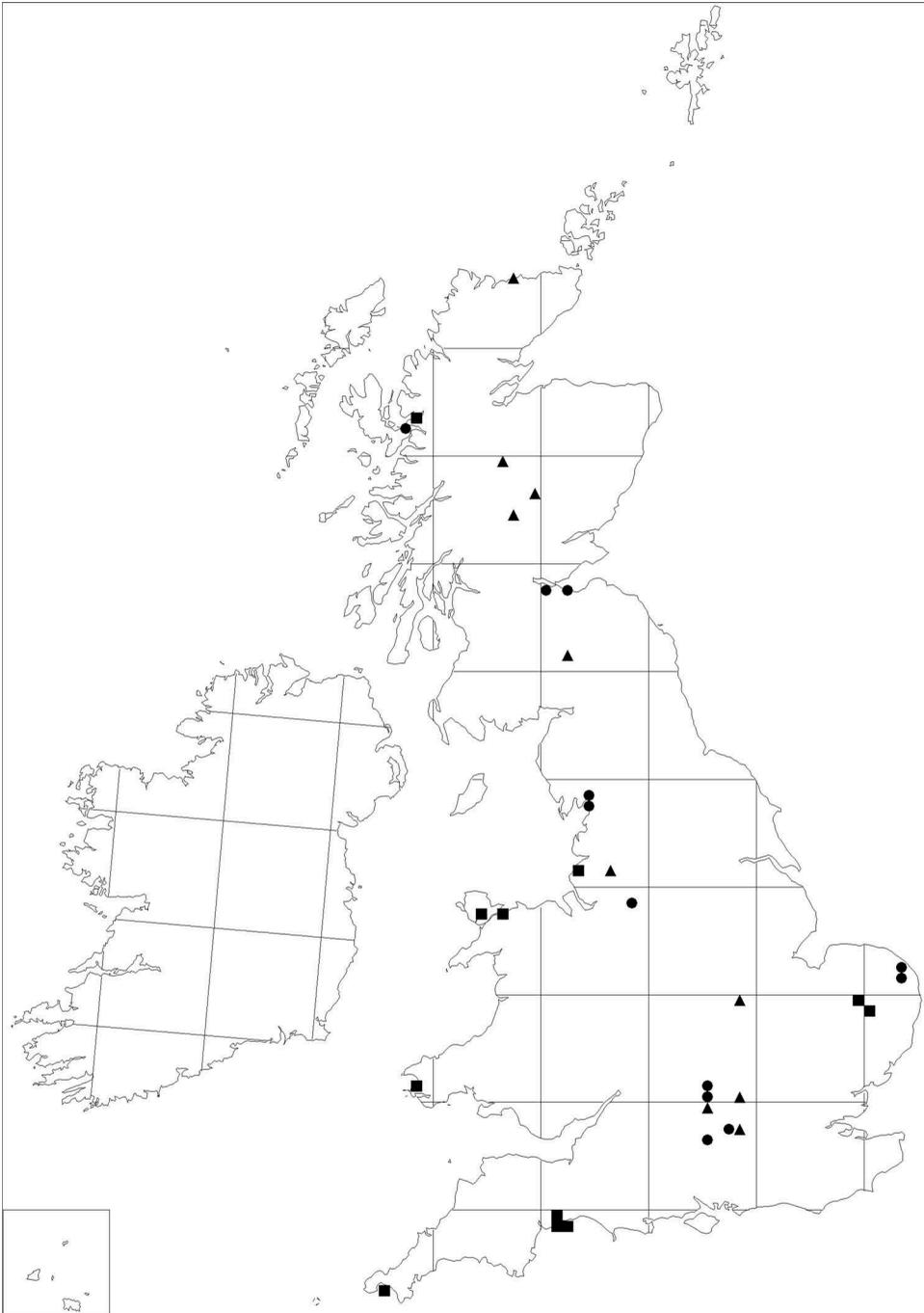


Figure 1. Principal collection regions: 10 km square of sites where one or more samples totaling 35+ hosts were collected are indicated by triangle (▲) for Generation 1 only, square (■) for Generation 2 only and circle (●) for both; only a single indication is made for the (many) situations in which different large samples were taken at different times from the same 10 km square.

Table 2. Best-sampled (informal) regions of Britain, sampling intensities and levels of parasitism found. For each region the number of large samples (35+) included is given as (x:y) for, respectively, first:second generations.

Region	Generation 1			Generation 2		
	Σ Larvae	Parasitoids	% parasitoids	Σ Larvae	Parasitoids	% parasitoids
1 (0:7)	6	3	(50)	460	167	36.3
2 (16:6)	1019	348	34.2	488	156	32.0
3 (2:5)	305	71	23.3	377	228	60.5
4 (4:7)	236	130	55.1	592	275	46.5
5 (8:3)	730	387	53.0	345	248	71.9
6 (4:2)	288	86	29.9	105	63	60.0

1 = Devon, Cornwall, Somerset, Pembrokeshire.

2 = Buckinghamshire, Oxfordshire, Berkshire, Hampshire.

3 = Cambridgeshire, Norfolk, Suffolk.

4 = North Wales, Cheshire, Lancashire, Cumbria.

5 = Lothians and South East Scotland.

6 = Central, North and West Scotland.

A total of 2650 first-generation host larvae were collected, resulting in 1030 mortalities due to parasitism (38.9% parasitism in the samples) by 10 primary parasitoid species (Table 1). Parasitism of the first generation (comprising host larvae that had overwintered) arose in two ways: parasitism in autumn of the preceding year by most species whose larvae then overwintered in the host, in contrast to attack in spring by *Lissonota stigmator*. In the second generation, or more accurately the coalesced summer generations, 2367 hosts suffered 1137 mortalities (48.0% in the samples, or 45.7% if 56 barren host arrests due to *Clinocentrus* are excluded) from 17 parasitoid species. The greater apparent level of parasitism in the second generation is highly significant ($P < 0.0001$) however the host arrests due to *Clinocentrus* are treated. As many as six primary parasitoids species (all Hymenoptera) were found to co-occur in several second-generation samples, and seven in one such.

Substantially more species of parasitoid were found in the second generation, although most of the additional species were represented by only a few specimens. The striking difference in the parasitoid complex between the generations (percentage similarity only 34.7%) was to a large extent the result of the commonest, by far, parasitoid of the first generation, *Lissonota stigmator*, being strictly univoltine and therefore wholly absent from the second generation, and a similar (nearly) complete absence in the first generation of the most abundant parasitoid in summer, *Clinocentrus cunctator*. In fact, under some circumstances (cool spring; northern sample) the latter can achieve a rare and small presence in the first generation if its adults emerge just in time, in mid June, to catch the last stragglers of the final-instar larvae before they leave to pupate, but its impact on that generation is invariably negligible. If these two dominant parasitoids are removed, the residual parasitism is still significantly higher ($P < 0.0001$) in the second generation (35.7%) than in the first (23.6%), but the similarity between the generations is much larger at 62.3%.

Of the seven species (discounting *C. cunctator*) that were found in both generations, three were significantly more prevalent in the second generation: *Diadegma fabricianae* ($P < 0.0001$), *Glyptapanteles fausta* ($P < 0.0001$) and *Triclistus anthophilae* ($P = 0.0008$). The difference for *Glyptapanteles lateralis* was in the opposite direction but it was not quite significant ($P = 0.06$). The remaining three species were present in only small numbers.

Constancy

Not surprisingly, the best-represented parasitoids in absolute terms tended also to be the ones present at the most sites (Table 1), and constancy scores were on the whole in line with overall representation. However, *Triclistus anthophilae* stands out as having a relatively lower constancy, particularly in the first generation (0.24), than might be expected from its moderately high numerical representation overall. This seems not to be a simple matter of geographical distribution, as it occurred in all persistently sampled regions; rather, it is presumably a sampling artefact because, unlike the other parasitoids, *T. anthophilae* oviposits only into final-instar hosts and these were represented by only a fraction of each sample. *Actia pilipennis* also had a low constancy score, being almost confined to just a few first-generation samples in which multiple rearings arose. One parasitoid, *Microgaster nixalebion*, caused 1.3% parasitism in the second-generation samples (2.7% of the parasitoids reared) but was absent from the first-generation samples. This, and also its rather low second-generation constancy (0.23), seems to be at least partly explained by both restricted and patchy distribution, as it was also absent from all northern second-generation samples; and in fact it has been reared from first-generation *A. fabriciana* in Britain by others (S. Wales: A. Davies, pers. comm.). More distributional detail is given in the section dealing with the biology of each parasitoid species.

Geographical variation

Figure 1 is presented largely to demonstrate that the sampling overall was moderately well distributed across England, Scotland and Wales (see also Table 2). At least a few large samples were collected in each of the six main regions in both generations, except that region 1 was barely represented in the first generation (Table 2). Owing to high variation between the individual collections, and insufficient sample sizes, it is futile to look for much meaning in the overall percentage parasitism found in summed samples in different geographical areas, but it is perhaps worth noting that parasitism in the more northerly areas, especially in the second generation, was not diminished in comparison with levels seen in the more southerly samples, despite the fewer parasitoid species found (see below). Region 2 (the most extensively sampled area overall, and particularly in the first generation) had relatively low levels in both generations, and it may be significant that on balance the sites sampled in this area tended to be the least (semi-)natural and/or were relatively small.

Hyperparasitism

Clearly, only true hyperparasitoids (i.e. koinobionts developing while the primary parasitoid was itself still feeding) were amenable to sampling, and even then their representation is particularly likely to be underestimated.

Of the main parasitoids, true hyperparasitism affected especially those primary ichneumonoid parasitoids that were fully accessible – that is, present in the host larva – which can be attacked by them early in its life, for a significant part of their own larval development. Essentially these would be all of the Ichneumonidae listed in Table 1 except *Triclistus*, and among the Braconidae all except *Clinocentrus*. Because of their developmental biology (see below) *Triclistus* (mostly) and *Clinocentrus* (completely) evade exposure to true hyperparasitism. For simplicity, further analysis of true

Table 3. Parasitism of the main primary larval and larva-pupal parasitoids by *Mesochorus pallipes*.

Primary parasitoid	Generation 1					Generation 2				
	N	unP	<i>Mesochorus pallipes</i>			N	unP	<i>Mesochorus pallipes</i>		
			% P	♀	♂			% P	♀	♂
<i>L. stigmator</i>	527	474	10.1	37	16	0	–	–	–	–
<i>D. fabriciana</i>	92	85	7.6	4	3	287 ^a	208	27.5	51	28
<i>Glyptapanteles</i>	315	300	4.8	8	7	226	174	23.0 ^b	29	22
<i>M. nixalebion</i>	0	–	–	–	–	31	22	29.0	3	6
<i>T. anthophilae</i>	70	70	0	–	–	92	89	3.3	1	2
<i>C. cunctator</i>	3	3	0	–	–	399	399	0	–	–

^a Excludes five parasitised by *Mesochorus atriventris*.

^b One unsexable (excluded from sex counts).

hyperparasitism (Table 3) is restricted to the main fully susceptible primary parasitoids (*Lissonota*, *Diadegma*, *Glyptapanteles* and *Microgaster*), although *Triclistus* and *Clinocentrus* are included in the table. All true hyperparasitism was due to *Mesochorus pallipes*, apart from five specimens of *Mesochorus atriventris* which are excluded from this part of the analysis. On this basis, there was significantly ($P < 0.0001$) more hyperparasitism in the second generation (25.6%) than in the first (8.0%). However, the situation is complicated because hyperparasitism in *Lissonota* in the first generation must have arisen entirely through spring attacks, while in the other fully susceptible species it might have arisen at least partly the previous autumn (perhaps even mainly so, although the relatively low overwinter load suggests not). At 10.1% *Lissonota* was significantly ($P = 0.0105$) more heavily hyperparasitised than other fully susceptible parasitoids in Generation 1 (5.4%), so the difference between the samples excluding *Lissonota* in the two generations was even more extreme (i.e. comparing hyperparasitism in strictly the same taxa of primary parasitoids): 5.4% as against 25.6% in the first and second generations, respectively ($P < 0.0001$). Heavy parasitism of *Lissonota* might result from hosts carrying that parasitoid normally persisting in the field somewhat later than those harbouring other parasitoids (as is undoubtedly the case) and coinciding better with the spring flight time of *Mesochorus pallipes*, possibly even including *Mesochorus* adults that had just arisen within the parasitoid complex from first-generation hosts via *Glyptapanteles* and *Diadegma*.

Table 4. Outcomes from the 59 cocoons of *Anthophila fabriciana* collected (combined generations). The sample size reduces to 37 if individuals that were parasitised before cocoon formation are excluded (i.e. leaving nine pupal parasitoids and 28 moths).

Outcome	Number reared
Moths	28
Primary larval parasitoids	
<i>Diadegma fabriciana</i>	12 (+3 parasitised)
<i>Clinocentrus cunctator</i>	3
Prepupal arrests (<i>C. cunctator</i>)	1
<i>Microgaster nixalebion</i>	3
Primary pupal parasitoids	
<i>Oiorhinus pallipalpis</i>	7 (18.9%)
<i>Itoplectis alternans</i>	2 (5.4%)
Pseudohyperparasitoids^a	
<i>Encrateola laevigata</i>	1
<i>Gelis areator</i>	2

^a All from cocoons of *D. fabriciana* within the host cocoon.

Thus, it is probably more meaningful to compare the levels of *Mesochorus pallipes* present in *Diadegma fabriciana* vs *Glyptapanteles* spp. and especially, since the *Glyptapanteles* species are much smaller than *D. fabriciana*, to compare sex ratios of the *Mesochorus* reared from the two. Summing generations, *Glyptapanteles* spp. suffered significantly ($P < 0.0001$) less from *Mesochorus pallipes* (12.4%) than did *D. fabriciana* (22.7%), but the difference in either generation alone (which is a more meaningful comparison) was not significant. The simplest interpretation for the difference may be simply that *Glyptapanteles* spp. leave the host part way through its final instar, whereas *D. fabriciana* erupts from the host prepupa, thus being exposed to parasitism by *Mesochorus* for longer. Neither was there evidence that *Mesochorus* was able to respond to any difference in quality between *Glyptapanteles* and *Diadegma* by choosing a different egg fertilisation strategy, as over summed generations the f:m sex ratio (Table 3) was not significantly higher in favour of the larger *Diadegma* ($P = 0.428$), and nor was there a significant difference in either generation considered separately, even though the adults reared from *Diadegma* were consistently larger.

Prepupal and pupal parasitoids

Parasitism of the cocooned stages of *A. fabriciana* that were casually encountered is given in Table 4. These limited data are unlikely to accurately reflect levels of parasitism or the range of parasitoid taxa using the host in these stages, though it is clear that both taxon specialists (*Oiorhinus pallipalpis*) and niche generalists (*Itopectis alternans*) occur (see below). Subtracting cocoons harbouring parasitoids of the larvae, the sample of hosts susceptible to (pre)pupal parasitoids is reduced to 37, of which nine had been parasitised (24.3%), suggesting that mortality at this stage may also be heavy. More information is given under the parasitoid species concerned.

Biological notes on the parasitoid species

Hymenoptera: Ichneumonidae

***Lissonota stigmator* Aubert (Banchinae)**

(Figure 2)

Primary koinobiont endoparasitoid, ovipositing into the host larva in early spring (certainly into second and third instars, perhaps more widely) and forming its cocoon within that of the host. Strictly univoltine; found in all regions, but only in the first generation, in which it is the dominant parasitoid. Known only from this host; absent from several large collections of *Prochoreutis* spp. (Choreutidae) (see Appendix 1), which is ecologically as well as systematically a close relative of *Anthophila*.

Some aspects of the biology of this species were observed in captivity. The adult emerges from its cocoon during mild weather in early spring, generally before mid March and often in February, having spent the last 8–9 months as a pharate adult in the cocoon – that is, with fully formed adult cuticle but still in its pupal cuticle, and consequently with wings unexpanded (Figure 2). This is an obvious adaptation allowing it to eclose in early spring, using the warmth of the previous summer to reach that state, mostly before the end of June. The overwintered host larvae are consequently open to attack more or less as soon as they are

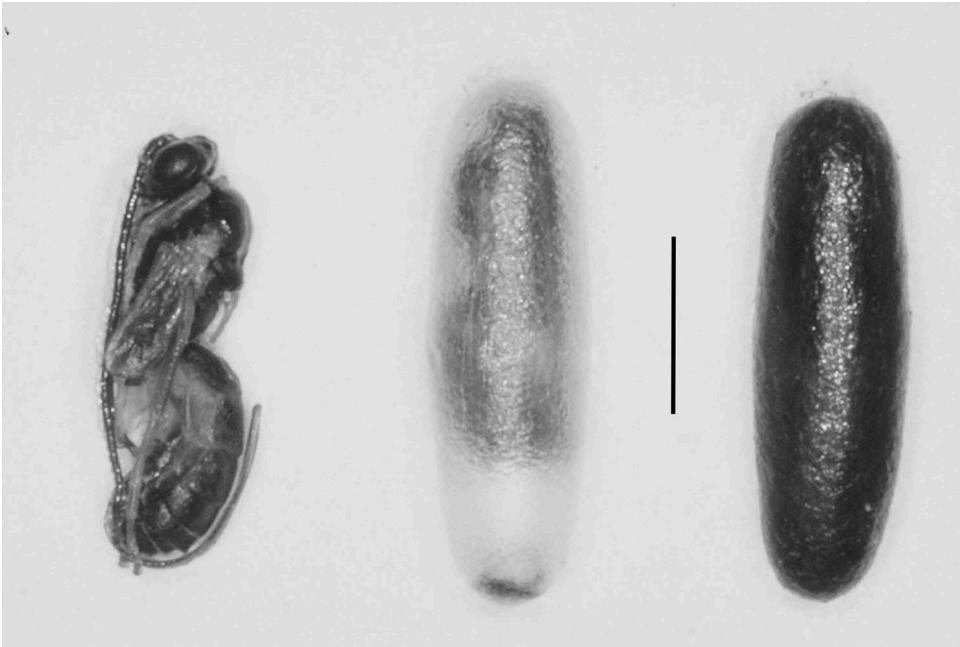


Figure 2. *Lissonota stigmator*. Pharate adult (removed from its cocoon), the state in which much of the summer and succeeding winter is passed, and cocoons formed under dry (centre) and moist (right) conditions. Scale bar = 2 mm.

able to feed on the developing new growth of nettles in the spring. Third-instar hosts offered naked were of little interest; instead the parasitoid probes larval spinnings (with its ovipositor unsupported by the sheaths), chasing the larva out of the web, whereupon it is grappled with and the egg is laid. Insertions of about 2 minutes seemed normal, with considerable thrashing around, as the host did not suffer temporary paralysis. Parasitisation by *L. stigmator* retards the host's growth more than by *Diadegma* and *Glyptapanteles*, its prolonged feeding period probably being behind the greater susceptibility of *L. stigmator* to hyperparasitism by *Mesochorus pallipes*. Final-instar hosts bearing *L. stigmator* invariably spun their cocoons in the lowest tissues in the rearing container – in nature this would probably be below the ground debris. Cocoons spun under dry conditions remain pale and translucent, but if spun under moist conditions (as in nature) they rapidly become opaque and practically black (Figure 2). Emergence in captivity was generally in mid to late afternoon, and the adults fed avidly on dilute honey and mated freely. Unfed females lived for over 3 weeks.

***Triclistus anthophilae* Aeschlimann (Metopiinae)**
(Figure 3)

Primary koinobiont endoparasitoid, ovipositing into the final-instar larva and emerging as an adult from the host pupa. Plurivoltine, overwintering in the host pupa. Found in both generations and in all regions except 6, with its apparently low constancy probably reflecting a sampling artefact (see above). This is a specialised parasitoid of Choreutidae, reared also from the arboreal *Choreutis pariana* (Clerck) (Shaw 1984) and, in France,

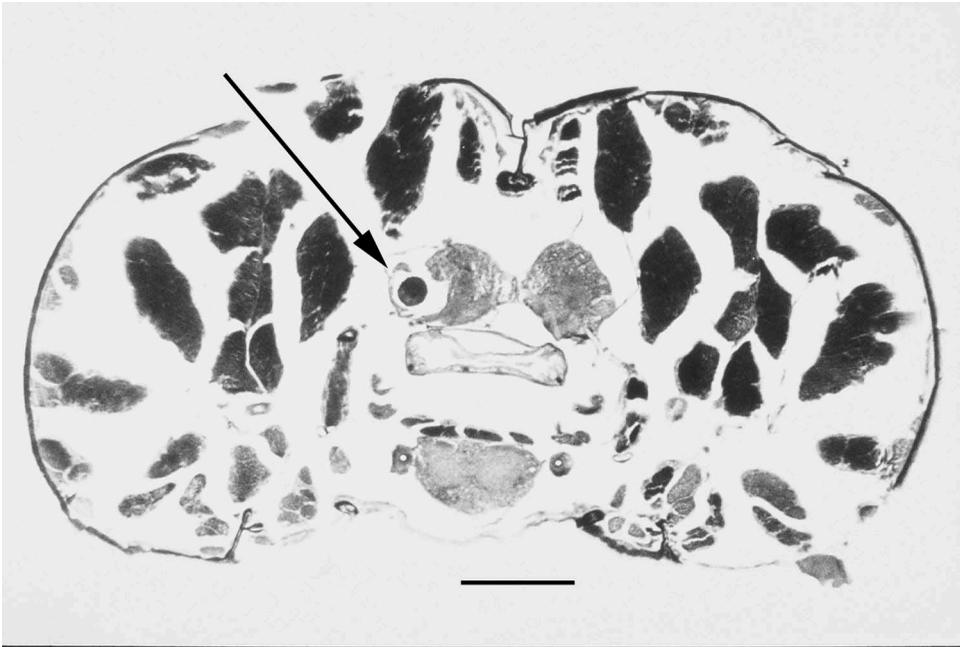


Figure 3. *Triclistus anthophilae*. Egg in supraesophageal ganglion ('brain') of final-instar *Anthophila fabriciana* larva. Scale bar = 0.1 mm.

Choreutis nemorana (Hübner), but not from large collections of *Prochoreutis* spp. (see Appendix 1). Its other hosts are much more patchily distributed than is *A. fabriciana*, making many populations locally monophagous.

This species was brought into short-term culture. It is thelytokous, although very occasionally males were reared. For oviposition, the parasitoid chases the host from its retreat then grasps it with its short powerful legs, aligned head to tail along its long axis dorsally (but positioned mainly at the head end of the host), bends the host's head downwards and oviposits with precision immediately behind the head and into the supraesophageal ganglion (Figure 3). Similar egg placement has been observed in other *Triclistus* species by Gerig (1960), Aeschlimann (1975) and Dijkerman (1988). This usually takes 3–5 seconds, during which the host is absolutely quiescent; however, it is not paralysed and vigorously wriggles away immediately after being released. The adult parasitoid normally runs or flies away straight after oviposition, which serves to limit (self)superparasitism. Hosts towards the end of the penultimate instar are accepted, but final-instar hosts are preferred – although rejected if very close to cocoon formation. Non-destructive host feeding on haemolymph was observed, from wounds made by the mandibles, but, although the hosts concerned fully recovered, no eggs were laid on these occasions. Probably the larva normally does not leave the ganglion until the host has become pupal (cf. Dijkerman 1988) and thus this species usually avoids attack from *Mesochorus*, but very rarely it is so parasitised (Table 3). Dijkerman (1988) records considerable growth of the first-instar larva in situ, and presumably it can be targeted there, and *Mesochorus* species are known to be able to parasitise ichneumonid larvae from the first instar (Zinnert 1969).

Campoplex lyratus (Thomson) (Campopleginae)

Primary koinobiont endoparasitoid, ovipositing into the host larva, erupting from the host prepupa and forming its cocoon within that of the host. Found only rarely in the second generation (regions 2 and 5). This is a common and widespread plurivoltine species in Britain, with a wide host range. Shaw et al. (2016) record it from 13 species in seven families of microlepidoptera, and also one each in Noctuidae and Nymphalidae. Although also reared sparingly from *Choreutis pariana* (see Appendix 1), it has no particular affinity with Choreutidae and it is clear that it enters the *A. fabriciana* parasitoid complex only casually. It is not known how it overwinters.

Campoplex pyraustae Smith (= *continuus* misident.) (Campopleginae)

Primary koinobiont endoparasitoid, ovipositing into the host larva, killing it as a prepupa and forming its cocoon within that of the host. Found rarely in this study, only in the second generation and only in regions 1 and 4. Despite more regular rearings from *Prochoreutis* spp. (see Appendix 1) this common and widespread plurivoltine British species has no special preference for Choreutidae, and is recorded by Shaw et al. (2016) from 15 species in eight families of microlepidoptera, and also one in Nymphalidae. It may habitually overwinter in its cocoon, which might limit attack on the first generation of *A. fabriciana*.

Campoplex tumidulus (Gravenhorst) (= *rufinator* Aubert) (Campopleginae)

Primary koinobiont endoparasitoid, ovipositing into the host larva, killing it as a prepupa and forming its cocoon within that of the host. Rare in the study (found only in the second generation, and only in region 2), but a common and widespread plurivoltine parasitoid in Britain, recorded by Shaw et al. (2016) from 33 species in 11 families of microlepidoptera, and also one in Nymphalidae. Several rearings from *Choreutis* and *Prochoreutis* spp. are included (see Appendix 1), but its use of Choreutidae is only casual. It habitually overwinters in its cocoon, probably limiting attack on the first generation of *A. fabriciana*.

Diadegma fabricianae Horstmann and Shaw (Campopleginae)

Primary koinobiont endoparasitoid, ovipositing into the host larva and forming its own cocoon within that of the host (almost always erupting from the host prepupa, but very rarely not killing the host until after it has pupated, in which case making its cocoon inside the semi-ruptured host pupa). Plurivoltine, overwintering as a larva in the host larva. Found in both generations and in all regions, with high constancy. Although not quite as specialised as was believed by Horstmann and Shaw (1984), who record various details of its biology in culture, this species is very strongly associated with *A. fabriciana*, but clearly also regularly uses crambid larvae feeding on *Urtica* and *Tussilago* (Shaw et al. 2016, who also give a single rearing from *Prochoreutis* sp.: see Appendix 1).

***Tranosemella citrofrontalis* (Hedwig) (Campopleginae)**

Primary koinobiont endoparasitoid, ovipositing into the host larva, killing it as a prepupa and making its own cocoon within that of the host. Found sparingly and only in the second generation, in regions 1, 3 and 4, but (non-reared) specimens seen also from regions 5 and 6. No additional hosts are recorded by Shaw et al. (2016), and it may be a specialist of this host, but it is a rare species in Britain (the male is distinctive, with a yellow face unusual in British Campopleginae, and it is unlikely to have been commonly overlooked). It appears to be plurivoltine, but its means of overwintering is uncertain.

***Tranosemella praerogator* (L.) (= *interrupta* (Holmgren)) (Campopleginae)**

Primary koinobiont endoparasitoid, ovipositing into the host larva, killing it as a prepupa and making its own cocoon within that of the host. Only one rearing resulted from this study, in the second generation (region 4). It is a widespread and common parasitoid in Britain, recorded by Shaw et al. (2016) from 22 species of Tortricidae (and a singleton doubtfully from a gracillariid), and it is clear that it entered the *A. fabriciana* parasitoid complex only freakishly.

***Oiorhinus pallipalpis* Wesmael (Ichneumoninae)**

Primary idiobiont endoparasitoid, ovipositing into the cocooned host prepupa or pupa (in culture equally successfully), and emerging as an adult from the host pupa. Reared in both generations, and found in regions 2, 4 and 5. This is a specialist parasitoid of Choreutidae, and Diller and Shaw (2014) give numerous rearing records from *A. fabriciana* and species of *Choreutis*, *Prochoreutis* and *Tebenna* (see Appendix 1). It is plurivoltine and overwinters as an adult.

***Itoplectis alternans* (Gravenhorst) (Pimplinae)**

Primary idiobiont endoparasitoid, ovipositing into and emerging as an adult from the host pupa; it is also capable of developing as a pseudohyperparasitoid within cocooned ichneumonoid pupae (cf. Shaw 2009) but the only two individuals reared (second generation, one site in region 2) in this study behaved as primary parasitoids. It is a common and widespread plurivoltine parasitoid in southern Britain, becoming rarer northwards, with an extremely wide host range comprising mainly microlepidoptera and ichneumonoid cocoons (Fitton et al. 1988), but without a particular affinity for Choreutidae although it has been reared from *Choreutis* (see Appendix 1).

***Mesochorus atriventris* Cresson (= *sylvarum* (Haliday) preocc.) (Mesochorinae)**

Koinobiont true hyperparasitoid, developing as an endoparasitoid in the still-feeding primary parasitoid which is killed as a cocooned prepupa. Found sparingly at one site each in regions 1, 4 and 5, and only in the second generation. It is rather a distinctive species but uncommon in Britain; it is unclear how important a component of its host range *Anthophila* is, but there is

(sparse) material reared from a wider range of hosts in NMS – including some from *Phytodietus* species (Ichneumonidae: Tryphoninae) parasitised as ectoparasitoids of tortricid hosts (Shaw 1993, as *M. sylvorum* Curtis in error for (Haliday)).

***Mesochorus pallipes* Brischke (= *crassicrus* Thomson) (Mesochorinae)**

Koinobiont true hyperparasitoid, developing as an endoparasitoid in the still-feeding primary parasitoid which is killed as a cocooned prepupa. Found in both generations and in all regions, with high constancy. Plurivoltine, capable of development in all the koinobiont larval endoparasitoids except *Clinocentrus*, and also (rarely) in the larva-pupal *Triclistus*. The reared *Mesochorus* material in NMS has not been thoroughly analysed, but it is apparent that this species is also important in the parasitoid complexes of *Epermenia chaerophyllella* (Goeze) (Epermeniidae) (Shaw and Aeschlimann 1994) and *Yponomeuta* spp. (Yponomeutidae), hosts that all live under webs, and it is also clear that host selection by *Mesochorus* species in general involves specialised orientation to the still-feeding caterpillar (etc.) species, within which it uses whatever ichneumonoid primary parasitoids are available (Shaw 1993). Although it does happen, parasitism of Tachinidae (Diptera) by *Mesochorus* species is very much less common (pers. obs.), and was not seen in this study.

***Encrateola laevigata* (Ratzeburg) (Cryptinae)**

Idiobiont pseudohyperparasitoid in the study; also capable of parasitising concealed microlepidoptera as a primary parasitoid. Develops externally on its concealed host. Twice reared from cocoons of *Diadegma fabriciana* (and once from a *Glyptapanteles* cocoon); regions 1, 2 and 4, second generation only. This is a common, probably plurivoltine and widespread parasitoid of a wide range of (mostly cocooned) small microlepidoptera and their ichneumonoid parasitoids (Schwarz and Shaw 2000) and, although it has been reared from *Prochoreutis* (see Appendix 1), it does not have a particular affiliation with Choreutidae.

***Gelis areator* (Panzer) (Cryptinae)**

Idiobiont pseudohyperparasitoid in the study, but also commonly parasitises case-bearing and cocooned microlepidoptera as a primary parasitoid. Develops externally on its concealed host. Found only once, reared from a second-generation cocoon of *D. fabriciana* collected in Region 2. It is a very common and widespread parasitoid of a wide range of cocoons and cocoon-like structures, usually on trees and bushes but also on prominent field-layer plants (Schwarz and Shaw 1999), without a particular association with Choreutidae although it has been reared from *Choreutis* (see Appendix 1).

Hymenoptera: Braconidae

***Clinocentrus cunctator* (Haliday) (= *gracilipes* (Thomson)) (Rogadinae) (Figure 4(a),(b))**

Primary koinobiont endoparasitoid, ovipositing into final- or penultimate-instar hosts following a pre-oviposition injection of venom that switches the host to an arrested

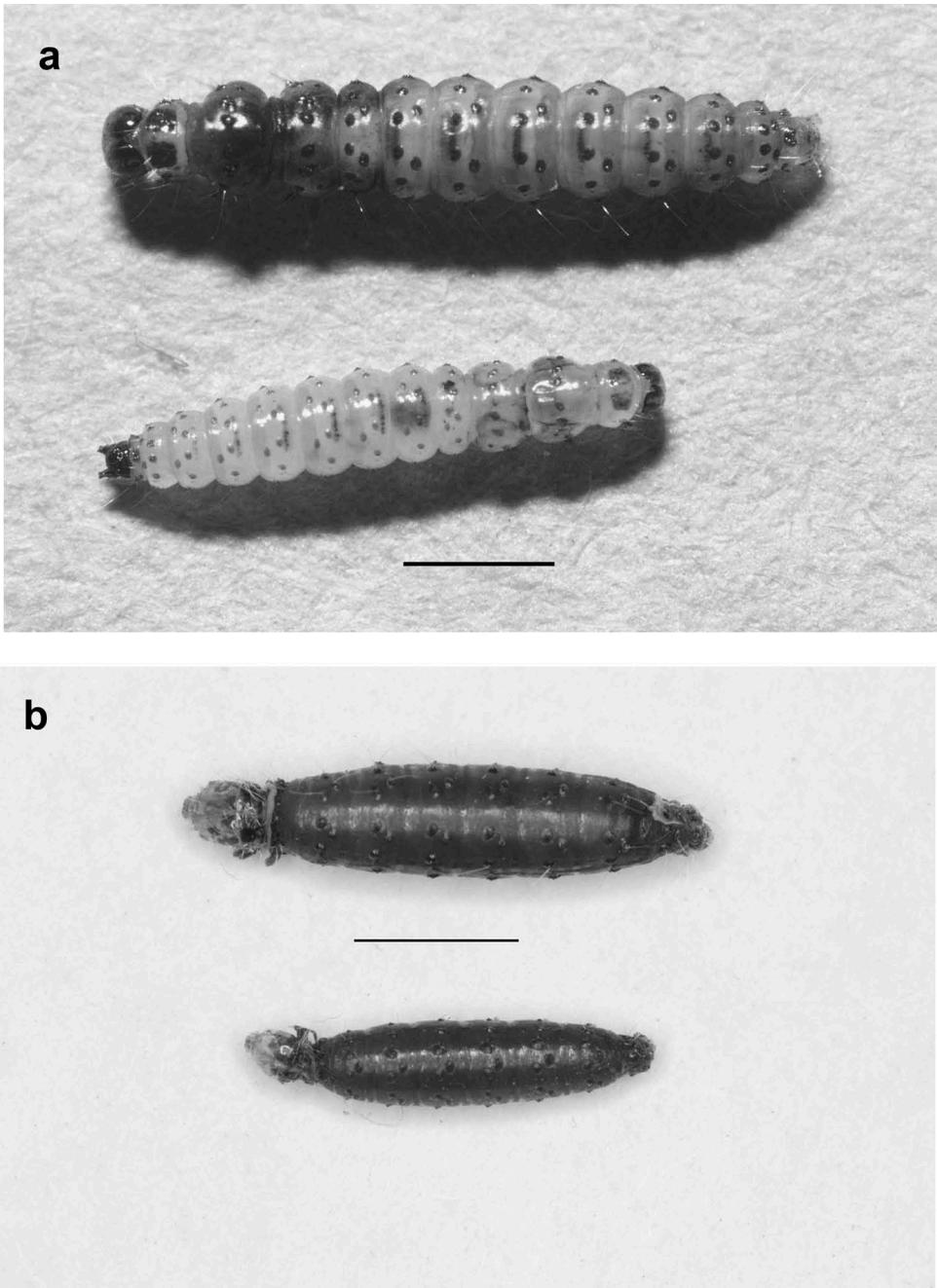


Figure 4. *Clinocentrus cunctator*. Penultimate and final-instar larvae of *A. fabriciana* (removed from cocoon). (a) arrested in a prepupal condition by the venom alone, both showing the same features of an underlying pupal cuticle such as wing cases and abdominal dorsal spines; (b) mummies in which the parasitoid pupates. Scale bars = 2 mm.

prepupal state (irrespective of instar, [Figure 4\(a\)](#)), overriding and preventing its next ecdysis (Shaw 1981, 1983). *Prochoreutis* species, which feed on the low-growing plant *Scutellaria*, are also heavily parasitised by *C. cunctator*, but it has not been reared from arboreal choreutids (see Appendix 1): however, in culture experiments (M.R. Shaw, unpublished data) it avidly and successfully parasitised *Choreutis pariana*, which feeds on rosaceous trees. This indicates a behavioural niche dimension to the host range of this specialised parasitoid of low-feeding web-making Choreutidae. As *Prochoreutis* species are very much more local than is *Anthophila*, *C. cunctator* particularly often has locally monophagous populations.

This species has been brought into short-term culture. The adult parasitoid probes the host's feeding web with its ovipositor, and stings the host to inject a venom that causes temporary paralysis, but the host can sometimes wriggle away before the venom takes full effect, and quite frequently the female parasitoid fails to relocate it in order to lay an egg. Whether or not an egg is laid, the host recovers to continue feeding through the rest of its instar, before leaving to spin a cocoon and become arrested as a prepupa. In the absence of an egg the prepupa simply dies, sometimes weeks later. If an egg is laid, the parasitoid hatches in the cocooned prepupa soon afterwards and eventually turns the host into a 'mummy' ([Figure 4\(b\)](#)), inside which it develops to the adult stage. The egg is placed just under the skin, transversely in the middle of a body segment, in which it is discernible externally. *Clinocentrus cunctator* is plurivoltine and emerges quickly from mummies formed relatively early in the latter half of summer, but individuals in late summer or early autumn overwinter as a prepupa in the mummy, and from these the first emergences take place in mid June the following year. This is the dominant parasitoid of *A. fabriciana* in the second generation (also *Prochoreutis* spp.; see Appendix 1) but, despite being at least predominantly plurivoltine, it emerges as an adult too late to parasitise the first generation of *A. fabriciana*, apart from very rarely catching late stragglers in exceptionally late springs (three individuals from two samples, region 5). Because hosts stung by *C. cunctator* leave to construct cocoons elsewhere so soon afterwards (and some are notionally penultimate instar, or even younger) mortality due to *C. cunctator* will have been underestimated by the sampling regime, perhaps substantially. Mummies of the 175 hosts successfully parasitised by *C. cunctator* up to the end of 1980 were scored as final instar (104) and penultimate instar (71). Seventy-three females and 31 males emerged from the former, and only six females with 65 males from the latter. The greater proportion of females to emerge from final-instar mummies as opposed to the smaller penultimate-instar mummies is significant ($P < 0.0001$). A very few male-producing mummies of second-instar hosts have also been noted (none before 1981). Although *C. cunctator* is not quite an idiobiont it is effectively using a host whose variable size is limited at the point of attack, so this efficient use of the overall resource is not unexpected. However, it is of considerable interest because the only part of the female that can contact the host, beneath its web, is the ovipositor (it is used unsheathed) – as has been observed in captivity many times and in nature twice – suggesting that the host's instar can be judged by the ovipositor, presumably either from cuticular properties or from its haemolymph in which the level of juvenile hormone may vary. As the egg does not hatch until after the host has left to construct a cocoon, *C. cunctator* is not susceptible to attack from *Mesochorus*.

***Microgaster nixalebion* Shaw (Microgastrinae)**
(Figure 5)

Primary koinobiont endoparasitoid, ovipositing into the host larva and killing the host usually in its cocoon, where a final external feeding phase takes place (Figure 5; illustrated fully by Shaw 2004). In this study found only in the second generation in regions 1, 2, 3 and 4, and even then with rather low constancy, but it has occurred in samples of the first generation reared by others (S. Wales: A. Davies, pers. comm.) and *A. fabriciana* is unquestionably a host in which it can overwinter. Plurivoltine; as with other *Microgaster* species, the need for concealment during its final feeding phase limits its host range (Shaw 2004) but it is common in summer on small larvae of the nettle-feeding nymphalid *Vanessa atalanta* (L.), as well as *Prochoreutis* spp. on *Scutellaria* (but not other choreutids; see Appendix 1). The widespread nettle-feeding crambid *Pleuroptya ruralis* (Scopoli) is an important host in which the winter is passed. This species is fully susceptible to parasitism by *Mesochorus pallipes*.

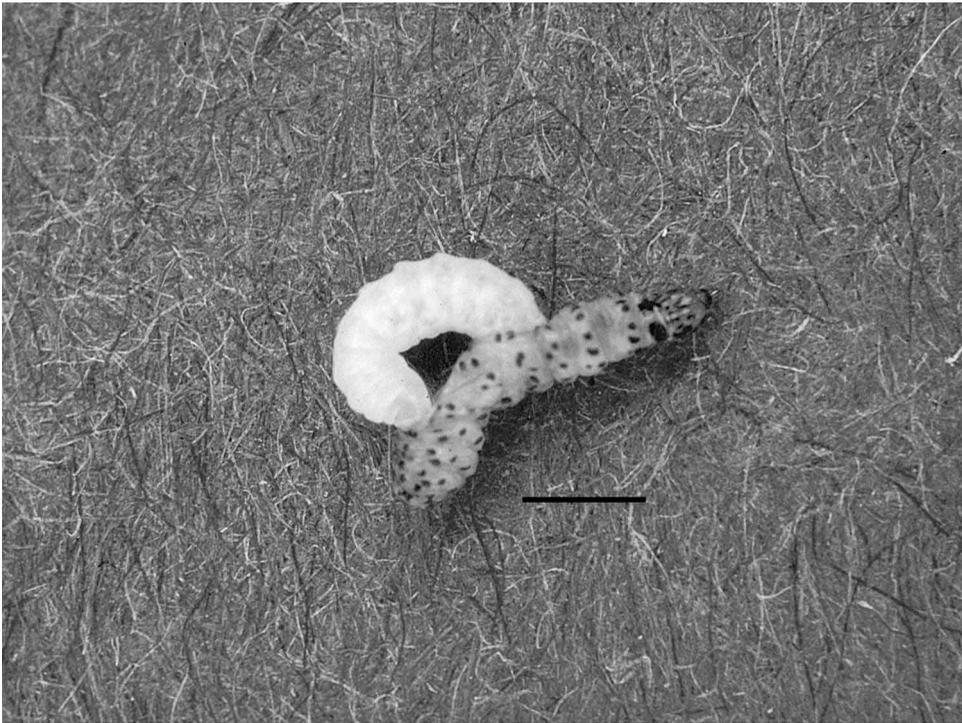


Figure 5. *Microgaster nixalebion*. The final-instar larva, having erupted from the final-instar *A. fabriciana* larva, completing its feeding from an external position. Scale bar = 2 mm.

***Glyptapanteles fausta* (Nixon) (Microgastrinae)**

Primary koinobiont endoparasitoid, ovipositing into the host larva and killing it part way through its final instar. Hosts can be successfully parasitised in first and second instars and oviposition is rapid. As this parasitoid is a haemolymph feeder, the host continues to live for a time after the parasitoid larva erupts, but it does not resume feeding and normally quite quickly leaves the site of its demise (often then falling from the plant altogether), leaving behind the small whitish parasitoid cocoon. Demonstrated to be thelytokous (Shaw 2012). Found in all regions except 6, and in both generations, but with rather low constancy. Two specimens have been reared from *Prochoreutis* species (see Appendix 1) at broadly similarly low relative frequency. Plurivoltine, overwintering in the host larva, and fully susceptible to parasitism from *Mesochorus*.

***Glyptapanteles lateralis* (Haliday) (Microgastrinae)**
(Figure 6)

Details as for *G. fausta*, except that it reproduces sexually (Shaw 2012), was found in all regions, has high constancy, and has been reared only from this host. The cocoons of the two species cannot be distinguished. In the two *Glyptapanteles* species the growing parasitoid larva becomes especially easy to detect externally as it distorts the host, usually displacing the gut line (Figure 6). However, this is not diagnostic as *Microgaster nixalebion* and the campoplegine parasitoids often cause similar (but usually less extreme) distortions.

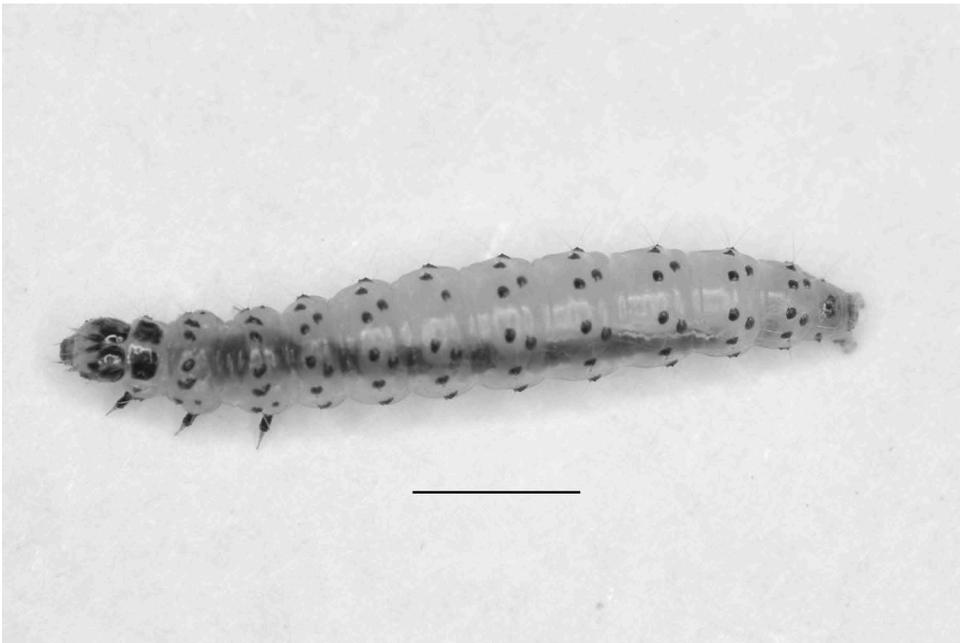


Figure 6. *Glyptapanteles lateralis*. The final-instar larva within that of its host, soon before eruption. (Not fully diagnostic, as larvae of several of the other parasitoids often become more or less evident in a similar way.) Scale bar = 2 mm.

***Chelonus contractus* (Nees) (Cheloninae)**

Primary koinobiont endoparasitoid, presumably (like known congeners, cf. Shaw and Huddleston 1991) ovipositing into the host egg but delaying final destruction of the host until it has constructed its cocoon, in which the parasitoid has a final external feeding phase. Found at only one site (generation 2) in this study, but several reared from *A. fabriciana* in Belgium and also reared from two collections of *Prochoreutis* spp. in Britain (Tobias and Shaw 2005; see Appendix 1). It may be specialised on Choreutidae, although the reared *Chelonus* (s. l.) material in NMS has not been thoroughly reviewed.

***Charmon cruentatus* Haliday (Charmontinae)**

Primary koinobiont endoparasitoid, with a very wide host range of more or less concealed microlepidoptera larvae of about the size of *Anthophila*, especially on trees, and very common in Britain (M.R. Shaw, unpublished data). Two individuals reared from one second-generation sample (region 4). It is clear that this was an abnormal undertaking, but of interest that a (presumably single) female successfully did it at least twice.

Hymenoptera: Eulophidae

***Elachertus anthophilae* Bouček (Elachertinae)**

Gregarious primary koinobiont ectoparasitoid, attacking final-instar larvae and killing the cocooned prepupa. Found at only two sites, at the very edge of reed bed/fen habitat (apparently absent a few metres distant) in regions 2 and 3, but in both generations. Despite its occurrence near fens (a typical habitat for *Prochoreutis* spp.), surprisingly it was not found in large collections of *Prochoreutis* on *Scutellaria* very nearby (M.R. Shaw, unpublished data; see Appendix 1). Plurivoltine, overwinters as pupae in the host cocoon. *Elachertus* species are known to inject a venom which permits the host to resume feeding but prevents its moult to the next instar (Umetasu and Sakanoshita 1987; Coudron et al. 1990). Final-instar hosts parasitised by *E. anthophilae* similarly recovered feeding activity and in this case were eventually consumed as arrested prepupae after cocoon construction.

This species was brought into short-term culture, but only limited observation was possible. For oviposition, the adults entered host retreats where they remained for over a day. This may suggest that they host feed and wait for their eggs to develop, but this could not be ascertained. There is certainly a pre-oviposition sting causing temporary paralysis from which the host initially recovers to resume feeding, but later succumbs from the venom alone. White barrel-shaped eggs are laid in a loose batch of about 4–8 (exceptionally up to 14) in more or less dorsal positions, on several adjacent body segments (not along intersegmental membranes, in contrast to *Eulophus* species (Shaw 1981)). The host does not die until it has constructed its cocoon, which seems to occur at about the time that the eggs hatch. Adults of some all-male broods raised experimentally failed to leave the host cocoon, possibly indicating that sib-mating at that location is normal.

***Stenomesus rufescens* (Rossius) (Elachertinae)**

Gregarious primary ectoparasitoid, attacking final-instar larvae. One brood of two reared in one second-generation sample (region 2). It has a wide range of hosts, and a regular association with *Choreutis nemorana* on *Ficus carica* in Europe (cf. Bouček and Askew 1968). From that host in France (Corsica) it was numerous in one sample collected from heavily browsed and essentially prostrate *Ficus* (M.R. Shaw, unpublished data; see Appendix 1) and appeared to be a koinobiont (similar in behaviour to *E. anthophilae*, but not well investigated), but it was not otherwise found as a parasitoid of Choreutidae.

Diptera: Tachinidae
***Actia pilipennis* (Fallén) (Tachininae)**

Koinobiont larval endoparasitoid, killing the fully grown host. Low constancy but causing significant mortality when found, it occurred in only three first-generation and one second-generation samples, in regions 4, 5 and 6. The larva, before eruption from the host, was evident as a swelling visible towards the anterior end of the host. Widespread in Britain and known to parasitise a wide range of microlepidoptera (www.tachinidae.org.uk, accessed 23 April 2016). One specimen was reared from *Choreutis* (see Appendix 1).

***Nemorilla floralis* (Fallén) (Exoristinae)**

Koinobiont larval endoparasitoid, killing the fully grown host. Two individuals reared from one first-generation sample (region 2). Restricted in Britain to the southern half but known to parasitise a wide range of microlepidoptera, often on *Urtica*, and more rarely macrolepidoptera (www.tachinidae.org.uk, accessed 23 April 2016).

Nematoda: Mermithidae
***Gen. sp.* indet.**

Found in both generations, but in only three samples (two rather marshy sites in regions 2 and 5, but it is not certain that the material is all conspecific). A rearing of a superficially similar individual from a different host is recorded and illustrated by Shaw (2014). The life cycle of Mermithidae is complicated and varied (Welch 1963; Kaiser 1991) but either the egg would have been ingested or the host penetrated by a preparasitic larval stage and, after its parasitoid larval phase, the mermithid would leave the host probably as a free-living predator. The association with *A. fabriciana* is believed to be merely casual, and it was not reared from other choreutids.

Discussion

This investigation of the parasitoid complex of a common and widespread moth was conducted on a wide enough scale to be reasonably confident that it is properly representative within Britain. Certainly, additional species will be found as parasitoids in British populations of *A. fabriciana* from time to time, but almost certainly not as regular primary parasitoids from either the host's or parasitoid's stance. In all, 19 species of primary parasitoid attacking the larval stage were found, with an additional two species of true hyperparasitoid using some of them. Very limited sampling of the cocooned stages, including primary parasitoid cocoons, added a further two primary parasitoids and two pseudohyperparasitoids, making a parasitoid complex comprising 25 species (although seven of these were found on only one sampling occasion). Further sampling of cocoons of the primary parasitoids would undoubtedly reveal a richer array of pseudohyperparasitoids, probably some of them as regulars.

Attention must be drawn to various potential sources of sampling bias, all of which make accurately estimating the generational percentage parasitism from the larval sampling practically impossible (in addition to the fact that any egg or pupal parasitism would not be included) in taxa that are not sedentary for their entire preimaginal life. Otherwise, even when only a single parasitoid species is under consideration, there are substantial difficulties in determining the true generational percentage mortality of the host attributable to that parasitoid (Lathrop and Newton 1933; Van Driesche 1983; Bellows et al. 1989; Thorpe et al. 1990; Van Driesche et al. 1990), and the situation is made more difficult still when a parasitoid complex is involved (Shaw et al. 2009). In the first place, unparasitised and parasitised larvae are likely to behave differently, and thus not be equally amenable to any sampling regime. For this reason, a sample (however extensive and proportional to distribution in the overall habitat) might not truly reflect the levels of parasitism present in the population at that time. A related issue is the extent to which parasitism may prolong or curtail the host's feeding period – that is, the length of time it spends in the sampling arena and hence its probability of being sampled. Whenever the sample is collected, some population mortality due to parasitism may have already occurred, with the consequent loss of those hosts from the potential sample, and also some of the unparasitised hosts collected might have later become parasitised had they been left alone. All of these general difficulties apply to the present study, and the percentage parasitism recorded for each (and summed) sample(s) is just that: a percentage found in the sample, but not an expression of generational larval parasitism. Nevertheless, comparisons between the various samples are believed to be meaningful, particularly because of the effort made to sample under approximately similar situations (when more than half of the sample was present as penultimate- and final-instar larvae), and, particularly, understanding the requirements and developmental biology of the component parasitoid species accounts rather well for the anatomy of the complex overall.

Parasitism was found to be significantly higher in the second sampling period ('generation') than in the first, which is a rather commonly found phenomenon for plurivoltine hosts under a variety of circumstances (e.g. Askew and Shaw 1974, 1979; Figueiredo and Araújo 1987; Stefanescu et al. 2012). In fact the real difference between the two generations in the present case is probably greater than indicated by the sampling as a result of biological properties of two parasitoids in particular. *Lissonota*

stigmator prolongs the host's feeding period, with a consequent tendency for its representation to be overestimated, and the reverse is true of *Clinocentrus cunctator* whose host's behaviour changes causing it to leave the arena soon after being stung, thereby leading to underestimation of its representation. As *L. stigmator* is exclusive to, and the dominant parasitoid in, the first generation, while *C. cunctator* has that position in the second, the difference between parasitism as sampled in the first (38.9%) and second (48.0%) generations is probably a substantial underestimate of the real generational difference.

Leaving aside cases like the seasonal change in form and position of cynipid galls on *Quercus* such that the two generations are, from a parasitoid's perspective, completely different hosts (Askew 1961), the situation whereby in each of the two (similar) generations there is a regular and specialised parasitoid that occurs only in that generation is highly unusual, the more so here as in each case that parasitoid is dominant within its generation. It has occasionally been reported that an apparently specialised parasitoid uses only one generation of its plurivoltine host (e.g. New 1970), but for this phenomenon to arise in both generations is on the face of it bizarre, although Stamp (1981) in passing recorded a similar pattern of presence and absence of two opportunistic pseudohyperparasitoids of *Euphydryas phaeton* Drury (Lepidoptera: Nyphalidae) via *Cotesia euphydryidis* (Muesebeck) (Hymenoptera: Braconidae) in different generations in an experimental arena. A possible explanation behind the present case may be that ancestrally *A. fabriciana* was univoltine and that when it became plurivoltine *L. stigmator* did not follow suit, and that the newly occurring summer generation became susceptible to parasitism from *C. cunctator*, originally restricted to *Prochoreutis* spp. But that speculation fails to address the overwintering mode of the hypothetically univoltine ancestral host, which is rather hard to envisage in the light of its present behaviour.

A recent recognition that some properties, formerly regarded as qualitative dichotomies, in parasitoid life history are graded and better expressed as quantitative indices includes a plea to score host range on a continuum between 'specialist' and 'generalist' on the basis of the number of host families and host species used (Boivin and Ellers 2016). Although a worthy sentiment, this begs not only a robust definition of host range, but also fails to address the enormous practical difficulties of discovering all the hosts used by a parasitoid species and indeed assessing the validity of records. Shaw (1994), in trying to address these and related problems, proposed a conceptual definition of host-range to include 'only the species of potential hosts that the parasitoid is usually able to attack successfully, following a pattern of searching behaviour enabling it to encounter them regularly' and advocated a quantitative approach towards host-range assessment such that freak events and mistaken records become marginalised and, as data accrue, can be excluded. Rather than attempting indexation, it seems that recognition and naming of characteristic nodes in a host-range continuum will be a useful approach. Thus, the 11 primary parasitoids and one true hyperparasitoid that appear to be regular parasitoids of *A. fabriciana* (in the case of rarely found species, at least from the perspective of the parasitoid), and also the remaining species found for which this host is of no real importance, can be divided into several categories reflecting different levels of specialisation to the host. The first, that might properly be called 'absolute specialists', on present evidence contains *Lissonota stigmator*, *Tranosemella citrofrontalis*, *Glyptapanteles lateralis* and *Elachertus anthophilae*, none of which appears to regularly parasitise any other host

species. Next are 'taxon oligospecialists' – that is, species that also regularly parasitise phylogenetically related hosts (in this case taken as other Choreutidae) but not others, to which belong *Triclistus anthophilae*, *Glyptapanteles fausta*, *Clinocentrus cunctator* and (probably) *Chelonus contractus* in addition to the pupal parasitoid *Oiorhinus pallipalpis*. Less specialised are 'niche oligospecialists', whose host range includes other, less phylogenetically related, hosts that share habitat or behavioural traits, exemplified by *Diadegma fabriciana*, *Microgaster nixalebion* and the true hyperparasitoid *Mesochorus pallipes*. The remaining species are best called either 'casuals' (exemplified by the three *Campoplex* species, the two tachinids and probably *Stenomesus rufescens*), reflecting no special relationship with the host but that the host falls into a more general but still restricted phylogenetic group(s) and ecological space in which the parasitoid seeks and attacks its hosts (the important concept being that the presence or absence of the particular host species would be of little consequence to the well-being of the parasitoid population), or 'strays' (exemplified by *Charmon cruentatus* and *Tranosemella praerogator* whose host ranges, as defined by Shaw 1994, clearly exclude *A. fabriciana*). No parasitoid is a true generalist, and the unqualified term 'generalist' should be avoided, but some parasitoids (especially pseudohyperparasitoids) can be important yet unspecialised components of a parasitoid complex, and the term 'niche generalist' is appropriate for that role. *Itoplectis alternans* and pseudohyperparasitoid Cryptinae found in the complex, such as *Gelis* species and *Encrateola laevigata*, should be categorised as niche generalists, consistent with their known host ranges (Fitton et al. 1988; Schwarz and Shaw 1999, 2000). Of course, a parasitoid population may act in a more restricted way than its potential; for example, when taxon or niche oligospecialists have only one of their several potential hosts locally available (as is frequently the case for *C. cunctator*, *T. anthophilae* and *O. pallipalpis*) their population dynamics will be those of specialists at that site and within that context they can be termed 'paraspecialists'.

This study provides both 'source web' data (i.e. parasitoids of a particular host) and 'sink web' data (other hosts that these parasitoids use, including information from the sources referenced) but, because the samples were collected neither simultaneously nor in the same place nor (in the case of other hosts) strictly quantitatively, it is inappropriate to force that together into a mythical quantitative 'food web'. Nevertheless, it is important to address parasitoid complexes in the way done here if we are to start to gain a proper understanding of the intricacies of relationships, which is surely the basic knowledge needed to address the conservation of biodiversity. On the basis of this study *Elachertus anthophilae*, being not only an absolute specialist but also known from very few sites (Catfield in the Norfolk Broads, and Woolhampton/Thatcham in Berkshire: Bouček 2002), starts to emerge as a species of potential conservation concern.

A final point is of relevance to Shaw and Hochberg's (2001) contention that our knowledge of parasitoid wasps on various fronts is a long way behind that of almost all other insects and that even in the British fauna, which is supposedly the best known in the world, this constitutes a huge impediment to the conservation of this particularly specialised and vulnerable trophic level. Four of the hymenopterous parasitoid species found (*D. fabriciana*, *T. anthophilae*, *M. nixalebion* and *E. anthophilae*) were formally described and named from material reared in this study; another five (*L. stigmator*, *C. lyratus*, *C. pyraustae*, *C. tumidulus* and *T. citrofrontalis*) had not yet been recorded from Britain at the start of it; and two more (*T. praerogator* and *C. cunctator*) were known

under an invalid specific epithet (compare Broad 2016; Broad et al. 2016; with Fitton et al. 1978). Even if there were literature host records for some of these species, they would be extremely hard to trust or interpret (Shaw 1994). The situation has certainly improved in the last few decades but there is still a long way to go and, with decreasing numbers of people finding employment to research the taxonomy and biology of parasitoids, there can be little confidence that this important group of organisms will ever take its proper place in the understanding of ecosystems, or biodiversity concerns and conservation planning.

Acknowledgements

Determination of the parasitoids often involved help from specialists of the group, as is clear from the cited publications, and in addition Klaus Horstmann determined the infrequent species of Campopleginae. Neil Ravenscroft kindly prepared Figure 1; and John Kennaugh sectioned and Les Lockey photographed the host's head for Figure 3. I am also grateful to Andrew Davies for sharing experience from his study of *A. fabriciana* in south Wales and to Louise Lewer for help with image manipulation.

Disclosure statement

No potential conflict of interest was reported by the author.

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Appendix 1

Primary parasitoids reared from other Choreutidae in Britain and Europe in parallel with this study. For each host/parasitoid pair the number of sampling occasions is given in brackets. Included are rearings by the author, and specimens reared by others and sent to the author for determination: in the latter cases the numbers of hosts collected are not necessarily known so overall sample sizes are not given. Material is preserved in NMS. * (pre)pupal parasitoid. † does not occur in Britain.

Choreutis diana (Hübner) [A very local species. Larva feeds under a web on *Betula*. Samples from Scotland].

Braconidae

Apanteles xanthostigma (Haliday) 2 (1)

Protapanteles immunis (Haliday) 1 (1)

Choreutis nemorana (Hübner) [Although this has recently been recorded from Britain, all samples are from the Mediterranean region where its larva is generally abundant feeding under a web on *Ficus carica*].

Ichneumonidae

Diadegma armillatum (Gravenhorst) 14 (4)

Campoplex tumidulus (Gravenhorst) 2 (2)

Triclistus anthophilae Aeschlimann 2 (2)

**Itoplectis alternans* (Gravenhorst) 2 (1)

*†*Itoplectis tunetana* (Schmiedeknecht) 1 (1)

Braconidae

†*Choeras semele* (Nixon) 2 (1)

Dolichogenidea candidata (Haliday) 4 (1)

Eulophidae

Stenomesus rufescens (Rossius) 10 (1) broods

**Elasmus* †sp. 1 (1) brood

Pteromalidae

**Pteromalus semotus* (Walker) 2 (1)

Bethylidae

Goniozus †sp. 65 (3) broods (+ 13 arrests)

Tachinidae

†*Cadurcia casta* (Rondani) 3 (1)

Pseudoperichaeta nigrolineata (Walker) 2 (1)

Choreutis pariana (Clerck) [A widespread species. Larva feeds under a web on various rosaceous trees (Shaw, 1984). Samples largely from Britain].

Ichneumonidae

Campoplex lyratus (Thomson) 4 (1)

Campoplex tumidulus Gravenhorst 5 (1)

Diadegma armillata (Gravenhorst) 2 (2)

Enytus apostata (Gravenhorst) 2 (2)

Triclistus anthophilae Aeschlimann 8 (5)

**Bathythrix thomsoni* (Kerrich) 1 (1)

**Gelis areator* (Panzer) 2 (2)

**Oiorhinus pallipalpis* Wesmael 3 (3)

Braconidae

Dolichogenidea candidata (Haliday) 40 (3)

Tachinidae

Actia pillipennis (Fallén) 1 (1)

Millieria dolosana (Heydenreich) [A widespread but non-British species. Larva found leaf-mining *Aristolochia* in France, and pupating in a disc in the mine].

Ichneumonidae

Diadegma holopygum (Thomson) 38 (3)

Braconidae

Bracon osculator Nees 11 (3) broods [many *]

?*Pholetesor circumscriptus* (Nees) 3 (1)

Eulophidae

Pnigalio pectinicornis (Linnaeus) 1 (1)

Prochoreutis spp. [Larvae of the two British species *P. myllerana* (Fabricius) and *P. sehestediana* (Fabricius) both feed under a slight web on *Scutellaria* growing low in marshy places, and are indistinguishable. All samples are British].

Ichneumonidae

Diadegma rufata (Bridgman) 74 (17)

Diadegma fabricianae Horstmann and Shaw 1 (1)

Campoplex pyraustae Smith 14 (7)

Campoplex tumidulus (Gravenhorst) 3 (2)

indet. *Campoplex* spp. 7 (3)

**Scambus* sp. 1 (1)

**Itoplectis maculator* (Fabricius) 1 (1)

**Gelis agilis* (Fabricius) 3 (3)

Gelis hortensis (Christ) 1 (1)

**Encrateola laevigata* (Ratzeburg) 1 (1)

**Oiorhinus pallipalpis* Wesmael 7 (6)

Braconidae

Clinocentrus cunctator (Haliday) 82 (18) (+ 10 arrests)

Oncophanes minutus (Wesmael) 1 (1) brood

Microgaster nixalebion Shaw 26 (4)

Glyptapanteles fausta Nixon 2 (2)

Chelonus contractus (Nees) 7 (2)

Eulophidae

Elachertus inunctus Nees 3 (1)

Tebenna bjerkanarella (Thunberg) [A local non-British species. Mostly collected as pupae found gregariously under a web on prostrate *Cirsium* in France].

Ichneumonidae

Diadegma fenestrata (Holmgren) 1 (1)

*†*Tycherus vafer* (Wesmael) 16 (2)

Tebenna micalis (Mann) [A regular immigrant to S. England, sometimes established. Larva and pupa collected mostly from *Inula* and *Pulicaria*, on which it feeds under a web. Samples from Britain and Mediterranean region].

Ichneumonidae

Diadegma fenestrata (Holmgren) 7 (4)

Diadegma exareolator Aubert 1 (1)

Diadegma sp. 1 (1)

Scambus brevicornis (Gravenhorst) 1 (1)

Itoplectis maculator (Fabricius) 1 (1)

**Pimpla spuria* Gravenhorst 2 (1)

Encrateola laevigata (Ratzeburg) 3 (2)

Gelis agilis (Fabricius) 1 (1)

**Oiorhinus pallipalpis* Wesmael 15 (6)

*†*Tycherus vafer* (Wesmael) 3 (2)

Braconidae

†*Apanteles hemara* Nixon 7 (4)

Choeras dorsalis (Spinola) 2 (1)

In addition to regional differences in the general fauna, the low similarity between parasitoids of the various Choreutidae is probably partly a consequence of different feeding sites (host plant virtually concealed vs prominent, as well as low plants vs trees), and also to the mode of preimaginal existence in the case of *M. dolosana*. Differences in overwintering mode and voltinism probably also have an influence.