



## Chapter 1

# INTRODUCTION

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Although most people are blissfully unaware of them, the ichneumonoid wasps are one of the most diverse groups of insects, and in terms of their ecological role they are probably of enormous importance. No-one really has a good idea about how diverse they are and estimates vary widely. The total number of valid species described to date, 18,000 braconids and 23,000 ichneumonids<sup>1</sup>, is certainly a great underestimate, but by how much is still anyone's guess. Many works cite estimates of 40,000 and 60,000, based upon expert opinion (Townes 1969, Gauld & Bolton 1988). Similar values have also been obtained by various objective estimation measures, but it seems likely that these too are underestimates, and narrowing the numbers down is not going to be easy for the reasons explained in Chapter 15.

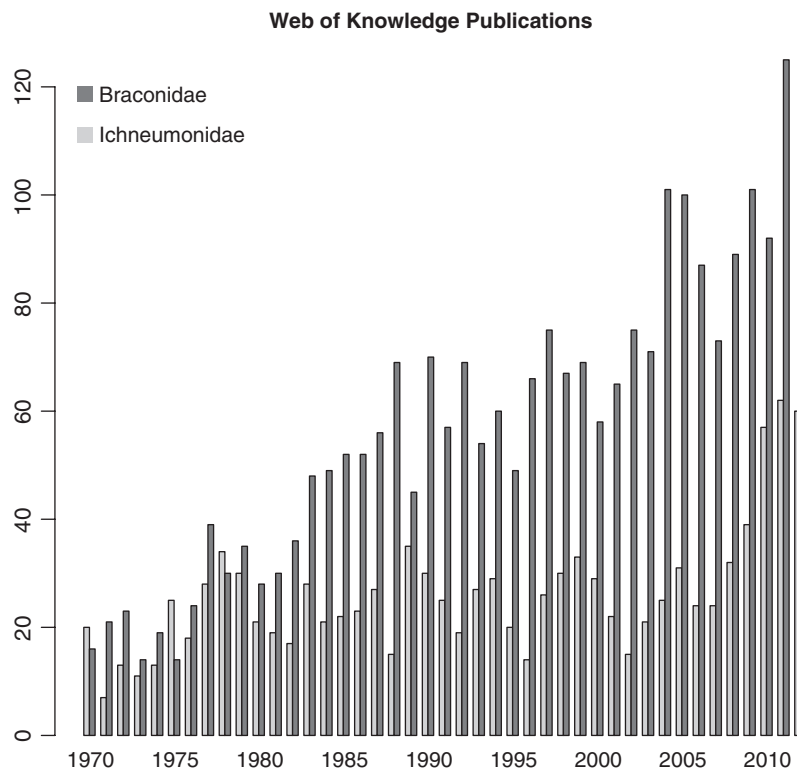
Unfortunately, neither family has attracted a lot of attention from amateur entomologists, which seems to be a prerequisite for a good knowledge of a group's taxonomy, distribution and biology. This may be partly because many of the species are rather small and often dull coloured, although this does not seem to have deterred generations of amateur coleopterists. Probably the most important factor has been the dearth, until fairly recently, of reliable and accessible identification guides to the major groups (subfamilies), confounded by the fact that the subfamily-level classification is only now becoming fairly stable, largely as a result of much new molecular work. Problems have been compounded because numerous names were mis-applied by early workers and, as these errors were slowly discovered and corrected, many groups accumulated a historical backlog of alternative names. In many fields of science, the really old literature seldom has to be cited, but in zoology, a great deal of excellent work on anatomy and biology was carried out 50 to 100 or so years ago. As this may be the only detailed work on a given group, it is still relevant today and the reader therefore has to deal with the sometimes confusing or even misleading nomenclature.

Difficulties in the correct identification of specimens, and publications dealing with incorrectly identified specimens, have also been a major stumbling blocks. To quote Perkins (1959), 'It is perhaps, not surprising that keys to subfamilies are very imperfect, as exceptions can be found to almost all characters that have been used in defining any subfamily, even in the limited British fauna'. Partly because of overall improving taxonomic and systematic understanding, published research on both families is growing, that dealing

with the braconids slightly more quickly than that for the ichneumonids (Fig. 1.1). There may be several reasons for this growth, not the least of which is that most researchers are now under great pressure to publish their findings quickly in bite-sized chunks and in high-impact journals, rather than presenting single, large tomes representing the results of many years of their work. The difference in the rate of publication between the families could well be due to the ease of identification – recognising subfamilies is generally easier for braconids and knowing what subfamily you are dealing with is the essential first step towards a proper identification.

The Ichneumonidae and Braconidae are each such large groups that few people since the early 20th century have attempted to work seriously on the whole of either one of them, so it is hardly surprising that in recent years almost no-one has attempted to tackle them both. This, of course, means that the similarities and differences between them may have been less well considered than they should have been. Superficially, it might seem that these two families essentially parallel one another, they are sister groups and they broadly occupy the same range of niches – they predominantly parasitise exposed and concealed moth and beetle larvae with a few incursions into attacking fly and Hymenoptera larvae, rarer ones into other insect groups and a few other ways of life such as spider egg predation and even a few instances of true phytophagy. However, things may not be as simple as they seem, because despite some remarkable parallels, they also show strong group differences in precisely what they do and in the types of adaptations they typically employ.

It should come as no surprise therefore, that ichneumonids and braconids do not 'behave' in the same way in so many aspects of their biology and morphology. If they did, it seems likely that one would have driven the other to extinction or pushed them a long way in that direction. That both groups are highly speciose seems very likely to indicate that they do not compete in a precise and consistent way, although many individual species no doubt do. Hence there are various sorts of adaptations that appear to evolve frequently in one family but not or only rarely in the other. For example, numerous braconids have evolved carapace-like metasomas where the basal 3 (or sometimes 4) metasomal terga are enlarged, frequently fused, or at least more or less immovably joined and conceal all more posterior ones (see Chapter 10, section *Carapacisation*). Only a very few ichneumonid groups have members



**Fig. 1.1** Numbers of papers on Braconidae and Ichneumonidae published each year in *Science Citation Index* (SCI) journals from 1970 to 2012.

with carapaces and the numbers of species involved is very small. Is this associated with the difference in articulation between the second and third metasomal terga, which is one of the diagnostic features for separating the two families? Endoparasitoid larvae belonging to several different braconid lineages have apparently independently evolved an everted rectum forming a structure called an anal vesicle (see Fig. 5.1) that serves a variety of physiological roles, but this adaptation, as far as is known, has only evolved in two genera within the Ichneumonidae. Similarly, very elongate mouthparts (although variously involving the glossa, malar region or maxillary palps) have evolved on numerous independent occasions within those Braconidae dwelling in relatively arid habitats (see Chapter 10, section *Concealed nectar extraction apparatus*), but the number of such occurrences in the Ichneumonidae is small (e.g. *Rhynchobanchus*: Banchinae). These modified mouthparts, collectively

referred to as a concealed nectar extraction apparatus, are an adaptation to obtain nectar from plants such as Asteraceae or Dipsacaceae, which in turn are adapted to prevent their nectar from drying up in places where water is in short supply. In this case, it may be because braconids tend to comprise a relatively larger proportion of species in such habitats, but the data are not really available to test this.

Ichneumonids collectively utilise a somewhat different spectrum of hosts than braconids. They include many more taxa that are parasitoids of other Hymenoptera, including both endo- and ectoparasitism, in addition to acting as pseudohyperparasitoids of other ichneumonids (see Fig. 13.1; cf. Fig. 12.2), and endoparasitism including developing as true hyperparasitoids within a host, as well as some being predators within aculeate wasp and bee nests. In the Braconidae, members of two tribes within the Euphorinae are endoparasitoids on adult Hymenoptera, a few

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ectoparasitoids attack leaf-mining sawflies and only a few members of the Ichneutinae are endoparasitic within sawfly larvae, and Gauld (1988a) plausibly suggested that these made the transition to sawfly hosts from ancestors that were endoparasitoids of leaf-mining Lepidoptera. Further, no braconids apart from the rather special case of a few euphorines parasitising adult ichneumonoids (see Chapter 12, section *Syntretini*), no braconids are hyperparasitoids or even pseudohyperparasitoids. Two subfamilies within Ichneumonidae, involving several evolutionary transitions, have become associated with spiders either as egg predators or as parasitoids of juvenile and adult individuals. All of these seem to be connected by their use of silk, or volatile or non-volatile compounds associated with silk, in the host location – because of its non-solubility, silk proteins themselves seem an incredibly unlikely source of host-finding cues. Nevertheless, at least some braconids do utilise cues from host silk trails (Ha et al. 2006), but it does not seem to have become an important part of their behavioural repertoire. Perhaps partly associated with this and the places where silk-cocooned hosts occur, ichneumonids appear to have evolved vibrational sounding (a sort of echolocation) as a host location tool on multiple occasions (and lost it on many also), whereas there is no evidence for this host location mode in the Braconidae (see Chapter 10, section *Antennal hammers and vibrational sounding*).

Another important question that we ought to consider is why the ichneumonoids and chalcidoids have not out-competed one another in one direction or another. Some niches occupied by chalcidoids are not available to ichneumonoids; for example, egg parasitism, which necessitates body sizes smaller than or at least at the very bottom range of that which ichneumonoids (e.g. *Miracinae* or *Cheloninae*–*Adeliini*) have thus far achieved. Ichneumonoids described to date are, in general, larger bodied than braconids (see Fig. 15.6), and this may correlate with some differences in host utilisation, since only braconids can attack small insect hosts such as psocids, aphids, plant bugs and tiny beetles (Čapek 1970).

It seems to me a very great shame that many traditional areas of study, such as those on comparative embryology and detailed descriptions of natural history, have suffered a serious decline in recent years and effectively have ceased in most Western universities. For a long time they have been largely restricted to

workers in parts of the world, such as the former Soviet block countries, where access to more trendy modern methods and thought were perhaps restricted. This means that many important descriptions of biology come from before World War II and sometimes before World War I. And although many of these are of high quality, they often deal with species serendipitously, as well as under unfamiliar names that have been lost in synonymy and therefore may require some detective work. However, these are the only sources of detailed biology for some groups.

A great deal of what we know about the biologies of various groups comes from efforts to use them for biological control (e.g. Wharton 1984). As a consequence, we know far more about some subfamilies than we do about others and obviously we know more about taxa that are readily easily brought into culture, which means that the host nearly always has to be easy to culture too, or at least easy to find and collect. There are a surprisingly large number of subfamilies for which we know absolutely nothing about the biology, not even the order of hosts that they attack or whether they are ecto- or endoparasitoids. Some of them include fairly common and frequently collected species.

Now that we have the powerful tool that modern phylogenetics provides, we are in desperate need of more such studies to help test hypotheses about the adaptive natures of particular character states within a comparative framework. Although it is possible in some cases to go out and obtain the necessary taxa, there is a general mismatch of people skills. Many excellent physiologists and molecular geneticists carry out their work on taxa of real or potential economic importance and a considerable amount of their research receives funding because of this. By their nature, the hosts of potential biocontrol insects are generally easy to obtain and culture, although admittedly wood-borers may pose more of a logistic issue than say grass-feeding aphids or cotton-feeding moths. The parasitoids that are therefore best investigated are those which attack these hosts with the consequence that much work has been carried out on a relatively small subset of taxa, aphidiine and microgastrine braconids and campoplegine ichneumonids being prime examples. Many of the laboratory researchers would love to obtain some other parasitoid taxa into culture to study, but this involves setting up host cultures, obtaining the parasitoids and working out rearing techniques, all probably with less funding available. Although there are numerous

exceptions, many laboratory-based experimentalists often do not have the field entomological or natural history backgrounds to facilitate the finding of some of the other taxa.

The other side of the skills mismatch is that there are, at least in many 'Western' and East Asian countries, excellent natural historians who are good at and enjoy going into the field in search of insects and rearing them, but they often do not necessarily know what more detailed pieces of information about an insect's biology are missing. Added to this is the problem that many taxonomically interesting taxa, which might well have particularly interesting biologies and associated physiology, biochemistry, etc., are simply rare, very local in distribution or attack hosts that are very difficult to obtain or bring into culture. There are multiple examples of all of these.

One of the aspects that really needs to be revisited, as soon as sufficient independent molecular phylogenies become available, is all the hypothesised evolutionary transitions and trends that have been based on purely morphological phylogenetic estimates. It is surprising how often the networks obtained from morphological and molecular analyses are similar, which is good, but the rooting is extremely different. Such different results may reflect either that the outgroups (if used) are too distant to provide much meaningful evidence of true ancestry or even that workers had a soft spot for an elegant biological story. It was certainly common practice in early cladistics studies to ignore characters that the worker 'knew' to be homoplastic. Currently available molecular data have provided a considerable number of new insights and reasonably well-supported big pictures for both families, but there are still many areas of the evolutionary tree where there is a real shortage of resolution and several taxa whose placements are far from certain. Quite possibly much of the radiation at subfamily level occurred subsequent to the Cretaceous period – there are few Cretaceous fossils that can be assigned to modern subfamilies with confidence, especially within the Ichneumonidae, yet the Eocene (53 to 33.7 Mya) fossil record contains many species that are fairly certainly recognisable to modern subfamilies and sometimes possibly to a genus.

The large size of both families mean that there are inevitably many scientific names which may seem daunting or confusing to beginners. Even when dealing with the relatively small number of frequently cultured species there are still many of them to get to grips with.

I think it is certain that the nomenclatural aspect of work on this group has been off-putting, not aided by the fact that some workers have employed alternative systems [see Chapter 13, section *Henry Townes (1913–90) and his idiosyncratic nomenclature*, although it is not just Townes' work where confusion can arise].

It is always difficult in a book such as this to decide whether to start with morphology, biology or taxonomy. I have opted for the first, but in order to be able to make some sense of the features, it is necessary to refer to some aspects of each of the others in this section. I have therefore included below very brief outlines of some of the important biological concepts and systematics to facilitate understanding. I have also chosen to arrange things in rather a small number of chapters, each consequently with a fairly broad remit. Nevertheless, some topics have had to be shoe-horned in at places where they might seem slightly incongruous. It also seemed logical to include a few physiological aspects within more broadly morphological sections since the understanding of the morphology is sometimes intimately linked with other processes. As this will be used mainly as a reference book, some facts are repeated in two or more places. I hope that in the end, the structure more or less makes sense.

## LIFE HISTORY

There are two important terms to be learnt here. The fairly obvious difference between parasitoids which (generally) lay their eggs within a host and whose larvae develop internally surrounded by wet host tissues, i.e. **endoparasitoids**, and those that lay eggs externally and whose larvae complete feeding from the outside, surrounded by air, i.e. **endoparasitoids**.

A second important distinction, – indeed, in many respects possibly more important – is between parasitoids whose hosts do not develop further after being parasitised, referred to as **idiobionts**, and those parasitoids whose hosts continue feeding and usually moulting after the parasitoid has oviposited (usually) in them, which are called **koinobionts**.

Ecto- and endoparasitism and idiobiont/koinobiont strategies both explain a great deal about other life history features and they are strongly correlated, although asymmetrically. Most koinobionts are endoparasitoids, but idiobionts can be either ecto- or endoparasitic, but endoparasitic idiobionts are almost entirely, within

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the Ichneumonoidea, parasitoids of host pupae and complete their development therein.

### SYSTEMATICS

Necessarily, many subfamilies and genera have to be mentioned, and typically members of the same subfamily show very similar biologies and members of genera even more so, although there are some exceptions. Both Braconidae and Ichneumonidae include a large clade whose members are all koinobionts and, with the exception of the Tryphoninae within the Ichneumonidae, endoparasitoids. In both families, the sister group to the entirely koinobiont clade is a predominantly idiobiont ectoparasitoid lineage with numerous independent transitions to endoparasitism and koinobiosis. In the Braconidae, members of this lineage are called cyclostomes (see Fig. 2.1b) in reference to their mouthpart morphology, although some members of the cyclostome lineage have secondarily become non-cyclostomes. When I use the term 'cyclostome'

in this book, unless specified otherwise, I am referring to the lineage rather than the condition. There is no equivalent term within the Ichneumonidae, although the biologically equivalent lineage of (predominantly) koinobiont endoparasitoids is dominated by a group informally referred to as the ophioniformes. The ending '-formes' is used throughout to indicate groupings of subfamilies that are believed to be monophyletic and usually have relatively consistent biologies.

Many readers will not know where a given taxon belongs, either within the above larger framework or to what subfamily it belongs. I have therefore very largely specified this as I go along, despite its clumsiness, because in that way the reader might most readily search for further information on other members of group of interest.

### ENDNOTE

1. Over 60,000 species names have been published so some 19,000 are synonyms.