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The evolutionary pattern of host use in the Bombyliidae (Diptera): a diverse family of parasitoid flies

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The larval host associations and mode of parasitism of Bombyliidae (bee flies) are summarized and analysed within an evolutionary framework. We discuss difficulties in extracting information from the (almost 1000) host records, noting that most observations are made by chance, often imprecise, and distributed unevenly across bombyliid taxa. These caveats aside, the vast majority of Bombyliidae are ectoparasitoid; endoparasitoids are known in only three tribes belonging to two distantly related subfamilies, the Toxophorinae (Gerontini and Systropodini) and Anthracinae (Villini). The recorded host range of Bombyliidae spans seven insect Orders and the Araneae; almost half of all records are from bees and wasps (Hymenoptera). No Bombyliidae have evolved structures to inject eggs directly into the host as is the case in many hymenopterous parasitoids. Bombyliid larvae usually exhibit hypermetamorphosis, and contact their host while it is in the larval stage. Bee fly larvae consume the host when it is in a quiescent stage such as the mature larva, prepupa or pupa. Records of hyperparasitism by Bombyliidae are uncommon, most occurring in genera of the Anthracinae. All bombyliids recorded as hyperparasitoids do not appear to have evolved in any close association with the primary host, and are best termed pseudohyperparasitoids. Both facultative and obligate pseudohyperparasitism has been recorded. Bombyliidae are difficult to place in the koinobiont/idiobiont classification used most extensively in Hymenoptera but they share most features of koinobionts. Provision-directed cleptoparasitism has been recorded in one genus. We propose an evolutionary scenario progressing from an ancestral substrate-zone free-living predator to ectoparasitoid, a broadening of host range to include the consumption of orthopteran egg pods, and the independent development of endoparasitism in two lineages. The suggestion that host range narrows as the intimacy of encounter between female parasitoid and host increases is supported in the Bombyliidae. Amongst the basal subfamilies which are parasitoids, host range is narrowest in the Toxophorinae. In the more derived subfamilies host range is generally broad, and is dictated by ecological context rather than host phylogeny. Bombyliidae violate the prediction of increased species richness in parasitic groups, and the broad host range of most bee flies is a possible explanation.

ADDITIONAL KEY WORDS:—endoparasite – ectoparasite – koniobiont – idiobiont – pseudohyperparasite.

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INTRODUCTION

There is no doubt that parasites are important to the structure and function of the biosphere: Price (1980) reasoned that at least half of the world's species are parasites. Parasites develop on or in the bodies of other organisms and play important roles in the natural regulation of populations (LaSalle & Gauld, 1991). Several of the most diverse lineages of insect parasites usually consume and kill a single organism during their development and are termed parasitoids (Reuter, 1913; Waage & Greathead, 1986; Godfray, 1994).

Parasitoids employ a wide range of hosts and feeding strategies, and there have been a number of attempts to provide a biologically meaningful, functional classification. The feeding position of a parasitoid, whether outside (ectoparasitoid) or inside (endoparasitoid) the tissues of the host, provides a simple dichotomy. Searching for a more powerful correlate of host range, Askew & Shaw (1986) distinguished between those parasitoids that do not immediately immobilize or kill their host on contact, but allow it some further development (koinobionts), and those parasitoids that kill and consume their host in the state it is in when attacked (idiobionts). They argued that most koinobionts would tend to have relatively narrow host ranges because of the close adjustment required to the host's biology, and idiobionts would tend to have broader host ranges. Askew & Shaw (1986) found that these generalizations held true when tested on hymenopterous parasitoids attacking arboreal leaf-miners in Britain.

The purpose of this contribution is to synthesize what is known of the biology of a diverse group of dipterous parasitoids, the bee flies (Bombyliidae). We bring together three separate sources of information: (1) the outstanding compilation of host records and other biological information on the Bombyliidae by Du Merle (1975); (2) a database of information updating Du Merle's contribution, which is maintained by one of us (DG), and (3) the recent cladistic phylogeny of the Bombyliidae proposed by Yeates (1994). We present a table of Bombyliidae host records reported since Du Merle (1975) or overlooked by him (Appendix). We have compiled information from a total of 985 bombyliid rearing records. Our aim is to gain insights into three main aspects of Bombyliidae life histories and their evolution as follows: (1) details of host use and host shifts; (2) the degree of host specialization, and (3) the distribution of ectoparasitoid and endoparasitoid strategies.

Evolutionary scenarios have been developed to explain the evolution of parasitoid traits in particular taxonomic groups without an explicit phylogenetic framework (e.g. Gauld, 1988). Cladistic methods allow much more explicit hypotheses of character evolution to be discovered and tested (Brooks & McLennan, 1994; Grandcollas, Deleporte & Desutter-Grandcollas, 1994). By mapping biological features onto a bee fly phylogeny, we prepose an evolutionary scenario for the development of parasitic strategies in the family. We examine the idiobiont/koinobiont classification from the perspective of our findings on Bombyliidae. Host use data may also provide additional characters to test the current phylogeny based on morphology (Miller & Wenzel, 1995).

Parasitoid definitions

Most definitions of parasitoid implicitly or explicitly restrict the term to the holometabolous insect Orders Hymenoptera, Diptera, Lepidoptera, Neuroptera and Coleoptera (Godfray, 1994). Eggleton & Gaston (1990) expanded the traditional definition of parasitoid to include some non-insect groups with functionally similar life histories. In order to clarify our usage of the term parasitoid, we list three attributes important to define them; the first two are not absolutely necessary, but are found in the vast majority of parasitoids.

We distinguish parasitoids from predators and parasites using the following characteristics:

(1) parasitoids differ from predators in that they (usually) consume a single prey item during their development;
(2) parasitoids are distinguished from parasites because (with rare exceptions) they kill their host, and
(3) parasitoids are further distinguished from parasites because the life cycle of a parasitoid includes a free-living reproductive stage that occupies a different niche from the developing stage.

These characteristics do not limit parasitoids to any taxonomic group. Limiting the term parasitoid to those organisms that consume a single host (Godfray, 1994) brings with it the unwanted consequence that some individuals of an otherwise parasitoid species may be classified as predators. For example, the larvae of the bee fly *Heterostylum robustum* (Osten Sacken) (see below) have the facultative ability to consume a second host if their first host is too small (Bohart, Stephen & Eppley, 1960). In addition, bee flies that consume numerous eggs in a single locust egg pod would be considered predators (e.g. *Systoechus* Loew). Both these groups share other life history traits with related flies that consume a single host, and it appears cumbersome to exclude them from the parasitoid category. We have referred to these latter species as ‘egg pod consumers’ below. Eggleton & Gaston (1990) emphasized that the essential feature of a parasitoid is that it kills its host. This has the disadvantage that some species (or individuals) otherwise belonging to a parasitoid group are excluded simply because their host survived after parasitism (e.g. De Vries, 1984), whether or not it survived to reproduce.

The characteristic free-living adult stage of parasitoids is critical in distinguishing them from true parasites [Askew (1971) termed parasitoids protelean parasites], and confers evolutionary advantages in dispersal and the ability to generate novel genetic combinations. Parasitoids have a free-living adult stage that allows them to disperse to new habitats. The dispersal stages of true parasites are usually not the adults, and usually disperse passively. The parasitoid adult free-living stage not only disperses but also feeds and reproduces, and often does so at some distance from its host. The majority of parasites reproduce in, on, or adjacent to their host.

Bombyliidae: biology and relationships

The bee flies (Bombyliidae), with the recent removal of the Proratinae (Yeates, 1992), are now considered monophyletic. The relationships between the various subfamilies (Yeates, 1994) are shown on the left side of Table 1 and in Figure 4. Although the morphological data are not particularly strong, the family is considered to be the sister-group to the remaining members of the superfamily Asiloidea (Woodley, 1989). The Bombyliidae were once grouped with two other families of cladistically basal Brachycera possessing parasitoid larvae (Rohdendorf, 1974), the Nemestrinidae and Acroceridae; these families are now thought to be cladistically outside the clade Asiloidea (Woodley, 1989; Yeates, 1994).

The Bombyliidae contains over 5000 described species and is thus one of the largest families of true flies. Species of Bombyliidae are most numerous in areas of Mediterranean climate (Hull, 1973) and they may represent another parasitoid group in which there is a decline in species richness toward tropical regions (Eggleton & Gaston, 1990). Most species are parasitoids or hyperparasitoids of other insects (see Fig. 1 for a typical life history), primarily the immature stages of the large endopterygote orders Coleoptera, Hymenoptera, Lepidoptera, and other Diptera (Hull, 1973; Du Merle, 1975). The parasitoid lifestyle has arisen numerous times in the Diptera (Oldroyd, 1964; Eggleton & Belshaw, 1992). Because other Asiloidea are mostly soil-dwelling predators, it is most likely that the ancestor of parasitoid Bombyliidae also had these habits (Eggleton & Belshaw, 1992). Adult bee flies are frequent flower visitors where they feed on nectar and pollen.

The female terminalia of almost all bee flies belonging to clade S of Figure 4 is modified to include a pouch immediately posterior to the genital chamber. This pouch, termed the 'sand chamber' (Schremmer, 1964), is surrounded by elongate setae and enlarged spines (Fig. 2b). Painter (1932) first drew attention to the complex oviposition behaviour exhibited by most bee flies. The sand chamber and its associated vestiture functions to gather and hold small particles of the substrate which are then glued to the eggs prior to deposition (Biliotti, Demoulin & DuMerle, 1965). In subfamilies that possess a sand chamber, egg deposition is almost always conducted while hovering.

Female Bombyliidae belonging to clade S may oviposit directly into nests of potential hosts (for example Bohart *et al.*, 1960) or more randomly onto the substrate (for example Du Merle & Delpech, 1973). Thus, host searching is at least partially the responsibility of the first instar (planidium) larva. The planidium searches for hosts predominantly in the leaf litter-soil interface, termed the substrate-zone habitat (Hlavac, 1971). A restricted number of genera belonging to clade S such as *Beckerellus* Greathead (Bombyliinae) (Greathead, 1995) and *Antonia* Loew (Antoniinae) have lost the sand chamber and the ovipositor is tubular. Although nothing is known of oviposition in these groups, behavioural changes have almost certainly been associated with the gross morphological modifications.

Little is known of the oviposition behaviour of the subfamilies basal to clade S in Figure 4. Many species in this group frequently attack hosts above the ground, suggesting that the presence of a sand chamber may tie bee flies more closely to hosts in the substrate-zone. *Systropus* Wiedemann (Toxophorinae) oviposits directly onto the body of the host limacodid larva (Lepidoptera) (Genty, 1972; Greathead, 1987). Female *Usia* Latreille (Usiinae) scatter eggs over the ground while perched on twigs (Du Merle, 1971). The hosts of other genera such as *Toxophora* Meigen are located above ground. Although no observations have been made, females of these groups may oviposit directly onto the host nest.

Egg production in Bombyliidae may be prodigious. *Heterostylum robustum* (Bombyliinae) and *Anthrax limulatus* Say (Anthracinae) can produce an estimated 1000 eggs per day (Bohart *et al.*, 1960; Marston, 1964), Gerling & Hermann (1976) estimated that *Xenox tigrinus* (De Geer) is able to produce 2000–3000 eggs, and *Comptosia biguttata* Yeates (Lomatiinae) is capable of producing about 800 eggs per day (Yeates, unpublished data).

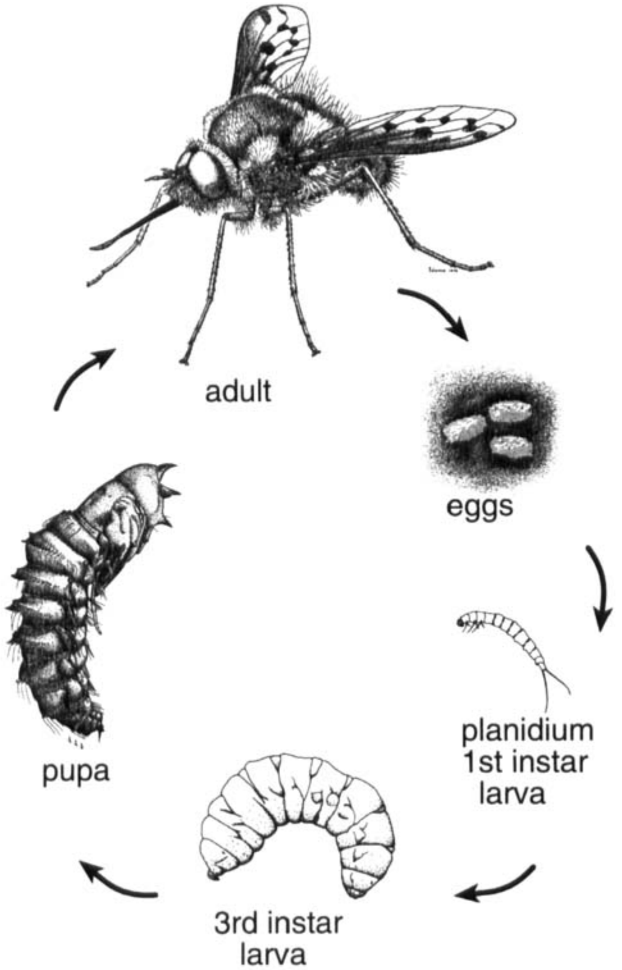


Figure 1. Generalized life-history of a parasitoid bee fly.

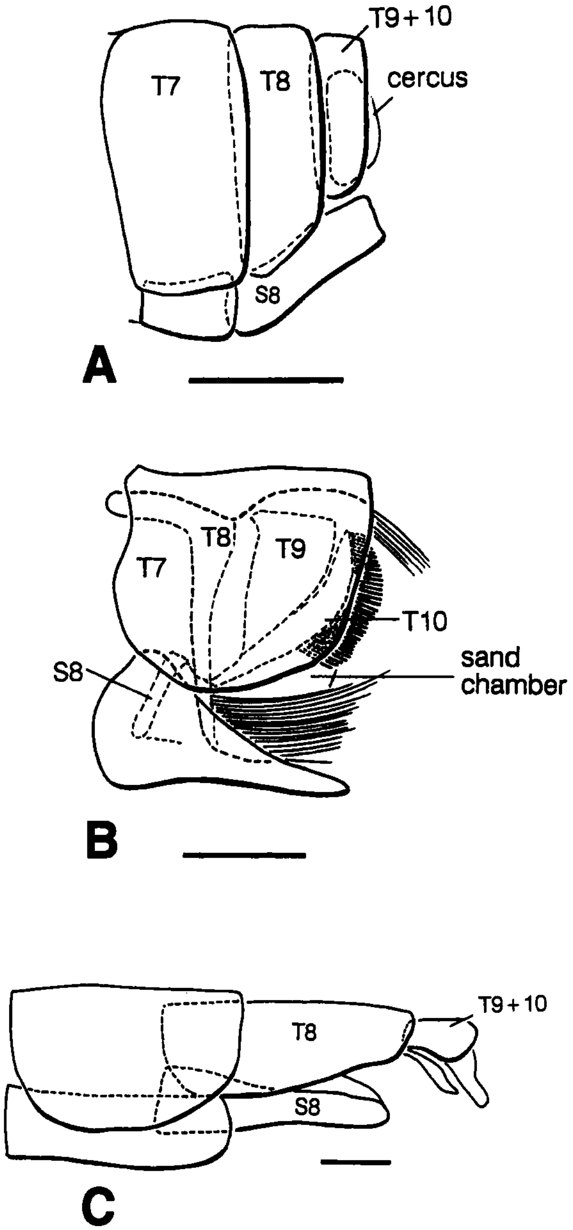


Figure 2. The diversity of female genitalic structure in the Bombyliidae. A, *Usia atrata* (Fabricius), a member of the Usiinae which plesiomorphically lacks a sand chamber and has a simple oviposition behaviour. B, *Bombylius major* Linnaeus, a member of the Bombyliinae which shows a sand chamber typical of many members of clade S (Figure 4). Tergite and sternite 8 are invaginated inside segment 7, and tergite 8 has a brush of long hairs on its posterior margin (only shown here dorsally and ventrally), and stout spines on tergite 10. Oviposition in this group is complex: the female first alights and loads the sand chamber with particles of the substrate; these are used to coat the eggs which are deposited while the female hovers. C, *Antonia suavissima* Loew (Antoniinae), one of the few members of clade S which has lost the sand chamber, and has a simple, tubular abdominal apex. Oviposition behaviour in this group is unknown. Scale bars = 0.5 mm.

It is instructive to compare the oviposition habits of Bombyliidae with another large, but distantly related, family of dipterous parasitoids, the Tachinidae. The simplest method of oviposition in the Tachinidae is the attachment of an egg to the host's integument (Wood, 1989). This is similar to the oviposition method found only in the bee fly *Systropus*. We do not know of any Bombyliidae that insert their eggs into the host's body, or deposit microtype eggs on plant surfaces which the host consumes, as found in some Tachinidae. Some Tachinidae and most species of Bombyliidae broadcast eggs in a habitat suitable for the host (e.g. many Tachininae and Dexiini and the members of clade S of the Bombyliidae). Tachinidae are much more diverse and numerous parasitoids of hosts above the substrate zone than Bombyliidae. The success of parasitic Hymenoptera and Tachinidae in this environment may have restricted the vast majority of Bombyliidae to hosts within the substrate zone, and may partially explain the diversity of bee flies with sand chambers in comparison with those more basal clades which have other oviposition strategies.

Almost all Bombyliidae undergo hypermetamorphosis, the first instar planidium differing morphologically from the other larval instars. The only exceptions appear to be species in the subfamilies Mythicomyiinae (Andersson, 1974) and Heterotropinae (Yeates & Irwin, 1992). Amongst hypermetamorphic Bombyliidae, the planidium larva functions to find and attach itself to the host. The morphology of the planidium is adapted for dispersal, whereas the morphology of later instars is clearly suited to a more sedentary existence. The planidium is elongate, has two long setae and fleshy pseudopods at the apex of the abdomen and a pair of long setae on each thoracic segment (for example Du Merle, 1972). Second and later instar larvae are stout, often scarabaeiform, and lack the long thoracic and abdominal setae (for example Hull, 1973).

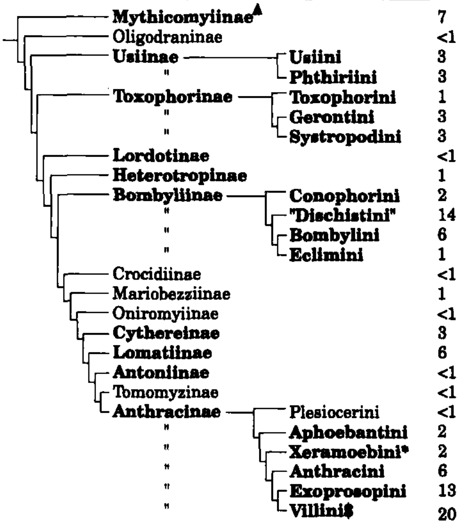
ANALYSIS

Data extraction

The one common thread linking almost all host records in the Bombyliidae is serendipity. A perusal of Du Merle (1975) reveals that most bee flies are reared by accident as their hosts are reared. Most records of parasitism are published as a biological oddity alone (for example Aiello, 1980), or in a work describing the biology of the host (for example Knisley & Pearson, 1981). Occasionally the host records are accumulated if the host rearing program is extensive (for example Brooks, 1952). Exceptions to these generalizations are the few papers published dealing directly with the biology of the parasitoid itself, such as the detailed study of the biology of *Systoechus somali* Oldroyd by Greathead (1958), or the research by Bohart *et al.* (1960), on the biology of *Heterostylum robustum*, and the series by Du Merle (1979a, b, c, 1981) on the biology of *Villa brunnea* Becker. All these studies are by-products of studies of an economically important host. *Systoechus somali* is a natural enemy of the desert locust *Schistocera gregaria* (Forskål), *H. robustum* is a natural enemy of the alkali bee, *Nomia melanderi* Cockerell, and *Villa brunnea* is a natural enemy of the pine processionary moth, *Thaumetopoea pityocampa* Schiff.

The chance nature of many host records in the Bombyliidae requires that we take extreme care in making generalizations from these data. As a recording of the host alone the chance records are adequate, but more detailed information is often absent, or obtained by indirect routes, and therefore unreliable. Du Merle (1975) was well aware of this problem, and flagged information in his catalogue with a single asterisk if he regarded it as "a little astonishing", two asterisks were reserved for information which he considered of "very little likelihood" and he used three asterisks to denote information which he rejected entirely. We have either ignored or draw attention to host records or biological information we consider doubtful or based on speculation, such as "adults seen ovipositing in nest entrances". The sparse nature of many of the records in many subfamilies may also give a false impression of host specialization.

Table 1 gives an overview of Bombyliidae host use at the level of subfamily and tribe for the parasitoid and at the level of Order for the host. This is just one of many levels we could have chosen to represent the information, and presents the 985 records in extremely abbreviated form. We chose this level because it is the one for which we have a complete phylogenetic hypothesis for the parasitoid (Yeates, 1994). Table 2 gives a more detailed summary, extending the level of analysis for the parasitoid to genus, rather than subfamily and tribe as in Table 1. Table 2 offers few further insights into the evolution of host associations in the Bombyliidae because we have little knowledge of the phylogenetic relationships among genera. Genera within a subfamily or tribe may have different host associations (for instance bee and wasp larvae or orthopteran egg pods in the Bombyliinae) but we have no way of discovering the evolutionary direction of these host shifts without more detailed knowledge of the relationships between the genera. More powerful evidence of host-



Subfamily	Tribe	% spp.	% recs	Parasitism Ecto-	Endo-	Orth.[¶]	Neur.	Host Order[§] Cole.	Dipt.	Lep.	Hym.
Mythicomyiinae[Δ]		7	<1	Predator		•					•
Oligodraninae		<1	-								
Usiinae	**Usiini**	3	<1	•				•			
"	**Phthiriini**	3	<1	•						•	
Toxophorinae	**Toxophorini**	1	3	•							•
"	**Gerontini**	3	1.5		•					•	
"	**Systropodini**	3	4.5		•					•	
Lordotinae		<1	<1	•							•
Heterotropinae		1	<1	Predator							
Bombyliinae	**Conophorini**	2	<1	•				•			•
"	**"Dischistini"**	14	3	•		•					•
"	**Bombylini**	6	10	•		•		•			•
"	**Eclimini**	1	<1	•				•			•
Crocidiinae		<1	-								
Mariobezziinae		1	-								
Oniromyiinae		<1	-								
Cythereinae		3	2	•		•					•
Lomatiinae		6	<1	?				•		•	
Antoniinae		<1	<1	?							•
Tomomyzinae		<1	-								
Anthracinae	Plesiocerini	<1	-								
"	**Aphoebantini**	2	<1	?		•				•	
"	**Xeramoebini***	2	3	•		•			•	•	•
"	**Anthracini**	6	34	•			•	•			•
"	**Exoprosopini**	13	5	•			•	•		•	•
"	**Villini$**	20	27	•	•	•	•	•	•	•	•

§ All are parasitoids of larval, prepupal or pupal stages, except in Orthoptera, where egg pods are consumed.
¶ Abbreviations for host orders are as follows; Orth., Orthoptera; Neur., Neuroptera; Cole., Coleoptera; Dipt., Diptera; Lep., Lepidoptera; Hym., Hymenoptra.
Δ Taxon names in bold are those for which we have some life-history informatin, for others we lack this information.
* One species recorded from a spider egg sac.
$ One species recorded from a cockroach ootheca.

Table 1. Summary of Bombyliidae host relationships.

TABLE 2. Summary of host record of Bombyliidae

Genus	No. of records	No. of spp.	Comments
MYTHICOMYIINAE			
Acridophagus	1	1	Egg-predator of Acrididae
Glabellula	2	1	Predator on larvae of *Formica* spp.
Mythicomyia	1	1	Ex Anthophoridae
Psiloderoides	1	1	Egg-predator of Acrididae
USIINAE: Usiini			
Usia	2	1	Ectoparasitoid on pupa of Tenebrionidae
USIINAE: Phthiriini			
Phthiria	4	4	Ex Gelechiidae & Tortricidae
TOXOPHORINAE: Toxophorini			
Toxophora	32	9	Ectoparasitoids in nests of solitary bees & wasps
TOXOPHORINAE: Gerotini			
Geron	22	10	Parasitoids (?endo) of larvae or pupae of Noctuidae, Psychidae, Pyralidae & Tortricidae in concealed situations, also hyperparasitoids
TOXOPHORINAE: Systropodini			
Systropus	47	21	Endoparasitoids of larvae & pupae of Limacodidae
LORDOTINAE			
Lordotus	4	1	Ex nests of Sphecidae
HETEROTROPINAE			
Heterotropus	1	1	Predators
BOMBYLIINAE: Conophorini			
Conophorus	2	2	Pupae in soil. No host association
Sparnopolius	2	2	Once ex nest of Anthophoridae, once as ectoparasitoid of Scarabaeidae
BOMBYLIINAE: Acrophthalmydini			
Acrophthalmyda	1	1	Hyperparasitoid of Tiphiidae on Scarabaeidae
BOMBYLIINAE: 'Dischistini'			
Anastoechus	18	6	Egg-predators of Acrididae & prey on other predators in egg-pods
Bombylisoma	2	2	Records speculative, based on adult behaviour
Heterostylum	11	3	Ectoparasitoids of solitary bee larvae & pupae
Triploechus	1	1	In association with Colletidae
BOMBYLIINAE: Bombyliini			
Bombylella	2	1	Ex dung balls of Scarabaeidae
Bombylius	38	9	Ectoparasitoids in nests of bees, one record from Eumeninae (Vespidae)
Parabombylius	2	1	Ex solitary bee nests
Systoechus	51	19	Egg-predators of Acrididae
BOMBYLIINAE: Eclimini			
Lepidophora	5	1	Ectoparasitoids in nests of Sphecidae & Eumenidae
Thevenetimyia	3	3	Ex borings of Cerambycidae & Ptinidae
CYTHEREINAE: Cythereini			
Callostoma	11	3	Egg-predators of Acrididae
Chalcochiton	1	1	Ex nest of Eumeninae (Vespidae)
Cytherea	9	5	Egg-predators of Acridiae
CYTHEREINAE: Cylleniini			
Cyllenia	1	1	Ex cocoon of Tenthredinidae in soil
LOMATIINAE			
Anisotamia	1	1	Ovipositing in association with fossorial Hymenoptera
Comptosia	2	2	One ex Hepialidae, one associated with ants
Lomatia	1	1	Ectoparasitoids of larva of Tenebrionidae
ANTONIINAE			
Antonia	3	3	Associated with mud nests of wasps, reared once
ANTHRACINAE: Aphoebantini			
Aphoebantus sensu stricto	7	2	Egg-predators of Acrididae (North America only)
Epacmus	1	1	Ex pupa of Ethmiidae
ANTHRACINAE: Anthracini			
Anthrax	306	70	Ectoparasitoids of larvae and pupae of bees and wasps. One record ex Mymeleontidae. *A. analis* endoparasitoid of Cicindellidae

TABLE 2. *(continued)*

Genus	No. of records	No. of spp.	Comments
Satyramoeba	2	1	Ex nests of Anthophoridae & Sphecidae
Spogostylum	12	4	Ectoparasitoids of solitary bees & wasps in soil also – from egg-pods of Acrididae & their Meloidae predators; cocoon of pyralid & its braconid parasitoid
Turkmeniella	1	1	Ex nest of Anthophoridae in soil
Walkeromyia	2	1	Ex nests of *Xylocopa*
Xenox	13	4	Ex *Xylocopa* spp
ANTHRACINAE: Xeramoebini			
Petrorossia	24	15	3 spp. ex puparia of *Glossina* spp., 2 spp. ex cocoons Tiphiidae, 1 sp. predator in spider egg-mass, rest ectoparasitoids of solitary bees & wasps
Xeramoeba	12	2	1 sp. egg predator of Acrididae also Bombyliidae & Meloidae predators. 1 ex pupae of Noctuidae
ANTHRACINAE: Exoprosopini			
Exoprosopa	25	12	Ex cocoons of Sphecidae, Pompilidae and Tiphiidae. Once from Scarabaeidae
Heteralonia	2	2	One ex 'dead unparasitized locust', one ex cocoon of Pompilidae
Hyperalonia	2	2	Ectoparasitoids on Sphecidae
Ligyra	14	5	11 ectoparasitoids in cocoons of Scoliidae and Tiphiidae. We consider records from Asilidae, Pompilidae & Sphecidae unreliable
Litorhina	3	2	2 ex nests of Sphecidae, 1 from Tiphiidae cocoon
Micomitra	3	1	Parasitoid of pupae of Myrmeleontidae
Pterobates	2	2	Ex cocoons of Pompilidae and indet Lepidoptera
ANTHRACINAE: Villini			
Chrysanthrax	6	5	3 ex cocoons of Tiphiidae, 1 ex nests of Anthophoridae
Dipalta	2	1	Ex pupa of Myrmeleontidae in cocoon
Exhyalanthrax	61	16	Most parasitoids in puparia of Diptera; also ex cocoons of Ichneumonidae, lepidopteran & diprionid hosts, 1 predator in ootheca of cockroach.
Exechohypopion	1	1	Ex pupa of Therevidae
Hemipenthes	52	6	Parasitoids in puparia of Diptera, cocoons of Ichneumonoidea, also their Lepidoptera and Diprionidae hosts. We consider records from Bombyliidae pupae, Andrenidae and Acrididae are unreliable
Lepidanthrax	4	1	One ex cocoon of Sphecidae, other records are not rearings
Marleymyia	2	2	Ex pupae of Cossidae
Oestranthrax	1	1	Parasitoid of Myrmeleontidae
Paravilla	11	9	Ectoparasitoids of bee pupae
Poecilanthrax	23	7	Endoparasitoids of Noctuidae pupae
Rhynchanthrax	1	1	Ex cocoon of Tiphiidae
Thyridanthrax	25	9	8 ex cocoons of Sphecidae, 15 as egg-predators of Acrididae, 2 ex pupae of Noctuidae, 1 ex pupa of Curculionidae
Villa	81	27	Endoparasitoids of Noctuidae, Lycaenidae, Tabanidae, 2 Tenebrionidae, 1 Myrmeliontidae

parasitoid evolution may become available once these lower-level phylogenetic hypotheses are complete and the hosts of more genera are known.

Taxonomic distribution of host records

The third and fourth columns of Table 1 indicate how representative Bombyliidae host records are in a taxonomic sense. The third column shows the percentage of described Bombyliidae species represented by that row, and the fourth column shows the percentage of host records represented by that row. For instance if the taxonomic sampling of host records was taxonomically even, then we would expect a subfamily representing 10% of species to account for 10% of host records. The degree to which the percentages from each column differ gives us an estimate of the degree to which bee fly host records depart from a representative sample. Not surprisingly, all of the subfamilies for which we have no host records (Oligodraninae, Crocidinae, Mariobezzinae, Oniromyiinae and Tomomyzinae) are represented by 1% or less of species. The subfamily Anthracinae accounts for just over 40% of the described species in the family, and over 60% of the host records. This imbalance is caused by the tribe Anthracini, which are represented by over five times as many host records (34%) as species (6%). We infer that some attribute of the Anthracini makes host records easy to collect. Most of these records are for the genus *Anthrax* Scopoli, a speciose, cosmopolitan genus of bee flies whose larvae are ectoparasitoids of bees and wasps. Perhaps the fact that female *Anthrax* can often be seen searching surfaces such as walls and embankments for suitable host nests has contributed to the large number of host records for this genus. More disturbing are the groups which represent a considerable percentage of described species but for which we have very few host records. In this category we place the Mythicomyiinae, Usiinae, 'Dischistini' (placed in quotation marks because evidence for the monophyly of the tribe is lacking) of the Bombyliinae, the Lomatiinae and the Exoprosopini of the Anthracinae. We infer that there is some attribute of these groups which makes their life histories cryptic to human observers.

Table 3 lists host records in broad host categories. Almost half the records (48%) are from bees and wasps, a great majority collected by ethologists. Agricultural and forestry entomologists have been important in accumulating records from moths, sawflies locusts and grasshoppers (39%) and hosts of medical and veterinary concern (tsetse flies) a further 5%. Taking the data from this table and the taxonomic representation of host records into account, we surmise that many groups of Bombyliidae for which life histories are poorly known probably feed on insect groups that are rarely reared-either because there is no economic impetus to do so or because of a cryptic lifestyle. For example, soil inhabiting Coleoptera larvae and insect immatures inhabiting decomposing logs may be underrepresented in rearing records compared to the real rate of parasitism of these groups by Bombyliidae.

TABLE 3. Summary of Bombyliidae host records by host

Hosts	No. of records (%)	Comments
Bees and wasps	482 (48)	308 for *Anthrax* spp.
Moths and sawflies	204 (21)	47 for *Systropus* spp.
Locusts and grasshoppers	147 (15)	
Tsetse flies	46 (5)	42 for *Exhyalanthrax* spp.
White grubs	32 (3)	
Horse flies	13 (1)	
Others	61 (6)	

Evidence after emergence

In the hope that this review stimulates the reporting of Bombyliidae host associations, we provide a few suggestions to improve the detail of those reports, and hence their utility. Most records of parasitism by Bombyliidae are recognized only after the parasitoid has emerged from its host's pupal shelter. Given that this will be the case for the majority of future rearings, we offer some suggestions which will allow as much information as possible to be extracted from post-emergence investigations. Detailed examination of the host's shelter and its contents provide telltale clues to the nature of parasitism.

There are several ways of determining, after emergence, whether Bombyliidae larvae feed externally or internally on the host (Fig. 3). Most Bombyliidae are ectoparasitic on host larvae, and after the emergence of the parasitoid we would expect to find (after careful dissection) a shrivelled host larval integument with only mouth-hook sized holes, a shed bee fly larval integument and a fully formed bee fly pupa (Fig. 3A). Almost all Bombyliidae pupae are easy to recognize because of the characteristic spines and hairs on the head, thorax and abdomen (e.g. see Hull, 1973). The bee fly larval integument can be identified by the characteristic head sclerites, particularly the prominent raised labrum (for example Bohart *et al.*, 1960, fig. 12). Endoparasitic Anthracinae consume of the host after it has pupated and undergo the larval-pupal ecdysis inside the host's pupal case. After parasitoid emergence in these circumstances two pupal cases should be present in the

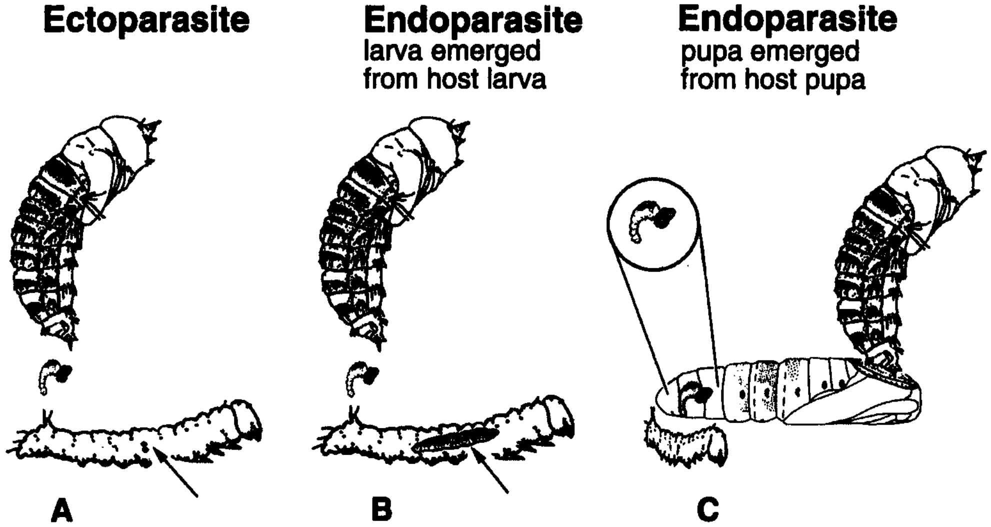


Figure 3. Evidence remaining after bee fly emergence regarding the nature of the parasitism. A, ectoparasitism: the bombyliid killed the host before the host reaches the pupal stage. We would expect a bee fly pupal case, cast larval integument and the deflated remains of the host with only small puncture marks. Bombyliidae pupae are recognizable because of the stout spines on the head and abdomen, those on the abdomen having anterior and posterior projections (see Hull, 1973). B, endoparasitism: the bee fly emerged from the host larva before it reached the pupal stage. We would expect the bee fly pupa and cast larval integument, and the deflated remains of the host with a large hole from which the mature bee fly larva issued. C, endoparasitism: the bee fly emerged from the host pupa. Then we would expect a bee fly pupa, host pupa with a hole from which the bee fly emerged, the cast larval integument of the host, and the cast larval integument of the bee fly inside the empty host pupal case. The cast larval integuments of the host and bee fly have different head capsule structures.

parasitised cocoon or host shelter – one host pupal case with an emergence hole in it, and the last larval exuvium of the bombyliid larva inside, and the Bombyliidae pupal case split along the dorsum of the thorax where the bee fly emerged (Fig. 3C). There is some circumstantial evidence that, in contrast to Anthracine endoparasitoids, those belonging to the Toxophorinae issue from the host larvae after it has formed a cocoon, but before it has pupated (Fig. 3B). The bombyliid then pupates in the host cocoon. The discarded host integument remains in the host cocoon and the bee fly larva would leave a relatively large emergence hole in the integument of the host.

Case histories

We have chosen to concentrate on three particular studies to illustrate particular aspects of larval bee fly biology. The work of Bohart *et al.* (1960) on *Heterostylum robustum*, a parasite of *Nomia melanderi* in northwestern U.S.A., is the most detailed account available of the biology of the immature stages of an ectoparasitic bee fly. *Heterostylum* belongs to the second most speciose subfamily, the Bombyliinae (Table 1, column 3), and its biology appears to be typical of many members of the subfamily. The series of papers by Du Merle (1964, 1979a, b, c, 1981) are the most complete account of the biology of the immature stages of an endoparasitic bee fly, *Villa brunnea*. This species belongs to the most speciose subfamily, the Anthracinae, and its biology may be similar in many respects to other endoparasitic Bombyliidae, most of which belong to the Anthracinae. Greathead (1958) conducted a detailed study of the life history of *Systoechus somali*, the larvae of which consume eggs of the desert locust *Schistocerca gregaria* in eastern Africa. This is a common form of larval feeding in a number of subfamilies such as the Bombyliinae and Cythereinae, and will allow us to examine in more detail the subtle differences between parasitoid Bombyliidae which consume a single host and ones which consume numerous hosts, in the form of orthopteran eggs.

All these case histories concern Bombyliidae that belong to clade S in Figure 4; females have a sand chamber and deposit substrate-particle coated eggs while hovering. Little detailed knowledge has accumulated regarding the biologies of bee flies primitively lacking a sand chamber, belonging to the subfamilies Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae, Lordotinae and Heterotropinae. The one exception is Du Merle's (1971), description of the biology of *Usia atrata* Fabricius. Ovipositing females alight on low foliage and release numerous bare eggs onto the ground surface. Although the natural hosts are the pupa of a tenebrionid beetle, *Asidia sabulosa* Fuessl., larvae were reared on ant pupae in the laboratory. Larvae are ectoparasitoids, and may enter diapause for more than a year. *Systropus* (Toxophorinae) oviposits large black eggs onto the integument of limacodid larvae (Genty, 1972) and apparently develop as internal parasites of the larvae, emerging from the host cocoons (Greathead, 1987).

An ectoparasite

The North American species *H. robustum* belongs to the bombyliine tribe 'Dischistini'. Females have a well-developed sand chamber typical of almost all Bombyliinae. It is the main parasite of the alkali bee *Nomia melanderi* in Washington, Oregon, Idaho and Wyoming, and parasitism rates reach 90% in some areas (Bohart

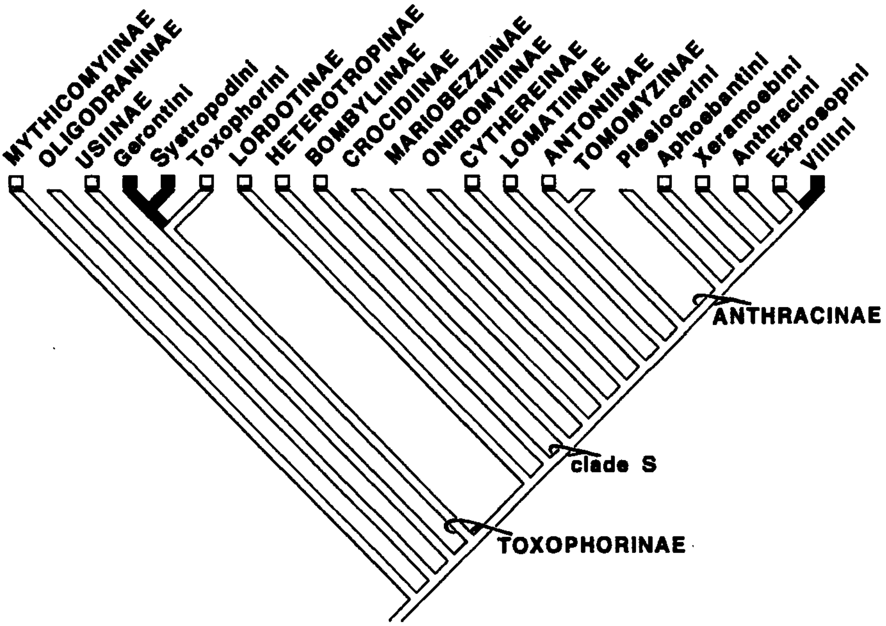


Figure 4. Cladogram of Bombyliidae subfamilies from Yeates (1994). Black stems indicate those groups with endoparasitic larvae, almost all the remainder are ectoparasitic. Life history information is only available for those groups with boxes below the name. Clade S indicates those subfamilies with a sand chamber (Figure 2b).

et al., 1960). The alkali bee nests in the ground and is an important alfalfa pollinator. The range of *H. robustum* greatly exceeds that of the alkali bee, and the bee fly uses other ground nesting bee hosts in other parts of its range. The female probably uses visual cues in host nest location; however, these cues are not particularly specific, as the female will oviposit into man-made depressions in the ground adjacent to bee nests.

The planidia are able to enter the bee nest cells after they have been sealed, and are occasionally found on the bee pollen ball in the cell, and may feed on the pollen mass itself. They are never found on the host larvae until it is in the final (5th) instar. The first instar bee fly larva remains on the host for about 36 hours, increasing in length from 1.8 to 2.3 mm, and increases in diameter more than 2 times. The first instar larva does not attach itself firmly, and often changes position. The second instar grows from 2.3 to 8.3 mm and increases in diameter three-fold. It usually remains in one place curved around the body of the host, but has no difficulty implanting its slender, knife-like mandibles again if disturbed. The host remains alive but noticeably shrunken during the feeding of the second instar bee fly. The third instar larva feeds for 3 or 4 days and doubles in length. The larva can complete development on a single host, but is also capable of moving between host cells to attack a new host. If the *H. robustum* larva attacks a new host it only consumes about half its volume. During larval development the bee fly larva increases its weight by up to 458 times and is very efficient at transferring the contents of its host, both having similar weights. After completing growth the *H. robustum* larva burrows from the bee brood chamber towards the soil surface and constructs an overwintering cell 5–8 cm below the soil surface. The larva overwinters before pupation.

The biology of this ectoparasite appears to be similar to other ectoparasites that are not closely related, such as *Anthrax*, belonging to the subfamily Anthracinae. Marston (1964) described the larval biology of *Anthrax limulatus fur* (Osten Sacken), parasitizing a mud-daubing wasp. On entering the host's cell, the planidium feeds sparingly on the larva for about 20 days, or until 9 days after the host begins to spin its cocoon, then moults to the second instar. The second instar grows rapidly and lasts 7 days, then moults into a third instar larva, which has an average duration of 4 days. The third instar larva grows rapidly, increasing in length by 2.5 mm per day. The *A. limulatus fur* larva pupates in the host cell.

An endoparasite

Villa brunnea is an endoparasitoid of the pine processionary moth, *Thaumetopoea pityocampa*, a European forest pest. Oviposition appears to be mediated by local terrain rather than host proximity (Billiotti *et al.*, 1965; Du Merle & Delpech, 1973), although this species has not been recorded from other hosts. Female *V. brunnea* scatter their eggs in the leaf litter, and planidia must find the host caterpillars once they have moved into the leaf litter in preparation for pupation. The planidium larva can live for one month without feeding on a host and can travel more than one metre from its oviposition site. The planidium penetrates the host only in the pupal stage; however, if it encounters a final instar larva the planidium clings to the integument of the host and is carried to the pupation site phoretically (Du Merle, 1979a). The planidium bores through the pupal integument, often at the base of an integumental fold (Du Merle, 1979b). After entering the host, the planidium remains close to the host's epidermis and does not feed. The host may encapsulate the larva at this stage (Du Merle, 1979c), and the parasite appears to stimulate the host to produce a breathing tube.

Little is known about the intermediate stages of larval development, but after a month the parasitoid has moulted to the third instar and consumed almost all the tissues of the pupa. The bee fly pupates inside the empty moth pupa. Once ready to emerge, the bee fly pupa uses the strong spines and hooks on its head and thorax to escape from the moth pupa and cocoon and tunnels to the soil surface. Eclosion of the bee fly occurs on the soil surface (Du Merle, 1964).

An egg pod consumer

All species of the genus *Systoechus* (Bombyliinae: Bombyliini), of which the early stages are known, consume the eggs of Acrididae (Orthoptera). *Systoechus somali* has been found attacking eggs of the desert locust *Schistocerca gregaria* in eastern Africa. The following account comes from the observations reported by Hynes (1947) and Greathead (1958).

Ovipositing adults hover at a height of 1–3 cm over depressions in the sand left by ovipositing locusts. Females flick eggs towards the depressions while hovering, the number of eggs laid per hole varying from 10 to 40. Eggs or first instar larvae could not be recovered from the soil. Infestation was patchy within and between egg fields, and rates of parasitism vary from 10 to 100%. Each *Systoechus* larva required about 8–10 eggs for development: this represents about 15% of the total eggs in a pod. From one to more than 60 larvae of different ages were found per egg pod, but the number was most often below ten.

Within the pod, the larva lies in a hollow at the side of the pod or in a cavity in the pod caused by egg consumption. Each larva applies its mouthparts to the middle of a locust egg. That egg, and others nearby, were dry and collapsed, their contents consumed by the bee fly larva. Larval development is very rapid; from 4 to 11 days after the egg pods were laid the *S. somali* larva is fully grown. The mode of larval feeding does not cause decay of the remaining eggs and in the majority of egg pods a proportion of the locust eggs develops normally. After feeding, the larva forms a small, oval chamber 1–2 cm from the egg pod and 5–10 cm below the soil surface. The larva can remain in diapause for more than a year. Each rainy period breaks diapause for a proportion of the larvae; in this way adults emerge at times when vegetation is green and hosts and adult food are likely to be present. Larvae have been kept in the laboratory for up to 3 years without pupating. During diapause larvae are able to move actively and form new cavities in the soil. The pupal period is short, approximately 9–15 days (based on laboratory observations). Once the pharate adult is ready to eclose, the pupa works its way to the soil surface using the strong spines and setae on its head and thorax. In the laboratory adults emerge from the protruding pupal case during daylight hours.

As we noted in the introduction, under some definitions *S. somali* would be classified as a predator because it consumes more than a single organism during its lifetime. Locust eggs are laid in a contiguous group, and function in nature as a single resource for potential consumers such as bee fly larvae. Each *S. somali* larva consumes part of an egg pod, but does not move between egg pods. In all other respects the biology of *Systoechus* is similar to closely related flies that consume a single larval host, such as species of *Bombylius* Linnaeus.

DISCUSSION

The evolution of parasitism in bombyliidae

Endoparasitism

The vast majority of Bombyliidae are ectoparasitoids as larvae (Table 1). However, endoparasitism has evolved in two separate lineages, and the details of parasitism are different in each lineage in accordance with their independent derivation (Fig. 4). Endoparasitism has evolved in at least three genera of the Villini of the subfamily Anthracinae (*Poecilanthrax* Osten Sacken, *Villa* Lioy and *Exechohypopion* Evenhuis). In these genera the parasitoid pupa emerges from the host pupa (Fig. 3c). Our lack of knowledge of the phylogenetic relationships within the tribe preclude an accurate estimate of the number of times that endoparasitism has evolved; however it may have evolved at least twice (Figs 4, 5), once in *Poecilanthrax* and once in *Villa* + *Exechohypopion.* Adults of the Gerontini and Systropodini (Toxophorinae) issue from their lepidopteran host cocoons, and the planidium enters the host larva before cocoon construction (Greathead, 1987). The host is consumed before it is able to pupate (Fig. 3b). Nothing is known of the mode of respiration in endoparasitoid bee fly larvae, or strategies they may employ to avoid encapsulation by the host. There are no obvious morphological modifications in *Villa* or *Poecilanthrax* larvae for respiration (for example Brooks, 1952).

The transition from ectoparasitoid to endoparasitoid is challenging because the parasitoid must overcome the host's internal immune system (Salt, 1938; Vinson &

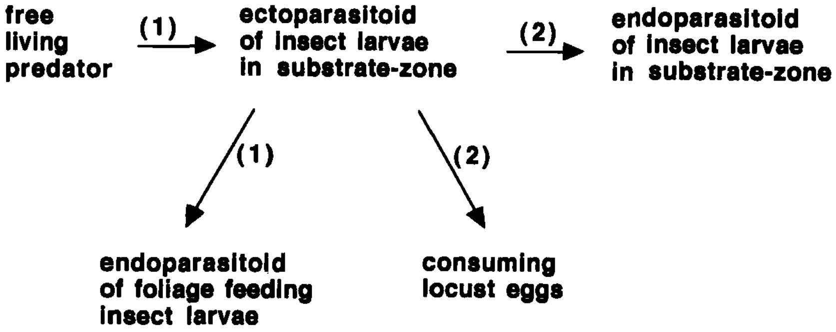


Figure 5. Scenario of parasitoid evolution in the Bombyliidae. The possible transitions, their direction and minimum number are indicated. Three different strategies have evolved from the plesiomorphic ectoparasitism on insect larvae in the substrate-zone. This figure is consistent with Eggleton and Belshaw's (1992) figure 2 which illustrates such evolutionary shifts for the entire Diptera.

Iwantsch, 1980). Our data indicate that the transition between host taxa even at the ordinal level (Table 1) has been made much more frequently than the transition from ecto- to endoparasitoid in the Bombyliidae.

Pseudohyperparasitism

A hyperparasitoid is an organism that parasitizes another organism that is itself parasitoid (Gordh, 1981). Du Merle (1975) and others have recorded species of a number of anthracine genera (*Chrysanthrax* Osten Sacken, *Exhyalanthrax* Becker, *Exoprosopa* Macquart, *Hemipenthes* Loew and *Ligyra* Newman), *Geron* Meigen (Toxophorinae) and a single bombyliine (*Acrophthalmyda* Bigot) as hyperparasitoids. Perusal of the records of hyperparasitic Bombyliidae shows that while bee flies have been reared from parasitoid hosts (for example Scoliidae, Tiphiidae, Tachinidae, Ichneumonidae and Braconidae), the primary parasitoid always spends at least some time exposed as a mature larva or prepupa after the primary host has been abandoned. In most instances it appears that the bombyliid attacks after the primary parasite has left its host. Bombyliids recorded as hyperparasitoids do not appear to have evolved in any close association with the primary host, and are best termed pseudohyperparasitoids (Shaw and Askew, 1976).

The pseudohyperparasitoid anthracine genera may be divided into two groups based on the host-specificity of their species. Some members of *Exhyalanthrax, Hemipenthes* and *Exoprosopa* attack a wide variety of parasitoids that have a variety of hosts. For example *Hemipenthes morio* Linnaeus has been recorded attacking Tachinidae and Ichneumonidae that were parasitoids of Noctuidae, Lasiocampidae, Lymantriidae, Thaumetopoeidae and Diprionidae as well as Sarcophagidae that were parasitoids of Thaumetopoeidae. Pseudohyperparasitoid species of *Exhyalanthrax* mostly attack muscoid dipteran parasitoids, and non-hyperparasitic species also attack muscoid dipteran parasites, notably tsetse fly larvae (*Glossina* Wiedemann). In these cases the bombyliids may have been attracted to the Diptera, but were able to attack other hosts associated with the flies. A species of *Exhyalanthrax* has recently been reared from a cockroach ootheca (Greathead & Grandcolas, 1995), an enclosed food source similar to muscoid puparia. Species of *Exoprosopa* have been recorded parasitising Sphecidae and Pompilidae as well as the parasitoid families Tiphiidae and Scoliidae. Additional records for individual species of *Exoprosopa* are needed to make further generalizations, but *E. fasciata* Macquart has been recorded as a parasite of scarabaeid beetles as well as a pseudohyperparasite of tiphiids, and *E. fascipennis* has been reared as a pseudohyperparasite on Tiphiidae as well as a parasite of Sphecidae. This first group of anthracine genera may contain both facultative and obligate pseudohyperparasites, as well as species that have not been recorded as hyperparasites. The second group consists of *Chrysanthrax* and *Ligyra.* Species of these genera have only been found attacking Tiphiidae or Scoliidae which are themselves external parasites of scarabaeid Coleoptera. These genera may be obligate pseudohyperparasites.

We conclude that pseudohyperparasitism in bombyliids developed under circumstances in which a normal ectoparasitoid bee fly with a broad host range was capable of feeding facultatively from ectoparasites which are already present on the host. In at least two lineages (Anthracinae and *Acrophthalmyda*) the pseudohyperparasitism may have become obligate.

Cleptoparasitoidism

Eggleton & Belshaw (1992, 1993) define a cleptoparasitoid as "an organism which develops at the expense of another single organism by usurpation of its food supply, killing the host as a direct or indirect result of that usurpation". Two distinct forms of behaviour in the Bombyliidae approach this definition. The first involves a planidium feeding on the provisions inside the host cell prior to feeding on the host itself. Eggleton & Belshaw (1992) term this host-directed cleptoparasitoidism. This form of behaviour has been observed or assumed in the Bombyliinae and Anthracinae, which use wasp or bee hosts developing in a provisioned chamber. In these cases the bee fly kills its host by directly feeding on it and feeding on the provisions by the bee fly larva is incidental.

The second form of cleptoarasitoidism has been found only in *Lepidophora* Westwood (Eclimini: Bombyliinae) (Krombein, 1967). In this form of behaviour, termed provision-directed cleptopredation by Eggleton & Belshaw (1992), the bee fly larva feeds exclusively on the wasp provisions (immobilized caterpillars or cockroaches), and the contents of several cells were necessary for the parasite to reach maturity. This feeding causes the host larva to starve and thus fits Eggleton and Belshaw's definition of cleptoparasitoid.

The idiobiont/koinobiont classification

Bombyliidae do not fit easily idiobiont/koinobiont classification of parasitoids proposed by Askew & Shaw (1986) and most often applied in the Hymenoptera. Most Bombyliidae attack endopterygote larvae, prepupae or pupae in the substrate zone. We assume that they most often contact the host in the location and state in which it is consumed (an idiobiont characteristic), although the host is not immediately paralysed or killed (a koinobiont characteristic). Most bee fly larvae feed externally and the host is killed only in the final stages of the development of the parasitoid. In the Hymenoptera, adult female idiobiont parasitoids inject a paralysing venom into the host (Gauld & Bolton, 1988). Bombyliidae do not possess anatomical features which allow the female to inject such a venom, and host searching within a suitable habitat is made by the first instar larva. Thus, in the sense that the term is used in Hymenoptera, Bombyliidae cannot be idiobionts. The distribution of these traits on the cladogram (Fig. 4) suggests that the koinobiont attribute was achieved before endoparasitism in the Bombyliidae. This transition mirrors part of the pathway found in rogadine braconids (Shaw, 1983).

Detailed evidence from some bee flies suggests that they may be able to facultatively switch between killing the host almost immediately (as idiobiont Hymenoptera do), or killing it at later stage (as koniobiont Hymenoptera do). Palmer (1982) studied two species of *Anthrax* that parasitize tiger beetle (Coleoptera: Cincindelidae) larvae. The *Anthrax* larvae could be found on all tiger beetle larval instars, but remained very small (second instar) for up to 9 months, depending on the stage of the host and time of year when they were contacted. Once the host constructs a pupal chamber, closes the burrow entrance and becomes a prepupa, the parasite grows rapidly, reaching full size in 7–14 days (Shelford, 1913). It appears that if the planidium larva finds its host as an early instar, it may remain on the host, feeding sparingly until the host has reached maximum size. The host will not be killed until some time after the parasitoid has made contact, fitting the definition of a koinobiont. If the planidium reaches the host when it is fully grown, the larva may begin feeding and developing immediately, thus killing its host quickly and approaching the definition of an idiobiont. Bohart *et al.* (1960) reported that the *Heterostylum* larva remained in the host larval chamber but did not feed on the host until it had reached the prepupal stage. During this time the bee fly larva obtained sustenance from the bee provisions. Du Merle (1979a) reported that larva of the internal parasite *Villa brunnea* contacted its host in various stages from caterpillar to pupa, but it was able to develop only on the pupa. The parasite remained phoretic on the host caterpillar until it formed a pupa. We do not know how widespread the ability to delay larval development is in the Bombyliidae. The ability of larvae to switch between koinobiont and idiobiont 'depending on the hosts developmental stage reduces the utility of these terms as functional categories, at least in the Bombyliidae.

Host usage

Bombyliidae that consume orthopteran egg pods are found in a number of subfamilies, ranging from the most basal subfamily (Mythicomyiinae) to one of the most derived subfamilies (Anthracinae) (Table 1). Orthopteran egg pod consumption has not been recorded in any subfamilies phylogenetically between the Mythicomyiinae and the Bombyliinae (Fig. 4). Although the intervening subfamilies account for only a small percentage of host records, this distribution does allow for the possibility that the ability to consume orthopteran egg masses has been acquired at least two times; at least once in the Mythicomyiinae and at least once in clade S (the sand chamber subfamilies) (Fig. 4). Within clade S the ancestral habit was probably ectoparasitoid on larvae in the substrate-zone, but the diversity of feeding modes in Mythicomyiinae precludes our identifying an ancestral habit in this subfamily.

Bombyliidae in the subfamilies Usiinae, Bombyliinae, Lomatiinae and Anthracinae have been reared from coleopteran larval hosts. In all instances the host was contacted in the substrate-zone. Coleoptera records make up a small proportion of total records, and host families include Cincindelidae, Scarabaeidae, Tenebrionidae, Meloidae, Cerambycidae and Curculionidae.

Dipteran hosts have been only recorded in the Anthracinae. Host families are all soil dwellers as larvae, and include the Tabanidae, Asilidae, Therevidae, Bombyliidae, Tachinidae, Muscidae, Glossinidae, Calliphoridae and Sarcophagidae. Some of these hosts are parasitoids themselves; however, they are probably parasitized during their brief pre-pupal stage when in the soil (see Pseudohyperparasitism above). Dipteran hosts belonging to the Cyclorrhapha ecdyse to become pupae inside the hardened integument of the last larval instar, termed the puparium. The bee fly parasitoid emerges from the host puparium, but we do not know how the larva penetrates it.

Lepidopteran hosts have been found in the related basal subfamilies Usiinae and Toxophorinae and in the closely related derived subfamilies Lomatiinae and Anthracinae. Hosts include the families Cossidae, Psychidae, Gelechiidae, Tortricidae, Limacodidae, Pyralidae, Noctuidae, Thaumetopoeidae, Lymantriidae, and Lasiocampidae; these are most often attacked as mature larvae or prepupae in the substrate-zone habitat. Bombyliidae rarely use exophytic larvae as hosts, and this distinguishes them from hyperdiverse parasitoid groups such as ichneumonids, braconids and tachinids.

By far the largest number of host records come from the insect order Hymenoptera (Table 1). Of the parasitoid subfamilies, hymenopteran host records are absent in only two, the Usiinae and Lomatiinae. Both symphytan and apocritan larvae are attacked, belonging to such families as Diprionidae, Tenthredinidae, Ichneumonidae, Scoliidae, Tiphiidae, Sphecidae, Vespidae, Pompilidae, and the bee families Colletidae, Halictidae, Megachilidae and Anthophoridae. Hosts are attacked either in the substrate zone or in their nests (which are sometimes not in the soil). Only in a few isolated cases have social aculeates been recorded as hosts. Some species of the anthracine genus *Anthrax* have been recorded ovipositing on mud nests (for example Marston, 1964). It would be interesting to know more of the role played by the female bombyliid and the planidium larva when invading the mud nests of aculeates.

Host specificity

Because host specificity is impossible to judge from single rearings we have limited our discussion to taxonomic groups that have been reared numerous times. Evidence suggests that (except in rare cases) the bee fly host spectrum is broad at the species level, and mediated through the ecological context of the first instar larva rather than the systematic affinities of hosts. For example, the larvae of egg pod consuming species have been found feeding on other larvae associated with the same resource. *Anastoechus mylabricidus* Zakhvatkin was found as an ectoparasite on a meloid beetle larva feeding on acridid eggs (Zakhvatkin, 1934). At generic level host ranges can be even broader, for example *Petrorossia* Bezzi has been reared from the egg sacs of Araneae, the larvae of various families of Hymenoptera and puparia of tsetse flies (Zaitsev & Charykuliyev, 1981). Members of the genus *Exhyalanthrax* have usually been reared from Diptera puparia in the soil, but have also emerged from cocoons of ichneumonid wasps, noctuid moths, diprionid sawflies and cockroach oothecae (Greathead & Grandcolas, 1995). These hosts appear to share only the feature of being located on or in the soil. However, those *Exhyalanthrax* species that have been reared from hymenopterous and dipterous parasitoids have also been reared from the primary hosts, thus all the hosts are from the same ecological nexus.

Why do Bombyliidae have such broad host ranges? Unlike Hymenoptera and a very few Diptera such as Pipunculidae and Tachinidae (e.g. *Compsilura concinnata*

(Meigen)), Bombyliidae have not evolved piercing ovipositors which would allow them to insert eggs directly into the host (Eggleton & Belshaw, 1993). In all cases the first instar bee fly larva is the invasive stage. Some isolated clades of Bombyliidae such as *Lordotus* (Lordotinae) and *Antonia* (Antoniinae) have evolved specialized female genitalia (Fig. 3C), which are associated with derived oviposition behaviour. These appear to be designed for insertion into a substrate rather than in host tissue.

Ovipositor morphology is not the only factor involved. Vinson (1976) suggested that as the intimacy of encounter between adult female parasitoid and host increases, host range tends to become narrower. This hypothesis is supported in the Bombyliidae. In most Bombyliidae, females scatter eggs in suitable habitats and the planidia make direct contact with the host. We suggest that planidia may come into contact with various possible hosts in the substrate-zone. In these cases, a selective advantage would accrue through the ability to develop on a variety of hosts, rather than on a narrow host spectrum which would be contacted with a reduced probability. Only one lineage of Bombyliidae, *Systropus* of the Toxophorinae, has evolved a more intimate encounter by the adult female with the host. This genus displays considerable host specificity and is only known to parasitize Limacodidae.

Price (1980) hypothesized that because parasites represent an extreme of specialized resource exploitation, rates of speciation and evolution may be high. Wiegmann, Mitter and Farrell (1993) compared species richness in sister-clades of parasitoid and non-parasitoid insect lineages and were able to substantiate this claim in only a minority of cases. This result may have been influenced by the different definitions of parasite used in the two works: Price included phytophagous insects but Wiegmann *et al.* excluded them. The broad host range of most Bombyliidae is a possible explanation for the lesser diversity of Bombyliidae (*c.* 5000 spp.) in comparison to their putative sister group, the remaining Asiloidea (*c.* 7000 spp.). Price's contention relies on the assumption that parasites are monophagous or narrowly oligophagous. Because most Bombyliidae have broad host ranges they are not as resource-specialized as parasites which have narrow host ranges. Thus the conditions that might lead to higher speciation in monophagous or narrowly oligophagous parasites do not apply with such force in the Bombyliidae.

Evolutionary trends

Table 1 shows that there is no close coevolution between host order and bee fly evolution at the subfamily/tribe level. As one moves from the more basal subfamilies to the more derived, a greater diversity of hosts are used per subfamily; for example, dipteran and neuropteran hosts are used only by Anthracinae. However, this may be an artefact of the higher diversity of Anthracinae, which represent over 60% of host records and over 40% of Bombyliidae species.

Two of the more basal subfamilies, the Mythicomyiinae and Heterotropinae, have larvae that are predatory rather than parasitoid. In the case of Mythicomyiinae, other parasitoid species are known in the subfamily, and predatory behaviour has probably evolved within this clade. Only a more detailed phylogeny for the subfamily and a greater taxonomic range of host associations within the subfamily will allow us to dissect this issue further. Heterotropinae larvae are known from a single record (Yeates & Irwin, 1992) and the predatory nature of the larvae was inferred from their morphology and behaviour in the laboratory. Our current knowledge of Bombyliidae phylogeny suggests that the acquisition of the predatory habit in Heterotropinae has occurred within the subfamily. Adult Heterotropinae have many plesiomorphic morphological features and analysis of further data sets may alter their phylogenetic position within the family and thus our hypotheses regarding evolution of their biological and morphological traits.

Toxophorinae

Because they represent only about 7% of species but 9% of host records the host associations of the Toxophorinae are relatively well known. The basal clade of the subfamily, the Toxophorini (Table 1, Fig. 4), are ectoparasitoids of solitary bees and wasps. The more distal clade comprises the Gerontini and Systropodini, which are endoparasitoids in Lepidoptera. This pattern of host use suggests a shift from Hymenoptera to Lepidoptera and a shift from ectoparasitoid to endoparasitoid along the node leading to the (Gerontini + Systropodini) clade. Some caveats are in order. This scenario is only tenable if the plesiomorphic state of host use in Toxophorinae is ectoparasitoid on solitary bees and wasps. While this is suggested because the plesiomorphic clade in the subfamily, the Toxophorini, has these attributes, comparisons with the (largely unknown) states present in more basal subfamily lineages of Bombyliidae are required to make this optimization unequivocal.

There is some evidence for additional evolutionary shifts in the Systropodini regarding the position of the host in the environment, means of host location and host range. Although some *Geron* species may attack concealed hosts above ground, evidence suggests that the plesiomorphic behaviour in the subfamily Toxophorinae is for hosts to be located in the ground or substrate layer. *Systropus*, on the other hand, locates and oviposits only on limacodid larvae that feed on foliage above the substrate. The hosts spin cocoons and pupate close to their feeding positions and never enter the substrate layer. There has been an additional shift in that host location in this genus is carried out by the adult female, rather than by the planidium first instar larvae, as in other Bombyliidae. Other genera of Bombyliidae for which we have a comparable number of host records (for instance *Systoechus* of the Bombyliinae) feed on hosts belonging to more than one family. These three evolutionary shifts are probably correlated — adult females are able to disperse and locate limacodid larvae in standing vegetation more efficiently than the tiny, legless planidium larva. Knowledge of the hosts and behaviour of other genera in the Systropodini, such as *Zaclava* Hull, may shed further light on the evolution of these features in *Systropus*.

Bombyliinae

Plesiomorphic members of this subfamily are external parasites of bee and wasp larvae found in ground nests and of other larvae found in the soil. It is interesting to note that no bombyliine has been recorded feeding on Lepidoptera larvae. Shifts to two different feeding strategies have occurred within the subfamily. The biologies of the 'dischistine' genus *Anastoechus* and the bombyliine genus *Systoechus* are relatively well known (a total of 69 records for 24 species), and all feed on orthopteran egg pods, predominantly of the Acrididae. The phylogenetic positions of these two genera lead us to suspect that they independently acquired this feeding mode from ancestors that were ectoparasitoids of soil-dwelling hosts, following the scenario of Eggleton & Belshaw (1992).

Lepidophora (Eclimini) has acquired an intriguing larval feeding mode termed provision-directed cleptopredation by Eggleton & Belshaw (1992). It is a little surprising that provision-directed cleptopredation has only been recorded once in the Bombyliidae as it appears to have at least two selective advantages to parasitoid larvae entering blood cells when the host itself is small: reduced development time and increased resource efficiency. In these cases the larva can begin feeding immediately on host provisions rather than waiting until after the host has itself consumed the provisions and grown to a suitable size to be consumed by the bee fly larva.

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APPENDIX 1

Records of hosts of Bombyliidae not in Du Merle (1975)

Notes

1. Includes records since publication of Du Merle (1975) and a few he missed, excluding obviously suspect records.
2. Reviews cited for some records: Acrididae (Greathead, 1963 & Rees, 1973), tsetse flies (Greathead, 1980) and Limacodididae (Greathead, 1989) to limit length of reference list.
3. IIE ident. = identification by DJG for the International Institute of Entomology.
4. This list includes references in CAB Abstracts and BIOSIS on line to the end of 1994.

Genus/species	Host	Reference	Comments
MYTHICOMYIINAE			
Glabellula			
arctica Zettestedt	*Formica* spp. (Hym Formicid	Andersson (1974)	?predator
USIINAE: Usiini			
Usia atrata Fabricius	*Myrmecocystus cursor* Fonscolombe Hym Formicid) or *Heliopathes abbreviatus* (Cole Tenebrionid)	Xambeu (1898)	?status, near nest of ant and larvae of tenebrionid. Recent record (Du Merle, 1971) makes the latter more likely
USIINAE: Phthiriini			
Acreophthiria			
similis Coquillett	*Epinotia kasloana* (McD) (Lep Tortricid)	Pinto, Frommer and Manweiler (1987)	parasitoid
TOXOPHORINAE: Toxophorini			
Toxophora			
australis Hesse	*Euodynerus euryspilus* (Cameron) (Hym Vespid Eumeninae)	Gess & Gess (1991)	hyperparasitoid ex cocoon of ?*Chrysis hoplites* Mocsáry
	indet. (Hym Vespid Eumeninae)	FW Gess *in litt.*	ex cells cells provisioned with Pyralidae
diploptera Speiser	indet. (Hym Vespid Eumeninae)	Evenhuis *in litt.*	from south Africa in South African Museum
virgata Osten Sacken	*Stenodynerus claremontensis* (Cameron) (Hym Vespid Eumeninae)	Markin & Gittins (1967)	parasitoid ex prepupae
TOXOPHORINAE: Gerontini			
Geron			
aridus Painter	*Pristomerus spinator* (Fabricius) (Hym Ichneumonid)	Johnson & Smith (1981)	ex pupa from *Elasmopalpus lignosellus* Zeller larva
	Elasmopalpus l. ignosellus (Zeller) (Lep Pyralid)	Johnson & Smith (1981)	ex pupa, enters larva, 0–2.8% (mean 0.80%) parasitism
erythropus Bezzi	*Palpita unionalis* (Hübner) (Lep Pyralid)	IIE ident.	parasitoid
exemptus Bowden	*Spodoptera exempta* (Walker) (Lep Noctuid)	IIE ident.	
gibbosus Olivier	indet. (Lep)	IIBC Pakistan Station	pupa under bark of *Dahlbergia sisoo*
hybus Coquillet	*Epinotia kasloana* (McD) (Lep Tortricid)	Pinto *et al.* (1987)	parasitoid
nomadicus Hesse	*Macrocentris maraisi* Nixon (Hym Braconid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *Loxostege frustralis* Zeller
	Exorista xanthaspis (Wiedemann) (Dipt Tachinid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *L frustralis*
	Exorista sp. (Dipt Tachinid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *L frustralis*
	Nemorilla maculosa Meigen (Dipt Tachinid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *L. frustralis*

APPENDIX 1 *(continued)*

Genus/species	Host	Reference	Comments
TOXOPHORINAE: Gerontini (*continued*)			
Geron (*continued*)			
nomadicus Hesse	*Palexorista sp.* (Dipt Tachinid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *L frustralis*
	Pales sp. (Dipt Tachinid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *L. frustalis*
	unident. Meigenini (Dipt. Tachinid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *L. frustalis*
turneri Hesse	*Chelonus curvimaculatus* Cameron (Hym Braconid)	Möhr (1980, 1990)	hyperparasitoid in cocoon of *L. frustalis*
	Temelucha picta (Holmgren) (Hym Ichneumonid)	Möhr (1990)	hyperparasitoid in cocoon of *L. frustalis*
	Loxostege frustalis Zeller (Lep Pyralid)	Möhr (1990)	ectoparasitoid on larvae & pupae in cocoons
TOXOPHORINI: Systropodini			
Systropus			
acutus Painter & Painter	*Acharia pauper* (Dyar) (Lep Limacodid)	Adams & Yanega (1992)	larval/pupal endoparasitoid
colombianes Karsch	*Sibine nesea* Stoll (Lep Limacodid)	Aiello (1980)	ex cocoon, entered larva at least 2 moults earlier
	indet. (Lep Limacodid)	Posada & Garcia (1976)	
daveyi Bowden	indet. (Lep Limacodid)	IIE ident	
pelopes Bowden	*Parasa ?viridissima* Holland (Lep Limacodid)	Igbinosa (1985)	
polistoides Westwood	*Thosea bipartia* Hering (Lep Limacodid)	Greathead (1987)	
aff. *quadripunctatus* Williston	indet. (Lep Limacodid)	Teran (1974)	parasitoid
roepkei de Meijere	*Birthamula chara* Swinhoe (Lep Limacodid)	Greathead (1987)	
	Chalcoscelis albiguttatus (Snellen) (Lep Limacodid)	Yunus & Ho (1980)	
	Darna trima ajavana Holloway (Lep Limacodid)	Desmier de Chenon (1982)	
sp.	*Sibene* sp. (Lep Limacodid)	Teran (1974)	parasitoid ex pupa on *Annona muricata*
	Phobitron hipparchia (Cramer) (Lep Limacodid)	Teran (1974)	parasitoid, host on *Annona* sp.
	Sibene auremaculata (Schasi) (Lep Limacodid)	Teran (1974)	parasitoid, host on *Annona* sp.
HETEROTROPINAE			
Heterotropus			
spp.	?	Yeates & Irwin (1992)	predatory ? sifted from soil
BOMBYLIINAE: Conophorini			
Sparnopolius			
brevicornis Loew	*Diadasia ochracea* (Cockerell) (Hym Anthophorid Anthophorinae)	Eickwort, Eickwort and Linsley (1977)	ex nest nests in soil
BOMBYLIINAE: Acrophthalmydini			
Acrophthalmyda			
sp.	*Elaphoptera* sp. nr *nigripennis* (Smith) (Hym Thynuid)	Lloyd (1952)	hyperparasitoid on *Macrosoma glacialis* (Fabricius) (Melolonthinae)
BOMBYLIINAE: 'Dischistini'			
Anastoechus			
chinensis Paramonov	*Locusta migratoria manilensis* (Meyen) (Ort Acridid)	Du *et al.* (1993)	egg predator, overwinters as egg, up to over 75% pods infested

APPENDIX 1 (*continued*)

Genus/species	Host	Reference	Comments
BOMBYLIINAE: 'Dischistini' (*continued*)			
Heterostylum			
robustum (Osten Sacken)	*Anthophora urbana urbana* Cresson (Hym Anthophorid Anthophorinae)	Torchio & Trostle (1986)	predator, consumes more than one host
	Nomia melanderi Cockerell (Hym Halictid Nomiinae)	Bohart *et al.* (1960)	ectoparasitoid on larvae in cells
BOMBYLIINAE: Bombyliini			
Bombylella			
ornatus pleuralis (Bezzi)	*Oniticellus formosus* Chevrolat (Cole Scarabaeid)	Cambefort (1982)	pupa in dung ball
sp.	*Oniticellus formosanus* Chervolat (Cole Scarabaeid)	Davis (1977) in Cambefort (1982)	ex dung ball
Bombylius			
albicapillus Loew	*Halictus farinosus* Smith (Hym Halictid Halictinae)	Nye (1980) in Eickwort (1985)	nest in soil
canescens Mikan	*Halictus* sp. (Hym Halictid Halictinae)	Ebejer (1988)	nest in soil
discolor Mikan	*Andrena vaga* Panzer (Hym Andrenid Andreninae)	Müller (1944)	nest in soil
major Linnaeus	*Andrena fulva* (Hym Andrenid Andreninae)	Litt (1988)	nest in soil
	Halictus farinosus Smith (Hym Halictid Halictinae)	Nye (1980) in Eickwort (1985)	nest in soil
minor Linnaeus	*Andrena clarkella* (Hym Andrenid Andreninae	Oldroyd (1969)	nest in soil
pulchellus Loew	*Halicts ligatus* Say (Hym Halictid Halictinae)	Packer (1988)	predator on all stages
Systoechus			
atriceps Bowden	*Oedaleus senegalensis* (Krauss) (Ort Acridid)	IIE ident.	egg predator
autumnalis Pallas	*Dociostaurus crassiusculus* (Pantel) (Ort Acridid)	Greathead (1963), Soltani (1978)	egg predator
littoralis Bowden	*Oedaleus senegalensis* (Krauss) (Ort Acridid)	IIE ident.	egg predator
	indet. (Ort Acridid)	P Shah Coll.	egg predator
melampogon Bezzi	*Oedaleus senegalensis* (Krauss) (Ort Acridid)	GB Popov Coll.	egg predator
oreas Osten Sacken	*Melanoplus* spp. (Ort Acridid)	Rees (1973)	egg predator
BOMBYLIINAE: Ecliminae			
Lepidophora			
lepidocera (Wiedemann)	*Trypoxylon tridentatum archboldi* (Krombein) (Hym Sphecid Larrinae)	Krombein (1967)	on provisions (spiders)
sp.	*Penepodium goryanum* (Lepeletier) (Hym Sphecid Sphecinae)	Garcia & Adis (1993)	parasitoid
CYTHEREINAE: Cythereini			
Cytherea			
infuscata Meigen	*Calliptamus italicus* (Linnaeus) (Ort Acridid)	Greathead (1963)	egg predator
LOMATIINAE			
Comptosia			
brunnea Edwards	*Myrmecia* sp. (Hym Formicid)	Yeates (1991)	pupa at entrance of nest
ocellata Newman	*Oncopora* sp. (Lep. Hepialid)	Yeates (1991)	

APPENDIX 1 *(continued)*

Genus/species	Host	Reference	Comments
ANTHRACINAE: Aphoebantini			
Aphoebantus			
mus Osten Sacken	*Melanoplus* spp. (Ort Acridid)	Rees (1973)	egg predator
	Melanoplus spretus (Walsh) (Ort Acridid)	Greathead (1963), Rees (1973)	egg predator
Epacmus litus Coquillett	indet. (Lep Ethmiid)	Evenhuis (1985)	ex pupa
ANTHRACINAE: Anthracini			
Anthrax			
analis Say	*Cicindella hirticollis* (Cole Cicindellid) Say	Bram & Knisley (1982)	ectoparasitoid on III instar, development slow until after host diapause
	Cicindella marginata Fabricius (Cole Cicindellid)	Bram & Knisley (1982)	ectoparasitoid on III instar, development slow until after host diapause
	Cicindella punctulata Olivier (Cole Cicindellid)	Palmer (1982)	ectoparasitoid
	Cicindella scutellaris Say (Cole Cicindellid)	Bram & Knisley (1982)	ectoparasitoid on III instar, development slow until after host diapause
	Cicindella tranquebarica Herbst (Cole Cicindellid)	Palmer (1982)	on larvae, all instars – lays into holes
	Cicindella tranquebarica	Bram & Knisley (1982)	ectoparasitoid on III instar, development slow until after host diapause
angularis Thomson	*Sceliphron laetum* (Smith) (Hym Sphecid)	Dahms (1968)	
anthrax Schrank	*Osmia tricornis* Latreille (Hym Megachilid)	Vicens, Bosch and Blas (1994)	parasitoid in cocoon, 6.3% & 3.6% parasitism
aterrimus (Bigot)	*Trypoxylon politum Say* (Hym Sphecid Sphecinae)	Moloumby (1995)	parasitoid
badius Hesse	*Xylocopa* spp. (Hym Anthophorid Xylocopinae)	Watmough (1974)	ectoparasitoid
cana Greathead	*Megachile* spp. (Hym Megachilid Megachilinae)	Greathead (1989)	ex pupa
capicola Bowden	*Ceratina truncata* Friese (Hym Andrenid)	Evenhis *in litt.*	from South Africa in South African Museum
cintalapa Cole	*Lithurge apicalis* (Cresson) (Hym Megachilid Lithurginae)	Parker & Potter (1973)	feed in cocoons
confluensis Roberts	*Myrmeleon acer* Walker [Neu Myrmel]	Evenhuis *in litt.*	in Macleay Museum (Australia)
diffusus Wiedemann	*Chalicodoma murina* Friese [Hym Megachilid]	Evenhuis *in litt.*	in South African Museum
distigma Weidemann	*Megachile lanata* Lepel. (Hym Megachilid Megachilinae)	Chaudhray & Jain (1980) in Evenhuis (1992)	
	Megachile nana (Hym Megachilid Megachilinae)	Jain & Kapil (1986) in Evenhuis (1992)	
	Sceliphron madraspatanum (Fabricius) (Hym Sphecid Sphecinae)	Kusigamati (1986)	ex nest
	Vespa simillima xanthoptera Cameron (Hym Vespid Vespinae)	Martin (1988)	ectoparasitoid on pupa. 15 of 21 cells in one nest parasitized, 100 others not attacked
gideon Fabricius	*Pseudoxychila tarsalis* Bates (Cole Cicindellid)	Palmer (1982)	ectoparasitoid on all instars, lay into host holes
incomptus Walker	*Lithurge scabrosa* Smith (hym Megachilid Lithurginae)	Cheeseman (1936)	enter burrows to lay in holes in wood

APPENDIX 1 *(continued)*

Genus/species	Host	Reference	Comments
ANTHRACINAE: Anthracini *(continued)*			
Anthrax (*continued*)			
incomptus Walker	*Sceliphron laetum* (Smith) (Hym Sphecid Sphecinae)	Smith (1979)	2.3% mortality
	Chrysis sp. (Hym Chrysidid)	Smith (1979)	ex cocoon
	Paralastor sp. (Hym Vespid) Eumeninae)	Smith (1979)	ex nest
irrorata Say	*Anthocopa* spp. (Hym Megachilid Megachilinae)	Parker (1977)	
	Osmia marginata Michener (Hym Megachilid Megachilinae)	Tepedino & Parker (1983)	
	Osmia marginata Michener (Hym Megachilid Megachilinae)	Parker (1981)	nest 1 ex cell, nest in snail shells
	Osmia texana Cresson (Hym Megachilid Megachilinae)	Esmaili (1963) in Rust (1974)	
	Proteriades spp. (Hym Megachilid Megachilinae)	Parker (1978)	nests in holes in wood
	Stelis depressa Timberlake (Hym Megachilid Megachilinae)	Parker (1984)	ex cocoon in nest of *Osmia latiuscula* Michener
irrorata irrorata Say	*Megachile inermis* Provancher (Hym Megachilid Megachilinae)	Scott & Strickler (1992)	ex cells
	Megachile mendica Cresson (Hym Megachilid Megachilinae)	Baker, Kuhn & Bambara (1985)	
	Megachile relativa Cresson (Hym Megachilid Megachilinae)	Scott & Strickler (1992)	ex cells
koshunensis Matsumura	*Pachyodynerus nasidens* (Latreille) (Hym Vespidae)	Kim (1993)	
	Megachile sachauinslandi Aitken (Hym Megachilid)	Kim (1993)	
leucogaster Wiedemann	*Vespa orientalis* Fabricius (Hym Vespid Vespinae)	Wafa, El-Borolossy & Sharwaki (1969)	ex pupa
limatulus Say	*Trypoxylon politum* Say (Hym Sphecid Larrinae)	Brockmann (1980)	12.6% parasitism at one site
macquarti D'Andretta	potter wasp (Hym Eumenid) indet.	Norwich Castle Mus.	ex cell
maculatus Macquart	indet. (Hym. Apoidea)	Evenhuis in litt.	G.H. Hardy notes in Australian Museum, bred from nest of native bees
matilei Evenhuis	*Eumenes germaini* Lucas (Hym Vespid Eumeninae)	Evenhuis (1991)	mud pots on stems
plumipes Hesse	*Xylocopa lugubris* Gerstaeker (Hym Anthophorid Xylocopinae)	Watmough (1974)	host nests in branches & timbers
pluto pluto Wiedemann	*Coelioxys* prob. *funeraria* Smith (Hym Megachilid Megachiilinae)	Scott & Strickler (1992)	ex cells, host cleptoparasitoid *M. relativa* Cresson.
	Megachile inermis Provancher (Hym Megachilid Megachilinae)	Scott & Strickler (1992)	ex cells
	Megachile relativa Cresson (Hym Megachilid)	Scott & Strickler (1992)	ex cells
sp.	*Euglossa cordata* (Hym Apid Euglossinae)	Garofalo (1992)	ex cells

APPENDIX 1 *(continued)*

Genus/species	Host	Reference	Comments
ANTHRACINAE: Anthracini (*continued*)			
Anthrax (*continued*)			
sp.	*Heriades truncorum* Linnaeus (Hym Megachilid Megachilinae)	Almeida Correia (1976)	parasitoid
	Osmia californica Cresson (Hym Megachilid Megachilinae)	Rust (1974)	reared
	Osmia subfasciata Cresson (Hym Megachilid Megachilinae)	Neff & Simpson (1992a)	ex cells
	Penepodium goryanum (Lepeletier) (Hym Sphecid)	Garcia & Adis (1993)	parasitoid ex trap nests, prey cockroaches
	??	Pakistan Station IIBC	ex material from *Pinus excelsa*.
	Cicindella spp. (Cole Cicindellid)	Knisley (1987)	attaches to II instar, develops at pupation
	Diadasina distincta (Holmberg) (Hym Anthophorid Anthophorinae)	Martins & Antonini (1994)	ex cells
	Sceliphron laetum (Smith) (Hym Sphecid Sphecinae)	Naumann (1983)	ex cells
	Sceliphron formosum (Smith) (Hym Sphecid) Sphecinae)	Naumann (1983)	ex cells
	Agrotis spp. (Lep Noctuid)	Mohyuddin & Shah (1977)	
sticticus Klug	*Megachile argentata* (Fabricius) (Hym Megachilid)	Pashina (1971)	parasitoid
trifasciata Meigen	various (Hym Sphecid Megachilid Megachilinae)	Greathead (1989)	ex cocoons
?*tetraspilus* Hesse	*Tricarinodynerus guerinii* (Saussure) (Hym Vespid Eumeninae)	Gess & Gess (1991)	ex cells
	Tricarinodynerus sp. (Hym Vespid Eumeninae)	FW Gess *in litt.*	
Satyramoeba			
etrusca (Fabricius)	*Xylocopa valga* Gerstaeker (Hym Anthophorid Xylocopinae)	Dindo, Campadelli & Gambetta (1992)	
Spogostylum			
isis Meigen	indet. (Cole Meloid)	Greathead (1963)	parasitoid?
	indet. (Dip Bombyliid)	Greathead (1963)	parasitoid?
incisurale (Macquart)	*Macrocentrus maraisi* Nixon (Hym Braconid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *Loxostege frustalis*
	Loxostege frustalis Zeller (Lep Pyralid)	Möhr (1990)	ectoparasitoid on larva & pupa in cocoons
zonabriphagus Porchinskii	indet. (Dip Bombyliid)	Greathead (1963)	parasitoid?
	Arcyptera microptera (Fischer-Waldheim) (Ort Acridid)	Greathead (1963)	egg predator
Walkeromyia			
lurida (Walker)	indet. (Hym Apoidea)	Teran (1974)	
Xenox			
simpson habrosus (Marston)	*Xylocopa* spp. (Hym Anthophorid Xylocopinae)	Minckley (1989)	

APPENDIX 1 (*continued*)

Genus/species	Host	Reference	Comments
ANTHRACINAE: Anthracini (*continued*)			
Xenox (*continued*)			
tigrinus (De Geer)	*Xylocopa* sp. (Hym Anthophorid Xylocopinae)	Gerling & Hermann (1976)	ectoparasitoid
xylocopae (Marston)	Xylocopa micheneri *micheneri* Hurd (Hym Anthophorid Xylocopinae)	Minckley (1989)	ectoparasitoid, feed on large larvae
	Xylocopa spp. (Hym Anthophorid Xylocopinae)	Minckley (1989)	
ANTHRACINAE: Xeramoebini			
Petrorossia			
angustibasalis Hesse	*Glossina* sp. (Dip Glossinid)	WR Ingram coll.	ex puparium
feti Zaitsev & Tsarykuliev	*Uratea limbata* (Aranae)	Zaitsev & Charykuliev (1981)	ex egg-sac
flavicans Bowden	indet.	P Shah Coll.	pupa in soil near Acridid egg-pods.
hesperus tropicalis Hesse	*Glossina morsitans* Westwood [Dip Glossinidae]	Evenhuis *in litt.*	from Zimbabwe in South African Museum
sp.	indet. (Hym Andrenid)	Evenhuis *in litt.*	from Madagascar in MNHN Paris
	Tachysphex sp. (Hym Sphecid)	Evenhuis *in litt.*	from Madagascar in MNHN Paris
	indet. (Hym Braconid)	Evenhuis *in litt.*	from Madagascar in MNHN Paris
	indet. (Hym Vespid)	Evenhuis *in litt.*	from Madagascar in MNHN Paris
williamsi Evenhuis & Arakaki	*Sceliphron deforme* (Smith) (Hym Sphecid Sphecinae)	Evenhuis & Arakaki (1980)	ex mud nests
Xeramoeba			
oophaga (Zakhvatkin)	*Dociostaurus* sp. (Ort Acridid)	Greathead (1963)	egg predator
	Oedaleus senegalensis (Krauss) (Ort Acridid)	Popov (1980), Cheke, Fishpool & Ritchie (1980)	egg predator
ANTHRACINAE: Villini			
Chrysanthrax			
near *editita Say*	*Xylocopa submordax* Cockerell (Hym Anthophorid Xylocopinae)	FD Bennett *in litt.*	
Dipalta			
serpentina Osten Sacken	*Myrmeleon immaculatus* De Geer (Neu Myrmeleontid)	Leech & MacDonald-Leech (1989)	ex pupa in cocoon ?infect host larvae
Exechohypopion			
therephaga Yeates	*Parapsilocephala ambocerina* Irwin (Dipt Therevid)	Irwin & Yeates (1995)	ex larvae in soil
Exhyalanthrax			
abruptus Loew	*Glossina morsitans morsitans* Westwood (Dip Glossinid)	Carpels & Greahead (1989)	ex puparium
	Wohlfhartia pachytyli Townsend (Dip Sarcophagid)	Potgeiter (1929), Greathead (1963)	parasitoid, hosts in acridid egg-pods
alliopterus Hesse	*Glossina swynnertoni* Austen (Dip Glossinid)	Greathead (1980)	ex puparium
beckerianus Bezzi	*Glossina pallidipes* Austen (Dip Glossinid)	Greathead (1980)	ex puparium
	Didacus ciliatus (Loew) (Dip Tephritid)	J. Appert Coll.	ex puparium

APPENDIX 1 *(continued)*

Genus/species	Host	Reference	Comments
ANTHRACINAE: Villini *(continued)*			
Exhyalanthrax (continued)			
blattae Greathead	*Heterogamisca chopardi* Uvarov (Dic Polyphagid)	Greathead & Grandcolas (1995)	egg-predator in ootheca
flammiger Walker	*Glossina palpalis* (Robineau-Desvoidy) (Dip Glossinid)	Greathead (1980)	ex puparium
	Macrocentrus maraisi Nixon (Hym Braconid)	Annecke & Moran (1977)	hyperparasitoid in cocoon of *Loxostege frustalis*
	Cremnops frustalis Nixon (Hym Braconid)	Möhr (1990)	hyperparasitoid in cocoon of *Loxostege frustalis*
	Cardiochiles sp. (Hym Braconid)	IIE ident.	hyperparasitoid, ex *Heliocheilus albipunctella* (de Joannis)
	Loxostege frustalis Zeller (Lep Pyralid)	Möhr (1990)	ectoparasitoid on larvae in cocoons
lugens Loew	*Glossina swynnertoni* Austen (Dip Glossinid)	Greathead (1980)	ex puparium
	spp. (Dip Tachinid)	Möhr (1990)	hyperparasitoid in cocoon of *Loxostege frustalis*
	indet. (Dip Tachinid)	IIE ident.	ex puparium
	Macrocentrus maraisi Nixon (Hym Braconid)	Annecke & Moran (1997)	hyperparasitoid in cocoon of *Loxostege frustalis*
	Spodoptera exempta (Walker) (Lep Noctuid)	IIE ident.	ex puparium
	Loxostege frustalis Zeller (Lep Pyralid)	Möhr (1990)	ectoparasitoid on larva in cocoon
sp.	*Chelonus curvimaculatus* Cameron (Hym Braconid)	Möhr (1980)	hyperparasitoid on *Loxostege frustralis*
transiens Bezzi	*Glossina pallidipes* Austen (Dip Glossinid)	Greathead (1980)	ex puparium
viduatus Loew	indet. (Dip Tachinid)	IIE ident.	ex puparium ex *Spodoptera exempta*
Hemipenthes			
morio (Linnaeus)	*Acantholyda nemoralis* Thomson (Hym Tenthredinid)	Koehler (1957)	
?catulina Coquillett	*Cyzenis* spp. (Dip Tachinid)	Humble (1985)	once as hyperparasitoid on host in *Operophtera brumata* (Linnaeus) pupa
	indet. (Dip Tachinid)	Humble (1985)	ex puparium in pupal exuvium of indet. Geometrid
Oestranthrax			
myrmecaeluri Miksch	*Myrmecaelurus trigrammus* (Pallas) (Neu Myrmeleontid)	Miksch (1993)	parasitoid of II and III instar completes development after cocoon formation
Paravilla			
edititoides Painter	*Anthophora urbana urbana* Cresson (Hym Anthophorid Anthophorinae)	Torchio & Trostle (1986)	one larva overwintering in host cell nest in soil
flavicoma Coquillett	*Diadasia (afflicta)* Cresson? (Hym Anthophorid Anthophorinae)	Neff, Simpson and Dorr (1982)	abundant pupae in nest area - assumed parasitoid
flavipilosa Cole	*Diadasia opuntiae* Cockerell (Hym Anthophorid Anthophorinae)	Ordway (1984)	follow bees, wait, when bee goes flick eggs in hole
fumosa Hall	*Colletes kincaidii* Cockerell (Hym Colletid Colletinae)	Torchio, Trostle & Burdick (1988)	ex larvae in cells
vigilans (Coquillett)	*Diadasia rinconis* Cockerell (Hym Anthophorid)	Neff & Simpson (1992b)	
Thyridanthrax			
heliocheili Greathead	*Heliocheilus albipunctella* (de Joannis) (Lep Noctuid)	Greathead (1991)	ex pupa

APPENDIX 1 *(continued)*

Genus/species	Host	Reference	Comments
ANTHRACINAE: Villini (*continued*)			
Thyridanthrax (*continued*)			
sp.	*Dociostaurus maroccanus* (Thunberg) (Ort Acridid)	Soltani (1976)	egg predator
Villa			
albifacies Macquart	*Lycia graecarius* Stgr. (Lep Geometrid)	Kazemi & Damanabi (1983) in Evenhuis (1992)	
faustina Osten Sacken	*Phigalia plumogeraria* (Hulst) (Lep Geometrid)	Furniss & Epps (1981)	ex pupa
hottentotta Linnaeus	*Serracea punctinalis* Scopoli (Lep Geometrid)	Livinchuk & Agamalieva (1982) in Evenhuis (1992)	
manillae Evenhuis	*Leptotes trigemmatus* (Butler) (Lep Lycaenid)	Evenhuis (1993)	
myrmeleonostena Baba	various (Neu Myrmeleontid)	Baba *et al.* (1987)	endoparasitoid then ectoparasitoid?
paniscoides Bezzi	*Spodoptera exempta* (Walker) (Lep Noctuid)	IIE ident.	ex pupa
sp.	*Leucotabanus annulatus* (Say) (Dip Tabanid)	Goodwin (1976)	ex pupa, host collected as larva
	Agrotis segetum (Denis & Schiffermüller) (Lep Noctuid)	Bogush (1959)	
	Euxoa radians Guérin (Lep Noctuid)	Currie (1930–31)	
ventruosa Loew	various (Dip Tabanid)	Kadyrova & Narmatov (1979)	original reference not seen
vitripennis (Loew)	indet. (Lep Noctuoid)	Evenhuis *in litt.*	from South Africa in South African Museum
ANTHRACINAE: Exoprosopini			
Heteralonia			
sp.	*Pompilus cinereus* (Fabricius) (Hym Pompilid)	Evenhuis *in litt.*	from Madagascar in MNHN Paris
Litorhina			
tollini (Loew)	*Tiphia* sp. (Hym Tiphiid)	Bünzli & Butticker (1957)	hyperparasitoid on *Anomala exitialis* Pérris
Pterobates			
apicalis (Wiedemann)	indet. Lepidoptera	Evenhuis *in litt.*	from South African in South African Museum
sp.	*Myrmeleon inconspicuus* Rambur (Neu Myrmeleontid)	Pantaleoni (1984)	ex pupae