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Functional, evolutionary and ecological aspects of feeding-related mouthpart specializations in parasitoid flies

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This paper considers mouthpart specializations for feeding among dipteran parasitoids, and places them in both an evolutionary and an ecological context. Parasitoid flies display specializations in relation to feeding on solidified honeydew, removing floral nectar from long, narrow, tubular corollas, and feeding on host materials. No species have as yet been identified which display particular specializations for pollen-feeding, but we consider it likely that they exist. Marked sexual dimorphism in mouthpart structure appears to occur only in the Phoridae. Mapping the occurrence of apparatus for removing floral nectar from long, narrow, tubular corollas ('concealed nectar extraction apparatus' or CNEA) onto published cladograms for Diptera shows that the evolution of such feeding apparatus has occurred many times independently. In contrast to parasitoid Hymenoptera, possession of CNEA is more often an autapomorphy for taxa above subfamily level in apparently two cases for superfamilies (Acroceroidea and Nemestrinoidea). We conclude that whereas in parasitoid wasps the pattern of occurrence of CNEA is mainly attributable to ecological expediency, in parasitoid flies phylogenetic history has also played a major role. We discuss the fitness advantages of the different feeding specializations among parasitoids generally (i.e. both Diptera and Hymenoptera) in relation to various ecophysiological factors.

ADDITIONAL KEY WORDS:—parasitoids – Diptera – Hymenoptera – mouthparts – comparative morphology – foraging – mating system – flower visiting – nectar feeding – honeydew feeding – pollen feeding – host feeding – nutritional physiology – evolution – phylogeny – reproductive strategies – sexual dimorphism.

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INTRODUCTION

Parasitoid insects exhibit extensive mouthpart specialization in relation to a wide variety of functions: adult emergence, grasping of the partner in mating (phoretic copulation), searching for hosts, handling hosts, nest excavation and construction, and feeding (Jervis, 1998). Parasitoid wasps display all six of these specializations, although in general a particular mouthpart type serves only one of the aforementioned functions (some Pompilidae, Sphecidae, Multillidae and Scoliidae being exceptions). Parasitoid flies, however, show specialization only in relation to feeding. One feeding specialization, a device for removal of floral nectar contained in long, narrow, tubular corollas, is far more common in parasitoid flies than in wasps (Jervis, 1998). This makes an interesting contrast, and deserves exploration. The purpose of this paper is to review the evidence for feeding-related adaptive specializations in the mouthparts of parasitoid flies, and to place the hitherto highly scattered information in the context of what is known about parasitoid feeding biology. We conclude by discussing, in relation to parasitoids generally (i.e. wasps as well as flies), the possible fitness advantages of the various feeding-related mouthpart specializations, and the ecophysiological factors that have influenced their evolution.

MOUTHPART SPECIALIZATIONS FOR FEEDING

The foods of parasitoid flies

It is well known that the main foods of parasitoid flies are floral nectar, extrafloral nectar, homopteran honeydew and host blood (Jervis & Kidd, 1986; Nettles, 1987; Jervis, Kidd & Walton, 1992; Jervis, Hawkins & Kidd, 1996a; Jervis, Kidd & Heimpel, 1996b). A few taxa take pollen or other materials from plants, but evidence for such behaviour is rare.

According to Evenhuis, Hall & Neff (in Deyrup [1988]), pollen feeding is widespread among female Bombyliidae possessing functional mouthparts; some species are known to visit nectariless flowers (Graenicher, 1910; Deyrup, 1988). The bombyliid *Poecilognathus punctipennis* (Walker), which may be a parasitoid (its biology is unknown [Deyrup, 1988; D. J. Greathead, pers. comm.]) has been observed to ingest the pollen grains it gathers from anthers with its front tarsi (Deyrup, 1988).

Pollen grains have been recorded in the guts of some dipteran parasitoids: Bombyliidae (*Geron* sp. [and *P. punctipennis*] [Deyrup, 1988]) and some Tachinidae (N. J. Mills, pers. comm.). However, neither Herting (1960) nor Disney (1994) recorded finding pollen in the guts of Tachinidae and Phoridae respectively.

Pollenia rudis (Fab.) (Calliphoridae) and a few Tachinidae have been observed to feed on the sugary liquid secreted by rust fungi and ergot (*Claviceps purpurea* [Fr.] Tul.) and also on the juices that exude from ripe fruit (Rathay, 1883). It is also

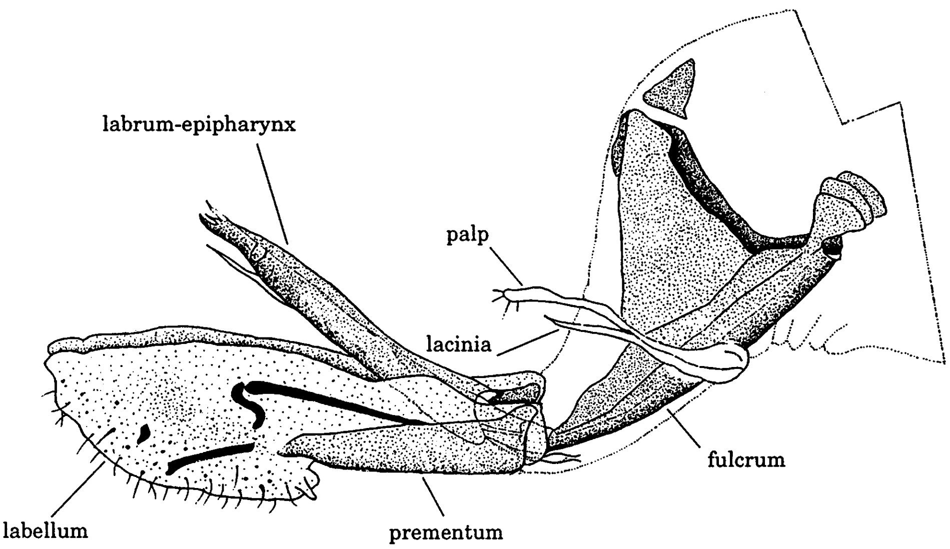

Figure 1. The basic structure of the higher dipteran proboscis (adapted from Schiemenz, 1957).

possible that parasitoid flies, like non-parasitoid flies, feed on plant leachates (Stoffolano, 1995), bird droppings (Hendrichs *et al.*, 1993), leaf surface bacteria (Hendrichs *et al.*, 1993; Vijaysegaran, Walter & Drew, 1997) and fungal hyphae and spores (Broadhead, 1984).

Mouthpart structure in Diptera

The terminology of the mouthparts of Diptera is confused, as in so much insect morphology, because of differing opinions concerning homologies: most studies of dipteran mouthparts are concerned with homologies of the different sclerites and with evolution (e.g. Gerstfeld, 1853; Becher, 1882; Peterson, 1916; Frey, 1921; Hoyt, 1952). Here we follow the terminology of McAlpine (1981). The mouthparts as described by McAlpine (1981) form a tubular sucking organ, the proboscis (Fig. 1), comprising two main parts:

(1) The *rostrum* is the basal part of the proboscis. In many taxa, particularly the Muscomorpha, the proboscis is extended by the sclerites of the cibarium (mainly the fulcrum) shifting into the proboscis (Fig. 1), forming the rostrum.

(2) The *haustellum* comprises two paired elements and three unpaired elements:

The two paired elements are: (i) the *mandibles*, which are usually absent, and are in any case only functional in females, normally of blood-feeding species; (ii) the *maxillae*, which often consist only of blade-like *laciniae*, bearing palps. The laciniae cannot be functionless in view of their powerful basal musculature, but their function has long been a puzzle (Schiemenz, 1957): they have been variously described as implements for pushing aside obstructing floral structures (Menzbier, 1880), or for forcing pollen into the labral food canal from the side.

The three unpaired elements are: (i) the *labrum* which generally forms the dorsal and lateral sides of the food canal, and often bears tooth-like projections

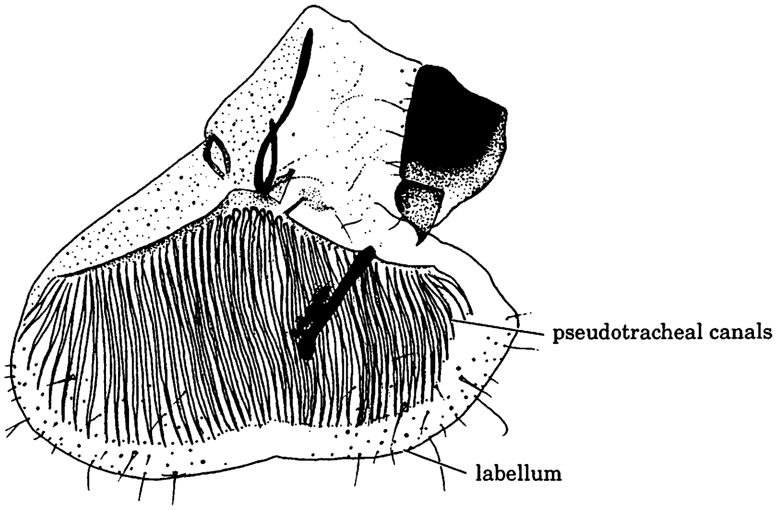

Figure 2. Labellum of higher Diptera, viewed from the inside to show the pseudotracheal canals. Drawn from a photomicrograph of *Episyrphus balteatus* (Diptera, Syrphidae).

or peculiar brushes at the tip; (ii) the *hypopharynx* which contains the salivary duct opening at its tip, and forms the ventral part of the food canal; and (iii) the *labium*, the largest of the mouthparts, which forms the ventral wall of the proboscis. The labium usually takes the form of a gutter in which the other mouthparts lie. It has three parts: the postmentum (often greatly reduced or absent), the prementum, and the paired *labella* at the distal end. The labella (note that the singular is labellum) consist of two membranous cushion-like lobes (Figs 1, 2), the inner surfaces of which bear varying numbers of sclerotized grooves, the *pseudotracheae* (Figs 2, 3). The structure of the pseudotracheae has been little studied, but contains remarkable variations between different taxa (e.g. Broadhead, 1984; Elzinga & Broce, 1986).

These basic elements vary considerably in size, shape and structure both among and within the different families of Diptera. Some remarkable structures have been recorded (*vide* the huge laciniae of the cecidomyiid *Farquharsonia rostrata* [Collin, 1921]), but rarely have they been related to their functions. The mouthparts of virtually all fly families are specialized fundamentally for fluid-feeding. There are various taxa at different taxonomic levels in which predatory or blood-sucking feeding modes have evolved, and their mouthparts have accordingly become specialized for either piercing (e.g. labrum, mandibles, maxillae and hypopharynx in Culicidae; the hypopharynx in Asilidae) or cutting (e.g. the labrum itself in many taxa; lateral tooth-like projections of the labrum in Dolichopodidae; the mandibles in Tabanidae; the prestomal teeth of the labella in *Glossina*, *Stomoxys* and *Scathophaga*).

Misinterpretations of the functional morphology of fly mouthparts are common in the literature, often as a result of authors studying dried or alcohol-preserved material. For example, Grimaldi (1988) shows the mouthparts of the bombyliid *Bombylius major* L. inserted into a flower with a long corolla (*Hedyotis caerulea* (L.) Hook), but he pictured the proboscis in its dried state, with the various mouthparts splayed apart and the labella folded back, utterly unlike their disposition *in vivo*. This

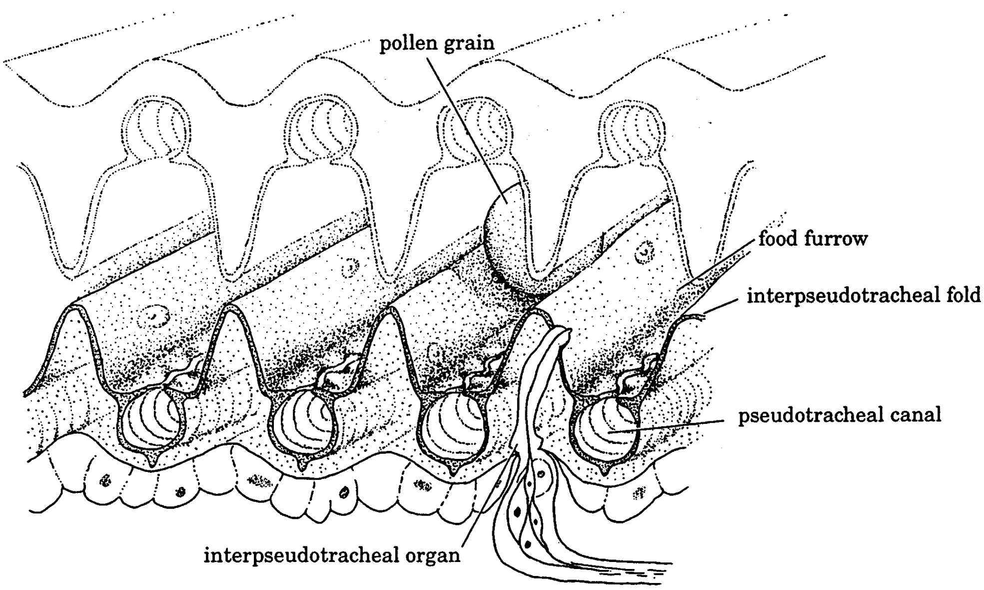

Figure 3. Fine structure of the inner labellar surface, indicating how pollen is collected in the food furrows (adapted from Schuhmacher & Hoffmann, 1982).

led him to misinterpret the way in which some of the mouthparts function: he described the laciniae as shaking pollen off the anthers into the food canal (which gapes open in his drawing), whereas in fact *in vivo* the laciniae are closely aligned with the labral food canal, within the labial gutter.

The mouthparts are often retracted into the head capsule (as in Cyclorrhapha), but in lower Diptera they are often relatively rigid, although even here (e.g. Bombyliidae, Nemestrinidae) they can be telescoped in and out, presumably by a combination of muscular action and haemolymphal pressure.

The structure of the labellum is reasonably well known in Diptera (e.g. Elzinga & Broce, 1986; Vijaysegaran *et al.*, 1997), and it is clear that the various components are very variable, even amongst the Muscomorpha (Elzinga & Broce, 1986). The pseudotracheal structures are particularly variable even between members of one family (Broadhead, 1984), with spines, brushes, blades, pores, and micropores all present (Elzinga & Broce, 1986). More studies are needed involving living flies, to enable precise determination of how the different mouthparts are used in feeding.

The very careful and critical work of Schuhmacher & Hoffman (1982) has clarified considerably the structure of the labella in the living fly, and hence the functioning of the mouthparts during feeding. By instantaneous freezing of feeding animals, these authors made a detailed study of the way in which the mouthparts operate in feeding hoverflies (Syrphidae): the basic mechanisms may be similar throughout the Diptera, at least in flower-feeding taxa. The key feature for pollen feeding is the interpseudotracheal folds maintained by haemolymphal pressure; these collapse in dried or alcohol-preserved material, and hence were not noticed previously. The folds create channels overlying the pseudotracheal canals (Fig. 3) in which fluids (e.g. nectar or wet honeydew with and without saliva, solidified honeydew or nectar

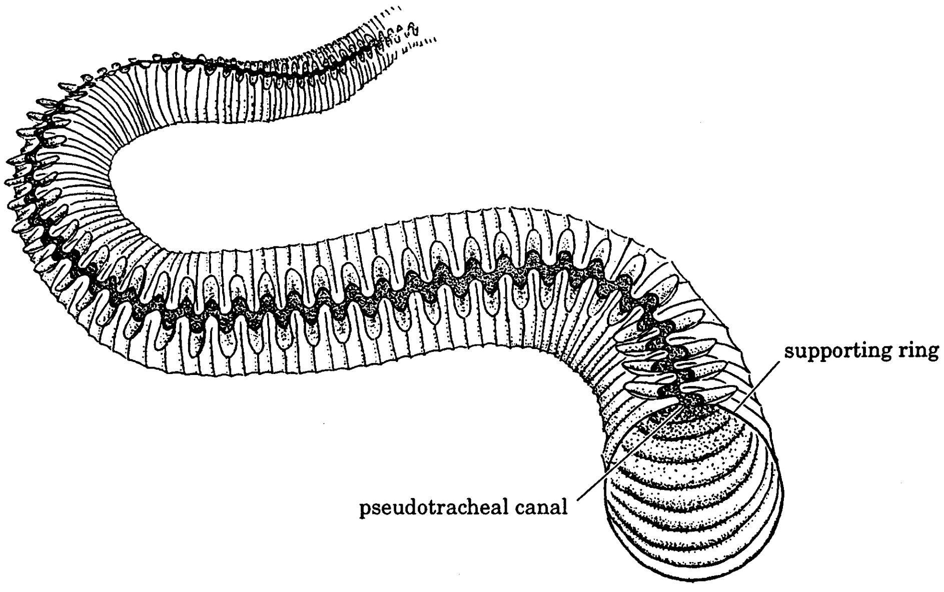

Figure 4. Arrangement of the supporting rings of the pseudotracheal canals. The pseudotracheal canal has been twisted in order to show the three-dimensional structure of the rings.

dissolved in saliva, pollen suspended in saliva) can be transported to the opening of the labral food canal.

In its basic mode, the proboscis is used to mop up and/or suck up liquids (Graham-Smith, 1930; Vijaysegaran *et al.*, 1997), either as liquid food (nectar, honeydew), or as solid material dissolved/suspended in salivary secretions. Studies of the functioning of dipteran mouthparts are relatively rare in the literature (Graham-Smith, 1930; Schiemenz, 1957; Schuhmacher & Hoffman, 1982; Vijaysegaran *et al.*, 1997) and there have been many wild guesses as to how the various parts operate, especially in feeding from flowers or on honeydew.

Feeding on honeydew and nectar

Many previous authors have hypothesized, experimented, or commented on the way in which the various mouthparts combine for fluid feeding, but the mechanism has often been misunderstood. Graham-Smith (1930) and many others envisaged the labella spread flat over the liquid surface, and the liquid food being taken up by capillarity into the small pseudotracheal canals, and thence via the common pseudotracheal duct to the opening of the labral food canal at the end of the labial gutter. This view may be incorrect for many Diptera, and is certainly incomplete.

In many flower-visiting species the pseudotracheal canals carry only saliva, which flows outwards from its source (the tip of the hypopharynx). The saliva wells out from pseudotracheal canals along their entire length through the narrow zipper-like openings of the incomplete support rings (Fig. 4) into the food furrows created by the interpseudotracheal folds; dissolved honeydew or nectar, or diluted nectar, are then sucked back to the labral food canal from all parts of the labella along the food furrows under the influence of the suction generated by the ‘prelabral pump’

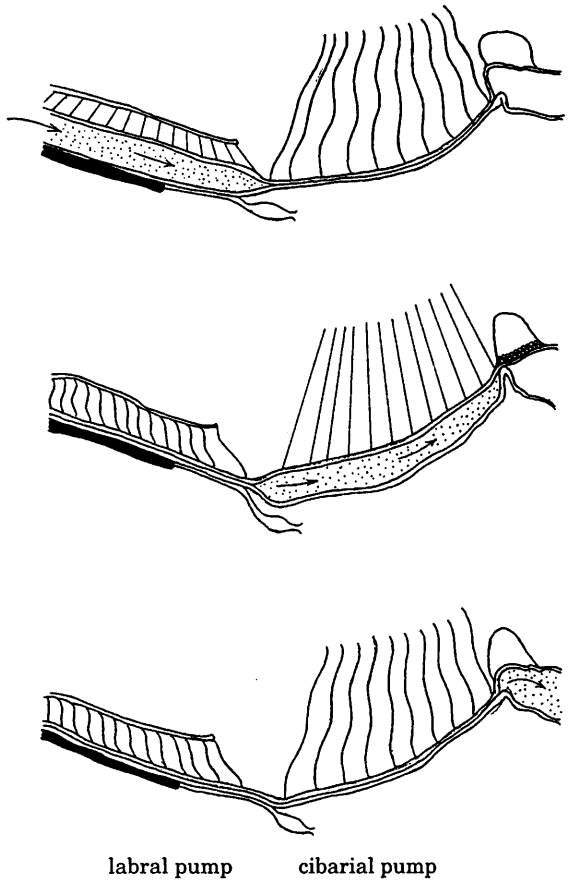

Figure 5. Double pump of the rostrum and haustellum of Brachyceran Diptera. The labral and cibarial pumps work out of phase to transport fluid into the pharynx and thence to the gut (Schiemenz, 1957; Rice, 1970; Dethier, 1976; Schuhmacher & Hoffman, 1982). To these must be added the pre-labral pump (see text).

(Schuhmacher & Hoffmann, 1982). The prelabral pump works via muscular contractions creating a space in the middle of the labella, generating suction that pulls the saliva/food mixture along the food furrows. One can observe the rhythmic pulsing (5–10 cycles per sec) of the labella in a feeding fly; fluid is drawn from far beyond the labella in a continuous flow of nectar. The prelabral pump is synchronized with two other pumps (the labral and cibarial pumps) that occur in series with it (Fig. 5), generating continuous suction from labella to pharynx.

The above account of feeding is most appropriate for the action of flies feeding on solidified honeydew deposits or the more or less solidified nectar present on exposed floral nectaries (such as occur in umbellifers [Apiaceae]) and extrafloral nectaries. In these cases, flies are dissolving sugars and other substances in their saliva, and sucking up the resultant liquid, presumably a very common behaviour amongst both parasitoid and non-parasitoid Diptera. For those taxa with closed pseudotracheal canals, which nevertheless dab their labella on surfaces in a superficially similar manner, both the food being taken and the mechanism of ingestion must be different, but we have very few relevant studies (but see Vijaysegaran *et al.* [1997]). This interpretation also does not always account for the way in which elongated mouthparts ('concealed nectar extraction apparatus' or CNEA, see companion paper by Jervis, pp. 461–493 bearing in some cases narrow, elongated labella, are used to obtain liquid nectar from flowers with long, narrow, tubular corollas.

One major additional factor for consideration is the hydrophilic inner surfaces of the labella, that draw nectar along hydrophilic pathways of the corolla; this hydrophily allows flies to obtain nectar from corollae that are deeper than the length of their mouthparts (Gilbert, 1981). A second difference of interpretation is that only a few pseudotracheae, or even just a single pseudotrachea, are sufficient for exclusive nectar feeding, demonstrated by the reduction in size (or at least the breadth, see below) of the labella and the reduction in the numbers of pseudotracheae in species that feed mainly on nectar from deep corollas (e.g. long-tongued tachinids, e.g. *Siphona*, Proctor, Yeo & Lack, 1996; long-tongued bombyliids, e.g. *Bombylius*, Proctor *et al.*, 1996; Zaitsev, 1982; Grimaldi, 1988; Yeates, 1994; Empididae, e.g. *Empis* spp. that consume floral nectar, Bletchly, 1954; Proctor *et al.*, 1996; Tabanidae, e.g. *Pangonia*, Mitter, 1917; and long-tongued syrphids, e.g. *Rhingia*, Gilbert, 1981). Some parasitoid flies with CNEA, such as many Bombyliidae (Yeates, 1994), certain Conopidae (Smith & Peterson, 1987) and certain Tachinidae (Proctor *et al.*, 1996), have elongated but narrow labella. The number of pseudotracheae per labellum in bombyliids is discussed below (see 'Evolutionary considerations', pp. 505–518).

There are also some indications of major differences in mechanism even among anthophilous Diptera. Schuhmacher and Hoffmann's (1982) account of nectar feeding by hoverflies is unambiguous in describing the pseudotracheal canals as conduits for saliva, but in some species with CNEA the canals may in fact have evolved to be mainly conduits for *nectar*. Zaitsev (1982) described what he called the pseudotracheal 'closing' apparatus in a large number of Diptera, especially Bombyliidae. While correctly noting that it was a mistake to apply uncritically Graham-Smith's work (1930) on *Calliphora* to all Diptera, he assumed that because nectar always travelled in the pseudotracheal canals, the latter had to be 'closed' by some mechanism. What he was describing was the zigzag zipper-like opening out of which saliva floods (Figs 3, 4). However, he described two main types, the normal 'dentate' type seen in most Diptera, and a 'spinose' type found mainly in bombyliid species with a very long CNEA. From his scanning electron micrographs, it seems unlikely that spinose types could work in the same way as in the syrphids so minutely described by Schuhmacher & Hoffman (1982), suggesting that the pseudotracheae might have converted to conduct nectar in these highly specialized anthophilous species. If this is correct, the conversion may have evolved independently in 'long-tongued' Tabanidae, the other family said to possess spinose edges to the pseudotracheae (Zaitsev, 1982). Elzinga & Broce (1986) did not see any clear distinction between spinose and dentate structures of the pseudotracheae, and probably this division is not useful. Instead, Elzinga & Broce (1986) describe a great diversity of different pseudotracheal elaborations that require a functional interpretation. For example, some non-anthophilous Diptera clearly possess complete support rings in their pseudotracheae. The gutter-like canals, with their zigzag openings, of the majority of Diptera are replaced here by closed pipes, accessible only via tiny micropores in the support rings themselves: these structures seem to be associated with the filtering of fluids on the surfaces of fruit and leaves and with the ingestion of fruit juices, leachates and bacteria (e.g. in some Tephritidae [Vijaysegaran *et al.*, 1997]). Presumably these canals are used both for exuding saliva onto the substrate, and for reingesting it together with suspended particles that pass through the micropores.

Feeding on pollen

There are many reports of whole pollen grains occurring in the guts of flower-visiting Diptera (Müller, 1883; Vine, 1895; Schiemenz, 1957; Haslett, 1983). However, many Diptera (including many flower visitors) do not ingest pollen. Downes & Dahlem (1987) dissected a 'very large number' of calyptrates without discovering pollen in the digestive tract. As we have already noted (see 'The foods of parasitoid flies', above), the available evidence suggests that few parasitoids, with the exception of some Bombyliidae and possibly some Tachinidae, feed on pollen.

Pollen feeding has traditionally presented problems to functional morphologists, since it is difficult to envisage how the pollen is removed from anthers and then ingested using the dipteran proboscis. Some authors (Zimina, 1957; Nayar, 1943; Percival, 1965) considered pollen to be ingested directly into the labral food canal with no involvement of the labella. Others (Künckel d'Herculais, 1875; Müller, 1883; Buckton, 1895; Lindner, 1919; McAlpine, 1965) recognized that pollen was removed from anthers by a twisting and rubbing motion of the labella. However, there have been several interpretations of the involvement of the various sclerites of the proboscis. The diagnostic, peculiarly shaped brushes at the tip of the labrum were thought either to brush pollen off the anthers (Vine, 1895) or to break apart lumps of pollen (Zimina, 1957). Percival (1965) reported that prestomal teeth rasped pollen off the anthers, despite there being no such teeth in the vast majority of flower-visiting Diptera (see McAlpine, 1981; Gilbert, 1981). Dimmock (1881) and Müller (1883) considered it the role of the pseudotracheae to convert lumps of pollen into strings suitable for ingestion.

As noted above ('The foods of parasitoid flies'), the bombyliid *Poecilognathus punctipennis* removes pollen from anthers using its tarsi (Deyrup, 1988). The grains are then transferred to the tip of the proboscis (*vide Eristalis tenax* [L] (Syrphidae); Holloway [1976]). Deyrup (1988) was unable to determine how pollen grains were conveyed from the proboscis tip to the mouth in *P. punctipennis.*

By freezing hoverflies in the act of feeding on pollen and subsequently cutting the mouthparts into sections, Schuhmacher & Hoffmann (1982) demonstrated clearly that the labella are vital both for collecting pollen from the anthers and for conveying it to the labral food canal but that, like nectar, the pollen never enters the pseudotracheal canals. Twisting movements of the labella placed around anthers abrade pollen masses down into individual grains which are then dispersed along the food furrows. The grains are held by surface tension since the inner surfaces of the labella are always kept moist by the labellar and main salivary glands. Subsequently, the labella are removed from the anther and are juxtaposed, thus generating tubular food tunnels. The main salivary gland produces a large quantity of saliva from the end of the hypopharynx, which spreads through the pseudotracheal canals (by capillarity and under the low pressure of secretion) and exudes into the food furrows, producing a suspension of pollen grains. The pre-labral pump then conveys this suspension along the food furrows to the labral food canal.

Measurements of the diameter of the food furrows in a variety of Syrphidae showed that it corresponds to the diameter of pollen grains that are taken by adults; flower species whose pollen grains are larger than this are not acceptable to the flies (Schuhmacher & Hoffmann, 1982).

It is possible that some parasitoid flies can consume the contents of pollen grains without ingesting the grains themselves, and therefore do not require specialized morphological structures for pollen feeding. Both sexes of the non-parasitoid *Drosophila flavohirta* Malloch (Drosophilidae) gather pollen grains from anthers using their normal-type labella, and moisten them with saliva. Pollen gathering alternates with 'quiescent' periods during which the large mass of accumulated pollen grains is continually vibrated. No pollen has ever been found in the guts of these flies, suggesting that nutrients are released by the combined action of saliva (i.e. the flies practise preoral digestion) and vibration, and are then ingested (Nicolson, 1994). This method of pollen nutrient extraction is similar to that practised by *Heliconius* butterflies (Gilbert, 1972). The cecidomyiid *Atrichopogon pollinivorus* Downes pierces pollen grains with its mouthparts (styliform labrum and labella?) and sucks up the contents, in the manner of Thysanoptera (Downes, 1995). The anthomyiid *Delia radicum* (L), which has short muscoid-type mouthparts, is able to remove sugars from the surfaces of grass pollen grains (Finch, 1974).

Given that honeydew on leaves is frequently contaminated with trapped pollen grains (derived from anemophilous plants such as grasses), it is likely that honeydew feeding will have given rise to a specialization for concentrating contaminant pollen in the diet, in the manner of *Xylota* hoverflies (see 'Evolutionary considerations', below).

There has been confusion over the fate of the pollen in the gut. There have been repeated fallacious claims that it is ground to a pulp (Hesse & Doflein, 1914; Lindner, 1919; Parmenter, 1953; Kugler, 1955; Percival, 1965; Elton, 1966; Faegri & van der Pijl, 1979), despite common knowledge that it is not (e.g. Haslett, 1983) (this probably applies widely to pollen-feeding insects, e.g. Dobson & Peng [1997]).

Feeding on host blood

Whilst in parasitoid wasps mouthpart specializations do not appear to have been developed in relation to host feeding behaviour (see companion paper by Jervis), in some parasitoid members of the fly family Phoridae they have, and this is reflected in sexual dimorphism (Disney, Khochare & Godase, 1992). The mouthparts of the female in *Megaselia chlumetiae* Disney have narrow labella and an expanded labrum from the tip of which protrudes the heavily sclerotized, piercing tip of the hypopharynx. Some *Phalacrotophora* species display the same specializations together with the occurrence of teeth on the inner faces of the labella. So far, females of the latter genus only have been observed to host feed (Richards, 1926; Delucchi, 1953; Disney *et al.*, 1992).

Sexual dimorphism in feeding specializations

Sexual dimorphism in mouthpart structure in Phoridae has been mentioned in the preceding section. It should be noted that in the non-parasitoid family, the Syrphidae, males generally have longer mouthparts than females, reflecting their low dependence on proteinaceous nutrients for gamete production (Gilbert, 1985b). The same dimorphism may occur in some anthophilous parasitoid flies, but as yet we cannot provide any examples.

Evolutionary considerations

Three main messages arise from this new understanding of the mechanics of feeding Diptera from flowers, extrafloral nectaries or honeydew deposits:

(1) In the case of feeding on solidified honeydew or nectar, the major limiting factor will be the area of the outspread labella that can be adpressed to the honeydew patch or (exposed) nectary surface, from which material can be dissolved and taken up. Thus, we can predict the combination of very short mouthparts with very broad labella and large numbers of pseudotracheae. Unless pollen is also being obtained from leaf surfaces, the width of the food furrows should be less important, and therefore we might expect them to be narrower than in species that feed mainly or exclusively on pollen (see [3] below), in order to accommodate more furrows into the labellar surface.

The evolution of the Diptera may well be intimately connected with adaptation to feeding on honeydew. Downes & Dahlem (1987) point out that floral nectar did not become available to Diptera until long after the Homoptera had evolved, and concluded that various dipteran characters (attraction to small shiny objects, presence of tarsal receptors, and klinokinetic walking behaviour following feeding on sugar-rich food) are adaptations for feeding on honeydew (see Disney [1994] on Phoridae). Since the labella and pseudotracheae occur even in the Tipulidae (Peterson, 1916; Proctor *et al.*, 1996), as well as some other Nematocera (e.g. Mycetophilidae, Ptychopteridae: Peterson, 1916; Hoyt, 1952; Hennig, 1973) and most Brachycera, they should be regarded as synapomorphies for the order Diptera as a whole (Hennig, 1981), although they are not listed as such by McAlpine (1981). This interpretation relies on the widely accepted view that the Tipulidae are the sister-group for the remainder of the Diptera (see Wood & Borkent, 1989); however, a recent dissenting opinion (Oosterbroek & Courtney, 1995) considers the Tipuloidea to be the sister-group of the Anisopodidae + Brachycera, which would place the evolution of the labellar-pseudotracheal system much later in the radiation of the order.

The labella may be principally an adaptation for feeding on films of solidified honeydew which sugars can be obtained without suffering accompanying water loss (Downes & Dahlem, 1987). Facilitation of feeding on exposed (solidified) nectar can be viewed as an additional benefit. The possession of short mouthparts with relatively broad labella is probably the plesiomorphic state for most Dipteran groups (*vide* the Bombyliidae, Yeates [1994]).

(2) Only a single pseudotracheal canal (the common collecting canal) is absolutely necessary for feeding on floral nectar from long, narrow, tubular corollas (where the nectar is nearly always relatively dilute, with low viscosity). Therefore, in species either exclusively or mostly feeding on such nectar, we can predict CNEA comprising an elongated proboscis with reduced labella and thus a reduced number of pseudotracheae, possibly also with conversion of the pseudotracheae into nectar-carrying rather than saliva-carrying channels (possibly evidenced by spinose pseudotracheal borders). Such specialized species are never very common components of anthophile assemblages. Because the distribution of corolla depths in natural communities of flowers is log-normal (i.e. many more species with short than with long corollas)

Table 1. The number of species of Tachinidae (Diptera) recorded visiting different food sources (data from Allen, 1929)

Proboscis length	Flowers only	Flowers, honeydew or extrafloral nectaries
Moderately long (=height of head) or long (>height of head)	17	10
Short (<height of head)	1	23

(Prys-Jones & Corbet, 1983), it is possible that the distribution of proboscis lengths in assemblages of nectar feeders might match it.

(3) The possession of food furrows overlying the pseudotracheae is a vital adaptation for pollen feeding, and therefore in species feeding mainly or exclusively on pollen we can predict a syndrome of short mouthparts with broad labella and a large number of pseudotracheal canals. The width of the food furrows should reflect the preferred size of pollen grains.

Some of these predictions are amply borne out by examination of the feeding habits and mouthpart structure of both the Syrphidae, a major flower-visiting taxon of Diptera, and the Tachinidae. In Syrphidae, larger species have an increased absolute requirement for nectar to fuel flight activity, spend proportionately less time flying than smaller species (indicating that energy may be limiting) (Gilbert, 1985a), and spend proportionately more time feeding on nectar (Gilbert, 1985b). Differences in proboscis length and labella size are strongly associated with variation in the observed nectar:pollen ratio; species with a short proboscis and broad labella are those observed most often taking pollen (Gilbert, 1981, 1985b). The distribution of proboscis lengths is indeed log-normal (F. S. Gilbert, unpublished data). Many species take honeydew from leaves, but this is a relatively infrequent component of the diet except in members of the genus *Xylota*, which specialize almost exclusively on feeding on pollen grains contaminating honeydew films on leaf surfaces (Gilbert, 1985b; Ssymank & Gilbert, 1993). *Xylota* spp. have exceedingly short mouthparts with enormous vacuum-cleaner-like labella densely provided with pseudotracheae, and the crops of individual flies are often packed with pollen (Ssymank & Gilbert, 1993); members of the genus worldwide appear to feed in the aforementioned manner, indicating that it is a synapomorphy for the genus (Ssymank & Gilbert, 1993).

Allen's (1929) survey of tachinid adult feeding habits (Table 1) clearly shows that, in accordance with our predictions, the possession of a short proboscis in Tachinidae is associated with feeding on honeydew and exposed nectaries, and that possession of an elongated proboscis is associated with specialized flower-feeding ($\chi_1^2 = 23$, $P \ll 0.001$).

Two bombyliids that apparently feed regularly on pollen, *Poecilognathus punctipennis* and *Geron* sp., do not display the predicted pollen feeding syndrome: they have an elongated proboscis (i.e. CNEA), not a short one. However, we do not know what proportion of the diet is represented by pollen, and suspect that nectar forms most of the food of these species.

Is CNEA associated with the parasitoid habit in Diptera? The rare occurrence of CNEA among parasitoid Hymenoptera and its frequent occurrence among non-parasitoid Hymenoptera (see companion paper) suggest that the answer to the above question is a categorical *no*. Table 2 lists the dipteran families with their mouthpart morphology, larval habit and adult feeding behaviour, where known. Eggleton & Belshaw (1992) showed, by mapping the occurrence of the parasitoid 'lifeway' onto phylogenies for the major groupings of Diptera advanced by Wood & Borkent (1989), Woodley (1989) and McAlpine (1989) (none utilizing mouthpart characters), that in flies the parasitoid habit has arisen probably over one hundred times independently among families. Mapping the occurrence of CNEA onto the same cladograms, we conclude that such feeding apparatus has also arisen many times independently among families, albeit much less frequently than the parasitoid habit. Families containing members with an elongated proboscis represent over half (54%, $n = 13$) of the 24 parasitoid-containing families (i.e. those containing at least one species displaying the parasitoid habit), whereas they represent around one eighth (13.6%, $n = 14$) of the 103 non-parasitoid families ($\chi_1^2 = 19.14$, $P \ll 0.001$). [Excluded from this analysis were families whose adults are not free-living. A similar result is obtained ($\chi_1^2 = 21.04$, $P << 0.001$), with the following additional exclusions: families in which the larvae are typically predatory or endoparasitic in vertebrates, those in which the larva receives internal nourishment from the mother, and those in which the female typically has mandibles]. While this could be taken as indicative of a link between the parasitoid habit and the occurrence of CNEA, it could well be misleading because while taxa may contain parasitoid and CNEA-possessing members, these may not be one and the same species.

Not surprisingly, elongated mouthparts are found among the majority (69%, $n = 20$) of the 29 dipteran families containing species that are obligate flower visitors, or which are commonly recorded at flowers, whereas they are found among a tiny minority (7%, $n = 7$) of the 98 non-flower visting families ($\chi_1^2 = 51.1$, $P \ll 0.001$). [Excluded from this analysis were families whose adults are not free-living (see above). A similar result ($\chi_1^2 = 44.8$, $P \ll 0.001$) is obtained when families in which the female feeds on vertebrate blood are additionally excluded]. This observation supports the hypothesis that flower-visiting behaviour promotes the evolution of CNEAs.

We do not have quantitative data, but it is our general impression that the syndrome of flower-visiting coupled with possession of elongated mouthparts, i.e. CNEA, is associated with a large average body size, there being a direct relationship between body size and absolute metabolic requirements (e.g. Gilbert, 1985a).

What broad patterns can be discerned within families? We address this question with reference to the Bombyliidae. We would like to have been able to have used also the Tachinidae, since all members of the group are parasitoids; however, their classification is one of the most difficult problems in the Diptera, and no phylogenetic schemes are known to us (see Wood, 1987). A CNEA is probably the apomorphic state in Tachinidae.

The Bombyliidae is well-known for the parasitoid larval and flower-visiting adult habits of many of its members. Despite this, the habits of many species remain unknown (Yeates & Greathead, 1997; M. Ebejer, pers. comm.), while the feeding biology of the adult flies is surprisingly poorly studied (see Toft [1983, 1984b] for exceptions). While some taxa (*Xenoprosopa* and the Villoestrini) have non-functional and reduced mouthparts, many have short retractile mouthparts with broad, fleshy labella (Anthracinae except *Stonyx*, Tomomyzinae, and Lomatiinae except *Comptosia*);

TABLE 2. The families ($n=131$) of the Diptera, their proboscis morphology, feeding behaviour, and the occurrence of parasitoids. Parasitoid-containing families ($n=24$) are indicated in bold type. Constructed using Ashburner (1981). Askew (1971), Broadhead (1984), Collin (1921), Colyer & Hammond (1951), J. C. Deeming (pers. comm.), Disney (1994), Downes (1955), Downes & Dahlem (1987), M. J. Ebejer (pers. comm.), Eggleton & Belshaw (1992), Ferrar (1987), Finch (1974), Lewis & Domoney (1966), McAlpine & de Keyzer (1994), McAlpine *et al.* (1981, 1987, 1989), Nettles (1987), Nicolson (1994), Proctor *et al.* (1996), Rathay (1883), Rupp (1989), Schlinger (1960), Schutz & Gaugler (1989), Smith (1989), Stubbs & Chandler (1978), Vijaysegaran *et al.* (1997), Yeates & Greathead (1997), Yeates & Irwin (1996), and Zaitsev (1982, 1988). Where mandibles are noted as present, they are only in females (males never possess mandibles). Non-parasitoid larval habits are also indicated.

Note that 'anthophilous' is a term widely used in the literature, and it is often applied both to the behaviour (i.e. frequent or obligate flower-visiting) and to the mouthparts of wasps and flies. However, floral materials of some sort can potentially be consumed irrespective of the particular mouthpart specialization. Thus, to avoid confusion, we have avoided using the term altogether in this table (we recommend that in future it be applied to behaviour only, as we have done in the text)

Family	Proboscis structure	Adult feeding	Larval feeding habit
Acarthophthalmidae	short & fleshy	not recorded at flowers	(? mycophages)
Acroceridae	vestigial or very small (*Acrocerca Ocneae, Ogcodes, Pterodontia*) very long (*Eulonchus*, *Lasia*, *Philopota*)	most spp. with functional mouthparts are obligate flower-feeders, taking nectar	all endoparasitoids in adult spiders, especially Lycosidae
Agromyzidae	short & fleshy; sometimes elongate	some spp. feed on 'nectar' of fungi	(phytophages – leaf miners)
Anisopodidae	reduced	only once recorded at flowers (*Heracleum*), possibly taking nectar	(saprophages, in sap flows)
Anthomyiidae	short & fleshy to long & tubular	regular at flowers; some are obligate flower-feeders, some feed on 'nectar' of fungi	(phytophages, saprophages, some coprophagous) *Acridomyia* (endoparasitoids in adult acridids) *Acyglossa* (endoparasitoids in adult acridids) *Eustalomyia* (provision-directed cleptoparasitoids in aculeate nests) *Leucophora* (provision-directed cleptoparasitoids in aculeate nests) *Tettigoniomyia* (endoparasitoids in adult acridids)
Anthomyzidae	short & fleshy	?	(phytophages in grass stems)
Apioceridae	short & fleshy; elongated (*Apiocera*)	?	(soil predators)
Asilidae	moderately elongated, sclerotized, fused to form a tube around the stilleto-like hypopharynx that injects saliva	predators; some visit flowers and feed on nectar, but they also prey on other insect visitors	(predators in soil or rotting wood) *Mallophora* (ectoparasitoid of scarabaeid larvae) *Hyperechia* (ectoparasitoid of xylocopid larvae?)
Asteiidae	short & fleshy	sap flows; 'nectar' of fungi: not recorded at flowers	(saprophages in fungi and plants)
Athericidae	short	honeydew, blood of vertebrates (*Suragina*)	(aquatic predators)

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Aulacigastridae	short & fleshy	?	(terrestrial saprophages)
Axymyiidae	vestigial	?	(rotting wood)
Bibionidae	short; occasionally elongate	frequent flower visitors; some spp. feed on 'nectar' of fungi	(terrestrial saprophages)
Blephariceridae	short; mandibles usually present in females	predatory (females); ?flowers (males)	(aquatic phytophages)
Bombyliidae	occasionally vestigial (e.g. *Oestanthrax*); short & fleshy (e.g. *Thyridanthrax*, *Villa*); long (e.g. *Geron*); very long (e.g. *Anastoechus*, *Bombylius*, *Heterostylum*, *Oligodranes*, *Systoechus*)	most are obligate flower-feeders, taking both nectar and pollen; pollen probably important only in some species (Toft, 1983, 1984b, Deyrup, 1988); honeydew feeding also reported. Some spp. important pollinators	vast majority are parasitoids, several genera are predatory in grasshopper egg pods *Acropthalmyda* (parasitoids of Tiphiidae) *Anthrax* (ectoparasitoids of solitary aculeates; also records from ant-lions and tiger beetles; others predatory in grasshopper egg pods) *Bombylius* (ectoparasitoids of solitary aculeates) *Exhyalanthrax* (most parasitoids in dipteran puparia, also recorded from Ichneumonidae and their hosts, one species predatory in cockroach egg mass) *Geron* ([endo?]parasitoids of Lepidoptera, also pseudohyperparasitoids) *Hemipenthes* (parasitoids in dipteran puparia; recorded from cocoons of Ichneumonoidea and their hosts) *Phthiria* (endoparasitoids in Lepidoptera) *Spongostylum* (ectoparasitoids of solitary aculeates, in cocoon of pyralid moth and its braconid parasitoid, some spp. associated with grasshopper egg pods) *Systropus* (endoparasitoids of limacodid Lepidoptera) *Thyridanthrax* (some parasitoids of sphecid wasps, most others predatory in grasshopper egg pods) *Toxophora* (ectoparasitoids in nests of solitary aculeates) *Usia* (ectoparasitoids on pupal tenebrionid beetles) *Villa* (endoparasitoids of Lepidoptera, Coleoptera, tabanid flies)
Braulidae	short & fleshy	liquid from bee mouthparts	(pollen in bee nests)

[*continued*]

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Calliphoridae	moderate & fleshy	some genera are regular visitors to flowers; *Pollennia rudis* and *Lucilia caesar* feed on juices exuding from ripe fruit and on 'nectar' of fungi	(saprophages, carnivores) Ameniinae, Melanominae and *Pericallimyia* (endoparasitoids in snails) e.g. *Angioneura*, *Eggisops*, *Melinda*, *Opelousia Belardia* (endoparasitoids in earthworms) some *Calliphora* (endoparasitoids in earthworms) *Lucilia bufornivora* (endoparasitoid in toads, frogs) *Onesia* (endoparasitoid in earthworms) Polleniini e.g. *Pollenia* (endoparasitoid in earthworms) *Protocalliphora* (blood-feeding on birds) *Stomorhina* (predator of locust egg pods)
Camillidae	short & fleshy	not recorded at flowers	(mouse nests)
Canacidae	short & fleshy	?	(marine saprophages)
Carnidae	prementum large and bulbous; labella short and inconspicuous	blood-sucking on birds (*Carnus*); *Meonura* at flowers	(coprophages in bird nests)
Cecidomyiidae	short except in *Farquharsonia* which steals regurgitated liquid food from worker ants practising trophallaxis	recorded at flowers	(terrestrial mycophages; phytophages, predators) *Endopsylla* (endoparasitoids of psyllids and tingids) *Endaphis* and others (endoparasitoids of aphids)
Celyphidae	?	?	(saprophages of plant decay)
Ceratopogonidae	moderate; blade-like mandibles; proboscis weak in males	vertebrate or insect blood (female); several spp. predators on swarming Nematocera; several spp. known to take floral nectar, and one sp. removes contents of pollen grains	(terrestrial saprophages, predators)
Chamaemyiidae	short & fleshy	?	(predators of Homoptera)
Chaoboridae	short & fleshy; sclerotized mandibles	?	(aquatic predators)
Chironomidae	reduced; long labrum in some spp.	non-feeding (most); nectar, honeydew; one spp. feeds on 'nectar' of fungi, can be important pollinators in tundra	([semi]-aquatic saprophages) *Tendipes* (one species an ectoparasitoid, another an endoparasitoid, of molluscs) *Simbiocladius* (ectoparasite on larval mayflies) *Demeijerea* (in sponges; ?parasitic) *Xenochironomus* (in sponges; ?parasitic)

Table 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Chloropidae	short & fleshy; long (*Olcella*, *Siphonella*)	some recorded at flowers taking nectar; some feed on 'nectar' of fungi	(phytophages, saprophages, several genera predators in spider egg cases and mantid oothecae, one genus predatory on aphids) *Batrachomyia* (under skin of frog) *Conioscinella* (spider egg cases, beetles, Lepidoptera) *Fiebrigella* (predator in acridid egg pods) *Oscinisoma* (endoparasitoid in eggs) *Polyodaspis* (endoparasitoid in larval Tortricidae) *Thaumatomyia* spp. predators on root aphids
Chyromyidae	short & fleshy	*Aphaniosoma* may be an obligate flower feeder	(?saprophages in bird nests, mouse nests, bat guano)
Clusiidae	short & fleshy	nectar, sap, rotting material	(rotting wood saprophages)
Coelopidae	short & fleshy	liquid from seaweed	(saprophages on seaweed decay)
Conopidae	geniculate, short (*Myopa*); long (*Conops*, *Physocephala*, *Zodion*); very long (*Stylogaster*)	obligate flower-feeders, taking nectar only	all endoparasitoids in bees, cockroaches, calyptrate flies *Conops* (bumblebees, solitary bees) *Dalmannia* (bees) *Leopoldius* (social wasps) *Myopa* (solitary and social bees, wasps) *Physocephala* (bumblebees, honeybee) *Physoconops* (bees) *Sicus* (bumblebees) *Stylogasterinae* (eg *Stylogaster*) (cockroaches, calyptrate and acalyptrate flies, spiders) *Thecophora* (solitary bees) *Zodion* (solitary bees, honeybee)
Cryptochaetidae	short & fleshy	honeydew	all endoparasitoids in Coccoidea *Cryptochaetum* (monophlebine coccids)
Culicidae	long and slender, stylet-like; mandibles present	blood (female); nectar (male, in some spp. the female)	(aquatic saprophages or predatory) *Toxorhynchites* (prey on larvae of other mosquitoes)
Curtonotidae	'well developed'	?	(?saprophages)
Cuterebridae	short or moderate	?	most on rodents *Cuterebra* *Dermatobia* (humans)
Cypselosomatidae	short & fleshy	?	(terrestrial saprophages)
Deuterophlebiidae	absent	non-feeding	(aquatic)
Diastatidae	short & fleshy	not recorded at flowers	(?)
Diopsidae	short & fleshy	plant exudates, liquids of decay, faeces	(phytophages, saprophages)
Dixidae	small & fleshy; non-functional mandibles	?non-feeding	(aquatic)

[*continued*]

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Dolichopodidae	short & fleshy with 6 + pseudotracheae; complex epipharyngeal armature	predators, occasionally recorded at flowers	(predators)
Drosophilidae	short & fleshy	most spp. rarely recorded at flowers, at least one sp. feeds on 'nectar' of fungi, female and male *Drosophila favohirta* feed on contents of pollen grains	(saprophages, phytophages) *Cacoxenus* (nest commensal of solitary bees) *Leucophenga* (commensal of cercopid spittle masses) *Cladochaeta* (possibly ectoparastoids of cercopids) *Zygothrica* (predator of frog egg masses)
Dryomyzidae	short & fleshy	liquids of decay	saprophages
Eginiidae	?	?	*Eginia* (millipedes)
Empididae	short; some elongated (e.g. *Empis*)	predators; nectar, occasionally pollen	([semi-]aquatic predators) endo- and ectoparasitoids of immature Trichoptera
Ephydridae	short & fleshy; some large with bulbous prementum	algae, bacteria, 'nectar' of fungi	(aquatic saprophages, some leaf miners) *Actocetor* (decaying locust egg pods, ?saprophage) *Trimerina* (predator in spider egg cases)
Fanniidae	short and fleshy	?	(saprophages, predators)
Fergusonidae	?	?	(phytophages)
Gasterophilidae	short and fleshy?	?	(endoparasitoids in mammals)
Glossinidae	long	blood-feeding (male and female)	(internal nourishment by female)
Helcomyzidae	short and fleshy?	?	(saprophages of seaweed decay)
Heleomyzidae	short and fleshy	not recorded at flowers, some spp. feed on 'nectar' of fungi	(saprophages)
Helosciomyzidae	?	?	(saprophages)
Hilarimorphidae	short; large prementum	recorded on *Salix*	?
Hippoboscidae	short; modified labium and labella	blood-feeding on birds and mammals	(internal nourishment by female)
Hybotidae	short	predators	(?same as non-parasitoid Empididae)
Ironomyiidae	?	?	(saprophages of plant decay)
Lauxaniidae	short & fleshy; modified labellar surface in some species for feeding on fungi	most not recorded at flowers, one sp. recorded feeding on juice exuded from ripe fruit; most forest-dwelling species consume fungal hyphae and spores	(saprophages in plant decay)
Lonchaeidae	short & fleshy	one sp. recorded feeding on 'nectar' of fungi	(saprophages in plant decay)
Lonchopteridae	short	occasionally recorded at flowers taking nectar; crop contents only nectar or honeydew	(mycophages)

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Megamerinidae	?	?	(under bark)
Mesembrinellidae	?	?	(unknown)
Micropezidae	short & fleshy	at least one sp. feeds on 'nectar' of fungi	(terrestrial saprophages)
Milichiidae	slender, short; elongate (*Aldrichiomyza*, *Eusiphona*)	often recorded at flowers	(?saprophages, many spp. develop in ants' nests)
Mormotomyiidae	?	?	(saprophages in bat dung)
Muscidae	moderate & fleshy; sometimes long & thin (Stomoxyinae)	very commonly at flowers, some obligate flower-feeders, some feed on 'nectar' of fungi, at least one species feeds on juices exuding from ripe fruit	(saprophages, phytophages, facultative predators, ectoparasites)
Mycetophilidae	usually short & fleshy. very long in some (eg *Antlemon*, *Asindulum*, *Gnoriste*, *Lygistorrhina*, *Macrorrhyncha*)	honeydew, 'nectar' of fungi; Keroplatinae often at flowers, including spp. with long proboscis	(mycetophages, predators) *Keroplastes* (predatory) *Planivora insignis* (endoparasitoid of flatworms)
Mydidae	short & fleshy; some atrophied, some elongated (*Raphiomydas*, *Neoraphiomydas*)	most are obligate flower-feeders	(soil predators)
Mystacinobiidae	?	?	(saprophages in bat dung)
Nemestrinidae	vestigial (*Trichopsidea*); short & fleshy (*Hirmoneura*); very long (*Neorhynchocephalus*)	most are obligate flower-feeders; nectar taken by long-tongued species, some of which are important pollinators	(predators) endoparasitoids, in beetle larvae/pupae e.g. *Hirmoneura*, *Trichopsidea* *Neorhynchocephalus* (predator in acridid egg pods)
Neriidae	short & fleshy	?	(?saprophages in plants, sap)
Neurochaetidae	?	?	(?saprophages)
Nycteribiidae	short, with modified prementum and labella	blood-feeding on bats	(internal nourishment by female)
Nymphomyiidae	vestigial	?	(aquatic feeders on algae, one sp. ectoparasitic on insect larvae)
Odiniidae	short & fleshy	sap flows, not recorded at flowers	(saprophages in insect galleries in wood) *Turanodinia* (egg masses of coccid)
Oestridae	small, vestigial or absent	non-feeding	all parasitic in mammals *Cephenomyia* (deer nostrils) *Gedoelstia* (antelope) *Hypoderma* (cattle, horses, deer) *Oedemagena* (reindeer) *Oestrus* (sheep & goat nostrils) *Pharyngomyia* (deer nostrils)
Opomyzidae	short & fleshy	?	(phytophages in grass stems)
Otitidae	short & fleshy	one sp. recorded feeding on 'nectar' of fungi	(saprophages, some phytophages)

[*continued*]

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Pachyneuridae	short	?	(rotting wood)
Pallopteridae	short & fleshy	recorded at flowers taking nectar	(terrestrial predators)
Pelcorhynchidae	short; broad labella; some with reduced mandibles	some spp. feed from flowers	(wet soil)
Perscelididae	short & fleshy	sap flows: not recorded from flowers	(sap flows)
Phaeomyiidae	short & fleshy	?	(saprophages) endoparasitoids in millipedes
Phoridae	usually short & fleshy; sometimes moderately long & sclerotized (*Crinophleba*, *Dohrniphora*, *Rhynocophoromyia*) females of some *Phalacrotophora*, spp. and some *Megaselia* spp. have enlarged labrum and narrow, teeth-bearing labella associated with feeding on host blood frequently sexually dimorphic	all probably taking nectar; at least one sp. feeds on 'nectar' of fungi, pollen has never been found in the crop or digestive system of any phorid: some parasitoid spp. consume host blood *Anevrina* *Beckerina* *Borophaga* *Chonocephalus* **Conicera* *Dohrniphora* **Diplonevra* *Gymnoptera* **Megaselia* *Melaloncha* **Metopina* **Phora* *Puliciphora* *Spiniphora* **Triphleba* * = commonly recorded at many flowers	(saprophages, phytophages, mycophages, predators) endoparasitoids: *Acanthophoroides* (ants) *Aenigmatias* (ants) *Apodicrania* (ants) *Apocephalus* (spiders, beetles, bees, ants) *Auxanommatidia* (ants) *Borophaga* (flies) *Cremersia* (ants) *Dacnophora* (ants) *Dicranopteran* (termites) *Diocophora* (ants) *Diplonevra* (earthworms, termites) *Iridophora* (ants) *Macrocerides* (ants) *Megaselia* spp. (molluscs & their eggs, spiders, diplopods, cockroaches, beetles, flies, Homoptera, ants, Lepidoptera) *Melaloncha* (bees) *Menozziola* (ants) *Microselia* (ants) *Misotermes* (termites) *Myrmosicarius* (ants) *Neodohrniphora* (ants) *Palpiclavina* (termites) *Phalactrotophora* (spiders, beetles, bees) *Plastophorides* (ants) *Pradea* (ants) *Prociniella* (ants) *Pseudacteon* (ants) *Puliciphora* (cockroaches, ants, termites) *Rhyncophoromyia* (ants) *Stenoneurellys* (ants) *Synneura* (Homoptera) *Trucidophora* (ants)
Phlebotomidae	short	normally nocturnal; females feed on both blood and honeydew, and their males also feed on honeydew, but floral nectar appears to be taken in some cases	(terrestrial saprophages)

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Piophilidae	short & fleshy	not recorded at flowers	(saprophages) *Neottiophilum* (blood-feeding on birds)
Pipunculidae	short & fleshy	honeydew, occasionally recorded at flowers taking nectar	all endoparasitoids in Homoptera Auchenorrhyncha
Platypezidae	short & fleshy	honeydew, recorded from flowers	(mycophages)
Platystomatidae	short & fleshy	dung; one sp. recorded feeding on 'nectar' of fungi	(?phytophages)
Pseudopomyzidae	?	?	(under bark)
Psilidae	short & fleshy	occasionally at flowers	(phytophages)
Psychodidae	short	normally nocturnal, recorded at flowers	(terrestrial saprophages)
Ptychopteridae	?	?	(aquatic)
Pyrgotidae	short & fleshy	fly at night	all endoparasitoids in adult scarabaeids
Rhagionidae	short & fleshy	blood (some); rarely at flowers	(?predators in wet soil)
Rhinophoridae	short & fleshy	*Rhinophora lepida* observed feeding on flowers of Asteraceae	all in woodlice
Rhinotoridae	elongate with very small labella	sap flows, rotting fruit	(?saprophages, in beetle galleries)
Richardiidae	short & fleshy	recorded at flowers	(phytophages)
Risidae	?short	?	?
Ropalomeridae	short & fleshy	?	(?tree sap)
Sarcophagidae	short & fleshy	only occasionally visit flowers, obtain sugars normally from honeydew, but some spp. feed on 'nectar' of fungi	(saprophages, facultative predators) Miltogrammini (provision-directed cleptoparasitoid of ground-nesting Hymenoptera Aculeata) *Dolichotachina* (predator of locust egg pods) *Hilarella* (endoparasitoid in adult Orthoptera) *Noditermitomyia* (endoparasitoids of termites) *Taxigramma* (endoparasitoid of adult acridids) Agriinae + Sarcophaginae (endoparasitoids in snails, adult Orthoptera, except: *Agria*, *Arachnidomyia* (Lepidoptera)

[*continued*]

TABLE 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
			Brachicoma (cleptoparasitoid of Hymenoptera) *Colcondamyia* (endoparasitoid of cicadas) *Doringia* (endoparasitoids of beetles, cicadas, mantids) *Nyctia* (endoparasitoids of weevils) Macronychiinae e.g. *Macronychia* (endoparasitoids in wasp and bee nests; adult Tabanidae)
Scathophagidae	moderate; small labella with strong prestomal teeth	commonly at flowers taking nectar and pollen: *Scathophaga stercoraria* also feeds on 'nectar' of fungi	(phytophages, saprophages in dung)
Scatopsidae	reduced; Ectaetiinae with large labella and single pseudotrachea	frequent flower visitors	(terrestrial saprophages)
Scenopinidae	short, retractile	not recorded at flowers	(predators in rotting wood and other substrates containing beetle larvae)
Sciadioceridae	?	?	(saprophages in carrion)
Sciaridae	short; very long in some (eg *Eugnoriste*)	some commonly on flowers, esp. Umbelliferae; at least one sp. feeds on 'nectar' of fungi	(terrestrial saprophages, often associated with fungi)
Sciomyzidae	short & fleshy	not recorded at flowers	(predators) endoparasitoids of snails and slugs *Antichaeta* (snail eggs)
Sepsidae	short & fleshy	fluids of decay, esp. dung 'nectar' of fungi; some recorded at flowers taking nectar, esp. *Sepsis*	(saprophages in dung)
Simuliidae	short; blade-like mandibles; proboscis weak in males	blood (females); nectar (males and females)	(aquatic saprophages)
Sphaeroceridae	short & fleshy	liquids of dung/decay; rarely at flowers	(saprophages, some carrion-feeders, some mycetophages)
Stratiomyiidae	usually short & fleshy; vestigial in some; very long (*Nemotelus*)	often at flowers, esp. Umbelliferae	(aquatic/terrestrial predators, saprophages, phytophages)
Streblidae	short; labium bulbous with needle-like tip; labella tiny	blood-feeding on bats	(internal nourishment by female)
Strongylophthalmyiidae	short & fleshy	?	(under bark)
Synneuridae	reduced; labella with single pseudotrachea	?	(rotting wood)
Syrphidae	short & fleshy; long (e.g. *Volucella*); very long (e.g. *Lycastris*, *Rhingia*)	obligate flower-feeders, although some spp. feed on 'nectar' of fungi	(saprophages, phytophages, mycophages, predators) *Volucella inanis* (ectoparasitoid of social wasp larvae)
Tabanidae	stout mandibles present; very long in some (eg *Esenbeckia*, *Pangonia*)	blood (females), nectar (males and females), honeydew (mostly males)	(predators in wet soil)

Table 2. *Continued*

Family	Proboscis structure	Adult feeding	Larval feeding habit
Tachinidae	very small (e.g. *Anthomyiopsis*); short (e.g. *Ametadoria*); moderate (e.g. *Estheria*, *Peleteria*, *Tachina*); very long (e.g. *Adejeania*, *Beskia*, *Clausicella*, *Crocinosoma*, *Epigrimyia*, *Eucoronimyia*, *Imitomyia*, *Prosenoides*, *Siphona*, *Trochilodes*)	mainly honeydew; long-tongued spp. tend to be obligate flower-feeders, taking nectar; some spp. feed on 'nectar' of fungi; *Eucelatoria bryani* consumes host blood from oviposition punctures	all endoparasitoids Dexiinae (e.g. *Dexia*, *Trixa*, larval beetles) Dufouriini (adult beetles) Voriini (Lepidoptera) Exoristinae (larval Lepidoptera, Coleoptera) Goniini (e.g. *Gonia*, *Zenillia*: larval Lepidoptera, sawflies) *Trichopareia* (larval Diptera) *Ocytata* (earwigs) Phasiinae (e.g. *Gymnosoma*, *Alophora*: Heteroptera) Tachininae (larval Lepidoptera, Coleoptera) *Eloceria* (centipedes) *Exoristoides* (centipedes) *Hyalurgus* (sawflies) *Loewia* (centipedes) *Lypha* (spiders) *Siphona* (larval Diptera) *Triarthria* (earwigs)
Tachiniscidae	?	?	(?parasitoids, one sp. reared from thyridid gall)
Tanyderidae	short, long palpi	?	(aquatic/soil saprophages
Tanypezidae	short & fleshy	?on flowers	(?saprophages)
Tephritidae	short & fleshy; sometimes long & reflexed (*Dioxyna*)	occasionally recorded at flowers taking nectar; some feed on honeydew, fruit juices, plant leachates, leaf surface bacteria and possibly bird droppings	(phytophages, including gallers)
Teratomyzidae	short	?	(feed on microflora on fern fronds)
Tethinidae	short & fleshy to moderate	?	(?saprophages)
Thaumaleidae	short	?non-feeding	(semi-aquatic phytophages)
Therevidae	small, retracted	nectar; honeydew (some spp.)	(soil predators)
Tipulidae	short (Limoniinae) or moderate (Tipulinae)	occasionally recorded taking nectar at flowers	(aquatic/soil phytophages and saprophages)
Trichoceridae	reduced	not recorded at flowers	(terrestrial saprophages)
Trixoscelididae	short & fleshy	often recorded at flowers	(?)
Vermileonidae	short & fleshy; some very long with tiny labella (*Lampromyia*)	obligate flower-visitors	(predators making pitfall traps)
Xylomyidae	large & fleshy	not recorded at flowers	(under bark)
Xylophagidae	short & fleshy	not recorded at flowers	(?predators in rotting wood)

the proboscis is elongate in the majority of the Geronini, Systropodini, Bombyliinae (except *Conophorus*), Usiiniae and Eclimini. The broad fleshy labella of short mouthparts have 5–30 pseudotracheae each, but the narrow labella of elongate mouthparts have fewer: 3 in *Bombylius major*; 2 in *Cytherea*; 1 in *Geron*, *Heterostylum*, *Sericosoma*, *Corsomyza* and *Oniromyia* (information from Yeates [1994]).

The distribution of proboscis lengths among adult bombyliids is highly left-skewed (Zaitsev, 1984) and is probably log-normally distributed, with many more short-tongued than long-tongued species. The plesiomorphic state is almost certainly a short proboscis with broad, fleshy labella containing 10–20 pseudotracheae (Yeates, 1994). Yeats (1994) suggests that elongated mouthparts (i.e. CNEA) are an adaptation to feeding while hovering. The spinose edges to the pseudotracheal canals of 'long-tongued' bombyliids are considered by Zaitsev (1982) to be filters of nectar, preventing the entry of particulate matter. The available phylogenetic schemes (Mühlenberg, 1971; Yeates, 1994; the latter based partly on mouthpart characters) suggest that changes in the length of the mouthparts probably occurred only rarely in the evolution of the family, i.e. mouthpart length is not evolutionarily labile. Keys to genera often use mouthpart length as a major component (e.g. Zaitsev, 1988). If Mühlenberg's (1971) phylogenetic scheme (Fig. 6) is correct, mouthpart length may have changed essentially only once. Yeates' (1994) cladogram suggests more changes, but still very few. There seems to be no association between adult mouthpart structure and larval habit.

DISCUSSION

In adult parasitoid insects, mouthpart specialization for feeding has involved one of the following:

(A) Development of devices for facilitating nuptial feeding during courtship and copulation: (a) in males for facilitating conveyance of a nuptial food gift (nectar, honeydew, regurgitated in some species) to the female (maxillae and/or labium with long, recurved setae); (b) in females for facilitating receipt and consumption of such a gift (reduction in components of labiomaxillary complex) (thynnine tiphiid wasps) (discussed in the companion paper);

(B) Development of very broad labella with a large number of pseudotracheae and food furrows for solidified honeydew feeding (various fly families);

(C) Additional development (assuming our prediction is correct) of a system of pollen grain ingestion conduits (multiple food furrows) for pollen feeding (various fly families);

(D) Elongation of the maxillary palps and the development of curved hairs on both these and the labial palps, for pollen feeding (scoliid and mutillid wasps) (discussed in the companion paper);

(E) Elongation of certain mouthparts in both wasps and flies (accompanied by elongation of the labella in many flies), enabling exploitation of floral nectar in long, narrow, tubular corollas into which the insects potentially can neither enter bodily nor place their heads (i.e. CNEA) (some ichneumonid, braconid, leucospid, chrysidid and pompilid wasps [see companion paper], various parasitoid fly families);

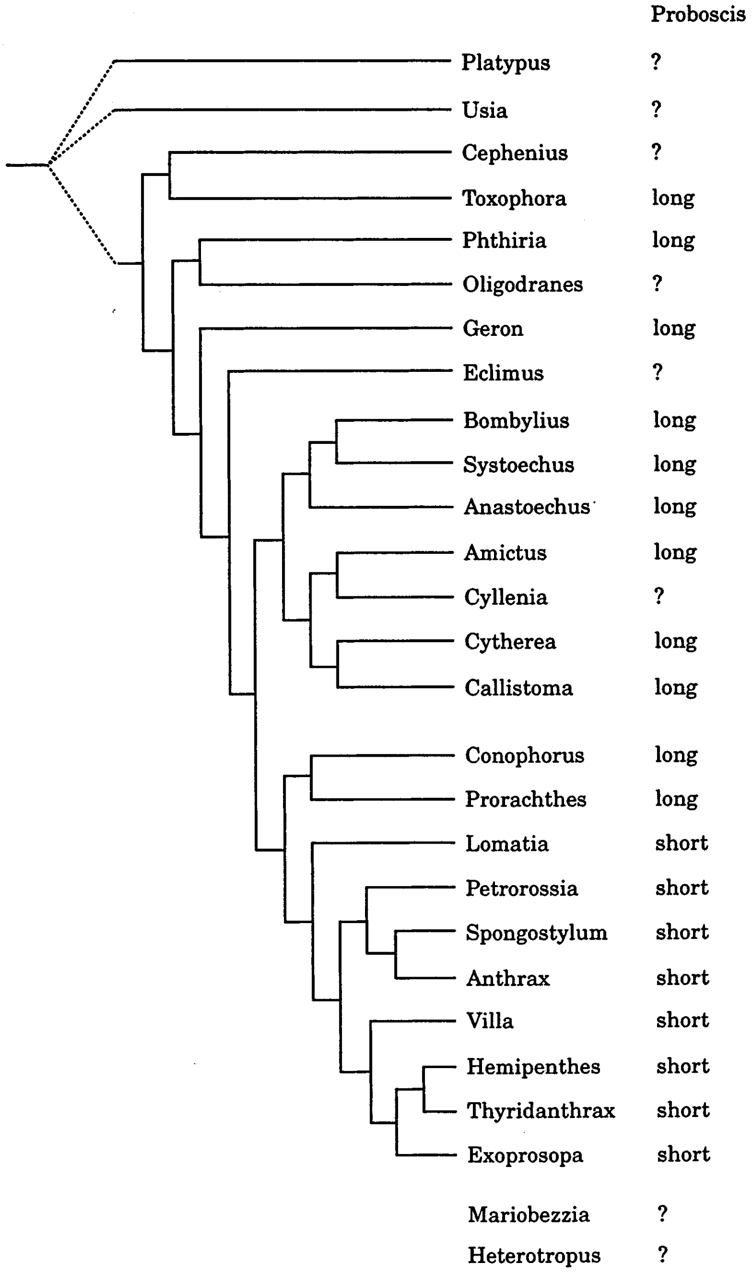

Figure 6. Mühlenberg's (1971) phylogeny of Bombyliidae.

(F) Enlargement of the labrum, the narrowing of the labella (and, in some species, the development of teeth on their inner faces), and the heavier sclerotization of the tip of the hypopharynx, for feeding on host blood (females of a few phorid flies).

One obvious consideration when attempting to explain the functional significance of mouthpart structure in parasitoids with respect to feeding is the potential nutritional value of foods. The results of analyses of the biochemical composition of the different major food types are not easily comparable. However, a broad generalization based on biochemical information in the literature (Barbier, 1970; Wigglesworth, 1972; Stanley & Linskens, 1974; Maurizio 1975; Faegri & van der Pijl, 1979; Baker & Baker, 1983; Woodring, 1985; Harborne, 1988; Dafni, 1992), is that the rank order (weight/weight or weight/volume), in terms of proteinaceous material content is, among the major food types: pollen ≥ host blood>honeydew>nectar. The rank order of foods in terms of carbohydrate content is: honeydew>nectar ≥ pollen>host blood. With the exception of some pollens (Dafni, 1992), the foods of parasitoids are lipid-poor. Host blood is superior to all other foods with respect to its essential vitamin and salt content (Jervis & Kidd, 1986; Heimpel & Collier, 1996).

The type of food females consume, and thus any mouthpart specialization shown, will depend on the following parasitoid-related factors:

(1) The species-characteristic potential lifetime pattern of ovigenesis. Flanders (1950) distinguished between pro-ovigeny and synovigeny in parasitoids (note that Flanders' concept of ovigeny is in need of revision [Heimpel, Rosenheim & Kattari, 1997a; Jervis *et al.*, in prep.] but that for present purposes we adhere to it). Pro-ovigenic parasitoids emerge with their full or very nearly full lifetime complement of mature eggs, so require no or few materials for egg production (Flanders, 1950). Females tend to be short-lived (Flanders, 1950), but any longer lived species are likely to require food to fuel their maintenance and locomotory metabolic requirements (Jervis *et al.*, 1993, 1996b). Synovigenic parasitoids, which form the vast majority of parasitoid wasps and flies (Jervis *et al.*, in prep.), mature eggs during adult life and tend to be long-lived (Flanders, 1950), so they need to feed to fuel both egg production and maintenance (Jervis & Kidd, 1986; Jervis *et al.*, 1996b).

Whether a species is pro-ovigenic or synovigenic, and in the case of synovigenic species, the proportion of oocytes that are mature upon female eclosion, will depend both on the extent of 'carry-over' of resources from the last larval instar to the imago (see [2] below and Boggs [1997a,b] on Lepidoptera) and on the pupal development time and its concomitant metabolic costs.

Among synovigenic parasitoids there is considerable interspecific variation in potential lifetime fecundity (Flanders, 1950; Jervis & Kidd, 1986); all else being equal (e.g. life span, egg yolk content) the higher the potential lifetime fecundity, the higher will be the external nutrient demand (more or richer food needed) for fuelling ovigenesis.

The external nutrient demand for fuelling ovigenesis in synovigenic parasitoids will also depend on the female's age. For example, the females of some host feeding parasitoid wasps spend the first few days of adult life feeding on sugar-rich materials, not on blood (Leius, 1960, 1961a,b), suggesting that the rate of ovigenesis is quite low for the first few days of life.

In some synovigenic parasitoids the rate of ovigenesis varies significantly with host availability. At higher levels of host availability females increase the rate of egg maturation during the earlier phase of adult life, so shifting their 'fecundity schedule'; lifetime realized fecundity is also higher (Mackauer, 1983; Sahragard, Jervis & Kidd, 1991; Jervis & Copland, 1996). The nature of any required change in feeding activity and/or diet will depend on the trade-off between the increased external nutrient demand for ovigenesis and the reduced demand for locomotion (see [4] below).

For discussion of the effects of diet quality on ovigenesis and fecundity, see below.

(2) The amount of fat body reserves present: the quantity of reserves acquired by the female either as a larva (i.e. 'carried-over') or as an imago (i.e. through feeding) (*vide* Lepidoptera [Boggs, 1997a,b]) [Note that the work of Ellers (1996) suggests that some parasitoid wasps cannot allocate to fat body storage nutrients acquired by feeding during adult life: radiotracer studies (see Boggs, 1997a,b) would be needed to verify this]. The quantity of fat body reserves in parasitoids declines with female age (when food is either present or absent, see Ellers [1996]), as reserves are metabolized.

As a point of information, at least three parasitoid families, the Acroceridae, Bombyliidae and Nemestrinidae, include members whose mouthparts are described as 'vestigial' (Schlinger, 1981; Hall, 1981; Teskey, 1981). It would be interesting to know whether such mouthparts allow feeding. If they do not, then 'carry-over' of larval resources must be adequate for all metabolic needs.

(3) Whether the eggs are yolk-rich ('anhydropic' or 'lecithal') or yolk-deficient ('hydropic' or 'alecithal'), and whether (if they are yolk-rich) the yolk contains or lacks protein inclusions (see Le Ralec [1995]). The work of Le Ralec (1995) suggests that parasitoids host feed in order to produce protein bodies in their otherwise lipid-rich egg yolk, although it is likely that proteinaceous materials in host blood are also converted to egg yolk lipids (Heimpel & Collier, 1996). A diet of host blood alone is sufficient for the egg production needs of some host feeding species, while other species need to feed also on sugar-rich foods to achieve maximal fecundity (Heimpel *et al.*, 1997a) (discussed further below).

It appears that in some non-host feeding parasitoid wasps the egg yolk lacks protein inclusions (Le Ralec, 1995), so the carbohydrate or the lipid content of food in these species is presumably of greatest significance so far as egg formation is concerned. Because most of the foods of parasitoids are lipid-poor, yolk lipids would have to be formed, via the tricarboxylic acid cycle, from carbohydrates in the diet.

So far as is known, egg yolk composition has not been studied in parasitoid flies. In non-parasitoid Diptera, both carbohydrates and proteinaceous materials are known to be required for ovigenesis (feeders on vertebrate blood being excepted), although in *Delia radicum* the latter are not required for production of the initial complement of eggs (Finch & Coaker, 1969; Finch, 1971).

(4) Host availability (via locomotory metabolic costs) (Kidd & Jervis, 1989); with both pro-ovigenic and synovigenic parasitoids the locomotory metabolic requirement will be higher if hosts are scarcer (Jervis *et al.*, 1996b).

(5) Factors that determine the profitability of food patches: (a) the average quantity of food available per patch, (b) the metabolic and time costs of travelling between host and food patches (see Kidd & Jervis [1989], Jervis *et al.* [1996b], Sirot & Bernstein [1996] and Jervis & Kidd [1998]), (c) the metabolic and time costs of removing the food.

(6) The parasitoid's maintenance metabolism (survival) requirements. Nectar, honeydew and pollen feeding can easily satisfy these requirements. The conventional wisdom has, until recently, been that host blood is a valuable source of nutrients for egg production only (Jervis & Kidd, 1986). For some host feeding parasitoids, however, host blood is also a valuable source of nutrients for maintenance metabolism (Heimpel & Collier, 1996; Heimpel *et al.*, 1997a). For further discussion of the effects of diet quality on survival, see below.

(7) The mode of locomotion in host-searching behaviour and the fuel used. In animals generally, running is energetically more costly, per unit distance travelled, than forward flight (Tucker, 1969; Schmidt-Nielsen, 1972), while walking as practised by many parasitoids during host location ought to be cheaper than other locomotory activities. Contrary to the traditional view (e.g. Casey, May & Morgan, 1985; Gaugler & Schutz, 1989), the metabolic rate in hovering flight (which does not constitute locomotion *per se*, but is practised by some parasitoids in host searching) has been found to be little different from that in forward flight (Ellington, 1991; Ellington, Machin & Casey, 1990). The substrate for flight in insects can be carbohydrate (glucose, trehalose, glycogen), lipid or amino acid (proline); of these, glucose, trehalose and proline are the substrates most likely to be obtained directly from the food, the latter two being obtainable from host blood in significant quantities.

(8) Morphological constraints. Parasitoids lacking the appropriate specialization (these include species with *unspecialized* mouthparts) may be unable to exploit certain food types. Smaller-bodied parasitoids lacking CNEA may be able to gain access, either bodily or by placing their head into the corolla, to nectar that is 'concealed' for larger-bodied parasitoids that lack CNEA (Jervis *et al.*, 1993; Patt, Hamilton & Lashomb, 1997). However, they are more likely to be prevented, by the stamens and petals, from exploiting exposed floral nectar (Patt *et al.*, 1997). Body size also has energetic consequences: larger-bodied parasitoids will have a larger absolute metabolic requirement than smaller parasitoids.

(9) Finally (obviously!), whether a particular food type is available to the parasitoid in its habitat.

The food *males* consume, and thus any mouthpart specialization shown, will depend on:

(1) Whether there has been sufficient resource 'carry-over' from last instar larva to adult for spermatogenesis to commence and for accessory gland maturation to be completed.

(2) The species' mating system (via metabolic and time costs, see factors [5], [6] and [7] for females). Given that in many parasitoids males are able to mate immediately (Godfray, 1994; van den Assem, 1996), they are, in general, unlikely to need food for reproduction. If they do require food, it ought to be mainly for fuelling motor activities, i.e. travelling to calling females, searching for female oviposition sites, searching for female feeding sites, maintaining a territory, participating in a lek (see Toft's [1984a, 1989a,b] Bombyliidae), and thus be highly

energy-providing. Yuval, Hollidayhanson & Washino (1994) showed that for male mosquitoes aerial swarming consumes over 502 of available calories, irrespective of body size.

(3) Parasitoid morphology (see factor [8] above, for females).

(4) Food availability (see factor [9] above, for females).

There have been numerous laboratory investigations into the effects of food availability and quality upon fecundity and longevity in parasitoids (reviewed by Jervis & Kidd [1986], van Lenteren *et al.* [1987] and Heimpel & Collier [1996]; see also Bleicher & Parra [1991], Hagley & Barber [1992], Idris & Grafius [1995]; Leatemia, Laing & Corrigan [1995], Olson & Nechols [1995], Dyer & Landis [1996], Morales-Ramos *et al.* [1996] and Heimpel *et al.* [1997a]). In many cases comparisons have been made of the effects of different food types, but few studies have involved measurement of the effects of food type on lifetime reproductive success *per se* (but see Heimpel *et al.* [1997a]), and even fewer have done so in anything closely approaching a realistic ecological setting.

Females given sugar-rich foods, either natural or artificial, have generally been found to be more fecund and longer-lived than those deprived of foods altogether (i.e. starved, usually given access to water); fecundity and life span are similarly improved by provision of sugar-rich foods in some host feeding species both when they are allowed to host feed (see below) and when they are prevented from doing so. Consumption of sugar-rich foods can also delay the onset of and decrease the rate of egg resorption in female host feeding parasitoids deprived of hosts (Heimpel *et al.*, 1997a). Male parasitoids given sugar-rich food are in general longer-lived than those given only water.

Some host feeding parasitoids are anautogenous, that is, even if they feed on sugar-rich foods, they cannot oviposit unless they have consumed host blood (Jervis & Kidd, 1986). In some *au*togenous host feeding species the females are more fecund when allowed to consume host blood but not sugar-rich foods than when prevented from consuming host blood but allowed to consume sugar-rich foods (Leius, 1961a, b). However, in other species no significant difference is produced between the two regimens (Heimpel *et al.*, 1997a). Life span in some parasitoid species is lower on a blood-only diet than in a sugar-rich food-only diet (Leius, 1961a; Morales-Ramos, Rojas & King, 1996; Heimpel *et al.*, 1997a). Heimpel *et al.* (1997a) showed that in *Aphytis melinus* DeBach host feeding can enhance both fecundity and longevity only if sugar-rich foods are available: there is a strong interaction effect.

Three types of mouthpart specialization (C,D,E) have been developed in relation to feeding on floral materials. In experiments examining the effects of flowers on fitness parameters (e.g. Lim, 1982; Foster & Ruesink, 1984; Hagley & Barber, 1992; Idris & Grafius, 1995) only Idris & Grafius (1995) established precisely which floral materials (pollen, nectar) were fed upon by the experimental parasitoids. Idris & Grafius (1995) showed with *Diadegma insulare* (Cresson) that longevity and fecundity vary significantly with flower species, and provide data which indicate floral morphology (which determines accessibility of the nectar and therefore the quantity of nectar that can be taken) to be an important explanatory variable. Thus, in studies involving floral food sources, it will often be difficult to disentangle the effects of food quality and quantity upon fitness parameters (for discussion of other pitfalls in the general experimental design of dietary studies generally, see Jervis & Kidd [1986] and Heimpel & Collier [1996]).

We now proceed to consider the probable fitness advantages of the different feeding specializations, i.e. what one can *reasonably surmise* concerning the different specializations. We are aware that 'fitness advantage' is not synonymous with relative fitness value e.g. the value, in terms of lifetime reproductive success, of the specialized state compared with that of the unspecialized or other specialized state.

The fitness advantage of specialization (A) in males (devices for nuptial feeding of female during courtship and copulation in thynnine tiphiid wasps) is presumably that a larger sugar-rich food gift can be delivered than would be possible with unspecialized mouthparts. The larger the gift, the greater the fitness gain for both sexes: more food is acquired by the female, so more eggs can be produced, and thus more eggs will be available for eventual fertilization (a male's sperm are stored in the female's spermatheca). The female's receptivity may depend upon the size of the gift, i.e. she may use the quantity of food on offer as a measure of male quality. Also, the larger the gift, the longer copulation may take, and so the less the likelihood of sperm competition occurring, through matings with other males. Alternatively (and more likely), provision of a large food gift simply minimizes the time devoted to each female (i.e. each female needs to be fed only once), so providing the male with more time for mate searching (J. Alcock, pers. comm.).

The fitness advantage of specialization (A) in females (reduction in size of labiomaxillary components in thynnine tiphiid wasps practising regurgitation feeding) is, presumably, that the food gift can be taken more readily and consumed relatively rapidly (by cibarial and pharyngeal pumping) without the involvement of the mouthparts. It is also possible that energy and materials that would otherwise be used for mouthpart construction are re-allocated to enhance some component of fitness such as fecundity.

The fitness advantage of feeding specialization (B) (for solidified honeydew and nectar feeding) is presumably that sugar-rich foods can be efficiently exploited. Honeydew appears to be a particularly 'cheap' food to exploit from an energy budget standpoint. Aphelinid wasps such as *Coccophagus* spp. and *Encarsia formosa* Gahan consume honeydew directly from the anus of their hosts (Cendaña, 1937; Yamamura & Yano, 1988). Compared with longer-distance foraging for most other foods (i.e. host blood excepted), such behaviour; (i) will take up a smaller proportion of foraging time; (ii) will be metabolically very undemanding; and (iii) will carry a relatively small predation risk (although in some cases attendance of the parasitoid's hosts by ants could reverse the differential, see Heimpel, Rosenheim & Mangel [1997b], for discussion of field predation of parasitoids). Although most parasitoids do not attack honeydew-producing hosts, many of those that attack hosts on foliage can rely upon non-host honeydew being available either in the close vicinity of host patches or within the patches themselves. As Downes & Dahlem (1987) have pointed out, entomologists have tended to underestimate just how widespread and abundant honeydew is in many habitats. However, it should be noted that the fecundity and/or life span of parasitoids given certain honeydews are lower than in insects given other sugar-rich foods (Leius, 1961a; Avidov, Balshin & Gerson, 1970; Idoine & Ferro, 1988), and in one study life span was as low as when insects were given no food at all (Avidov *et al.*, 1970). An inhibitory effect of honeydew on longevity and fecundity was also found in host feeding females that had access to hosts (Leius, 1961a). Such effects have been attributed to the occurrence, in honeydew, of oligosaccharides such as melezitose (Zoebelein, 1955; Leius, 1961a; Avidov *et al.*, 1970), which is also found in some floral nectars (Harborne, 1988).

The fitness advantage of specializations (C) and (D) (for consuming pollen) are, presumably, that a food with a high proteinaceous material, and in some cases a high lipid, content can be efficiently exploited (note that in the case of [C] the capacity for efficient consumption of sugar-rich food [honeydew] is retained). Morphological specializations for pollen feeding appear to be uncommon among parasitoids nevertheless. Low digestibility of pollen is unlikely to be the explanation for this, as pollen grains do not have to be ground in order for insects to extract nutrients from them. The evidence that some pollens, like some honeydews, can have an inhibitory effect on fecundity is limited to a few species (of Ichneumonidae [Leius, 1961a,b, 1963]). As far as parasitoid flies are concerned, several species possessing specialization (C) may exist but could easily have been overlooked, given the 'invisible' nature of the specialization. However, several species lacking such a specialization may have developed behaviour for the extraction of nutrients from pollen, in the manner either of *Drosophila flavohirta* or of *Delia radicum* (see 'Feeding on pollen', pp. 503–504). Many parasitoid wasps no doubt inadvertently ingest pollen grains that frequently contaminate nectar, honeydew and dew (which many ichneumonids certainly have a habit of drinking [Townes, 1958, 1972]), but the amount taken, and thus the nutritional gain, is likely to be very small (see companion paper).

The fitness advantage of specialization (E) (i.e. CNEA) is, presumably, that:

(1) Nectar 'concealed' in long, narrow, tubular corollas is usually relatively dilute and therefore of low viscosity (Dafni, 1992; Prys-Jones & Corbet, 1983); consequently, it can be extracted relatively rapidly (Heinrich, 1979). Unlike exposed nectar and honeydew, concealed nectar does not require dilution with saliva before ingestion.

(2) Sources of concealed nectar often offer a much greater volume of nectar than exposed nectar sources, and are usually more sugar-rich in absolute terms (Prys-Jones & Corbet, 1983). It is also generally the case that the deeper the corolla, the more dilute the nectar remains during the day; consequently, the greater the amount of nectar sugar that can be extracted, and in bumblebees (Prys-Jones & Corbet, 1983) the greater will be the net rate of energy return from feeding. The larger water intake that would result may present problems (i.e. osmotic stress and increased metabolic foraging costs; Schmid-Hempel, Kacelnik & Houston [1985]), but very little is known about how an excess of water is managed in nectarivorous insects.

(3) Where external sources of water are limited in supply, parasitoids can obtain significant quantities from 'concealed nectar'. Prys-Jones & Corbet (1983) and Willmer (1983, 1985, 1986) discuss water balance with reference to nectar foraging by bees, and Willmer (1986) showed that the need to maintain an appropriate hygrothermal physiological balance has an important influence upon the food foraging strategy of a xerophilous megachilid bee. It is noteworthy that many parasitoid wasps possessing CNEA, and most Bombyliidae and Nemestrinidae, occur in, and in some cases may be restricted to, arid or semi-arid habitats (e.g. Huddleston & Walker [1988], on *Cardiochiles* of the Sahel region of Africa).

The ability to exploit pollen is probably lost in parasitoid wasps possessing CNEA, as pollen grains are likely to clog up the nectar transport system. The presence of a particulate matter filter on the tips of the galeae of some wasps suggests this (see companion paper). However, the ability to exploit pollen appears not to have been lost in some parasitoid flies possessing CNEA (see Deyrup's [1988] observations on *Poecilognathus punctipennis* and *Geron* sp.). The ability to exploit honeydew and exposed nectar is probably lost in many CNEA-possessing parasitoids in both the Diptera and Hymenoptera; possession of some types of CNEA is also likely to preclude feeding on host blood (see companion paper).

CNEA is a more common feature of parasitoid flies than of parasitoid wasps, occurring in around one quarter of species among the former, compared with at most one thirtieth among the latter (see companion paper). How may we account for the relative rarity of CNEA among parasitoid wasps? Two explanations readily come to mind:

(1) There may be significant differences among parasitoid wasps and flies with respect to locomotory activity, and thus energy expenditure, during host searching and during mating *sensu lato*. Many parasitoid flies carry out sustained flight during both the early and the late stages of the host location or egg deposition site location process, whereas parasitoid wasps tend to fly during only the early stages, if at all, so perhaps searching behaviour in most wasps can be adequately fuelled by foods other than concealed nectar. Mating behaviour generally involves more flight activity in parasitoid flies than in parasitoid wasps; the mating system of many parasitoid wasps involves the males remaining at their emergence site (Godfray, 1994; van den Assem, 1996).

However, whereas Pipunculidae typically fly throughout the host location process, in all members of that family (including those whose homopteran hosts do not produce honeydew) the mouthparts are characteristically short with broad labella and numerous pseudotracheae, i.e. of the typical 'muscoid' type (Hardy, 1987). The same applies to Pyrgotidae whose members typically oviposit whilst in flight (Steyskal, 1987). Both in parasitoid wasps and in non-parasitoid flies such as Syrphidae the possession of short mouthparts does not preclude aerial swarming behaviour. Also, the above argument is based on the as yet untested assumptions that walking is the most common alternative to flying in parasitoids and that it is the least metabolically expensive of all major locomotory activities (running being the most expensive?) for these insects.

(2) In parasitoid wasps CNEA is not always essential for gaining access to concealed nectar:

(a) Many lacking CNEA might be able to exploit otherwise inaccessible nectar by chewing a hole in the base of the corolla, thereby behaving as 'nectar-thieves' in the manner of some short-tongued bees. Larger-bodied Ichneumonidae and parasitoid Aculeata certainly possess sufficiently robust mandibles for this purpose.

However, only one parasitoid wasp nectar-thief, the ichneumonid *Diadegma insulare* (Cresson), has been identified to date (Idris & Grafius, 1995, 1996), and given that no other species were recorded 'stealing' nectar during detailed observations made on a wide diversity of flower-visiting parasitoid wasps by Györfi (1945), Hassan (1967) and Jervis *et al.* (1993), we doubt whether many more species will be reported.

(b) A substantial proportion of all parasitoid wasps are small-bodied, so can enter narrow tubular corollas bodily. It is noteworthy that Chalcidoidea, extremely few of which possess CNEA, have been observed to gain access to the 'concealed' nectar in the tubular corollas of Asteraceae and other families either by inserting their heads into the corolla or by walking down it (Jervis *et al.*, 1993; Patt *et al.*, 1997). The only chalcidoids known to have CNEA are Leucospidae, a family whose adults are large-bodied by general chalcidoid standards (Bouček, 1974).

However, small-bodied parasitoid flies (e.g. Phoridae) and wasps (e.g. several Tersilochinae, some Cheloninae and many Braconinae) possess CNEA (see companion paper), so small size does not preclude the evolution of CNEA.

Mapping the possession of CNEA on what few cladograms are available for parasitoid groups suggests that its pattern and frequency of occurrence is mainly attributable to ecological expediency in the case of parasitoid wasps, but a combination of ecological expediency and phylogenetic history in the case of parasitoid flies. CNEA is more often a synapomorphy for taxa above subfamily level among parasitoid flies than among parasitoid wasps (see companion paper), the extreme examples being the Acroceroidea and Nemestrinoidea [note that according to Yeates (1994), the families Acroceridae and Nemestrinidae do not form a monophyletic group].

For both types of parasitoid (and non-parasitoids for that matter) one constraint upon the evolution of CNEA has presumably been the relative rarity of 'concealed' nectar sources, compared with exposed nectar sources, in most habitats; the opportunity has not existed for a larger proportion of the fauna to switch to feeding on concealed nectar.

Owing to the paucity of parasitoid-plant records, extremely little is known about the value of CNEA length as a predictor of flower use in parasitoids. We would expect there to be a close correlation between the length of a species' CNEA and the morphology (corolla length) of the plants it exploits. However, Harder (1985) has shown for bumblebees that whereas CNEA length is the morphological feature most closely associated with flower choice, its importance in determining the range of flower species exploited varies significantly with other insect morphological (body size) and plant ecological (abundance, species richness) factors (see Pyke [1982]).

There is some morphological evidence for evolutionary interactions between certain flowering plants and concealed nectar-feeding parasitoids. Grant & Grant (1965) discuss the Californian 'races' of *Gilia splendens* (Polemoniaceae) whose floral morphology closely matches CNEA length in the most frequent visitor/nectarivore. For the 'Widespread' race and the 'San Gabriel' race the match is between a bombyliid and an acrocerid, respectively. A close morphological match also occurs between: (i) *Linanthus androsaceus* (Polemoniaceae) and its visitor *Eulonchus smaragadinus* (Acroceridae) (Grant & Grant, 1965); (ii) a guild of several Iridaceae and Geraniacieae and two *Prosoeca* spp. (Nemestrinidae) that visit them (Manning & Goldblatt, 1996); and (iii) a member of the *Disa draconis* L.f. (Sw.) complex (Orchidaceae) and its visitor *Moegistorynchus longirostris* Wiedemann (Nemestrinidae) (Johnson & Steiner, 1997). Where such matches are found, one should not too hastily conclude that the selection pressure for the evolution and maintenance of elongated CNEA in the parasitoid comes from the plant race/species in question (zero selection pressure if the plant does not offer a nectar or other reward: *vide* the *Disa draconis* complex, members of which have long floral spurs but do not secrete nectar). The more likely explanation is that the evolutionary response relates to a guild of flowering plants (Johnson & Steiner, 1997). It is a valid generalization to say that most pollination systems are skewed towards morphologically specialized flowers with unspecific pollinators, i.e. it is usually difficult to attribute pollinator traits to a particular plant (S. D. Johnson, pers. comm.).

The fitness advantage of specialization (F) (for host feeding) is that host blood, which is high in proteinaceous materials, contains essential vitamins and salts that are either scarce or absent in other foods, and is thus valuable for both reproduction and (in some parasitoids), maintenance; it is conveniently packaged within hosts, and can be extracted efficiently. Note that the phorid flies that possess the only known specialization of this kind do not possess a piercing ovipositor (most other host feeding parasitoids [mainly wasps] imbibe blood that exudes from wounds made with the ovipositor [Jervis & Kidd, 1986]); this suggests that their host feeding behaviour evolved from opportunistic consumption of blood from hosts injured or killed by other agencies (*vide* Disney, 1994). The fitness benefits and costs of host feeding for parasitoids generally are discussed by Jervis & Kidd (1986, 1996a, 1998), Kidd & Jervis (1991) and Heimpel & Collier (1996); these authors agree that one cost is a long handling time. There are likely to exist, for some of those parasitoid wasps that use their mandibles to produce a host feeding site in the host's integument, strong selection pressures for the evolution of mouthpart specializations that minimize this cost. It is perhaps surprising that no mouthpart specialization whatsoever for host feeding is evident among parasitoid wasps (see companion paper).

In view of the known beneficial effects of sugar-rich food consumption in parasitoids with unspecialized mouthparts (see above), we consider it unlikely that parasitoids possessing specializations for host feeding would lose the ability to feed on non-host foods, particularly sugar-rich ones.

A final, general question that requires addressing is the infrequent occurrence of sexual dimorphism in feeding-related mouthpart specializations among parasitoids. Given the intersexual differences in the array of ecophysiological factors promoting/constraining the evolution of such specializations (see above), we would expect sexual dimorphism to be more common than is observed. An explanation for this mismatch that readily comes to mind is that mouthpart morphology is controlled mainly by autosomal alleles.

It is clear from the aforegoing discussion that both reproductive strategy and mating system must play a significant role in shaping the evolution of feeding strategy and therefore mouthpart structure in parasitoids. As well as feeding strategy influencing mouthpart structure, the opposite must apply; for example we have argued that in Diptera reduced size (or at least width) of the labella will tend to preclude pollen, honeydew and exposed nectar feeding. At the population level, the type of adult feeding strategy, combined with its reproductive and other physiological correlates, will determine the relative levels of parasitoid and host population equilibria and the stability/persistence characteristics of the population (Kidd & Jervis, 1989; Jervis & Kidd, 1992, 1995; Briggs *et al.*, 1995; Jervis *et al.*, 1996a,b; see also Owen & Gilbert, 1989, on Syrphidae, and Miller, 1996, on Lepidoptera). It is clear then, that studies on the functional morphology of parasitoid mouthparts should be viewed not as a mere adjunct to parasitoid biology, but as an integral component.

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REFERENCES

Allen HW. 1929. An annotated list of the Tachinidae of Mississippi. *Annals of the Entomological Society of America* **22:** 676–690.

Ashburner M. 1981. Entomophagous and other bizarre Drosophilidae. In: Ashburner M, Carson HL, Thompson JN eds. *The genetics and biology of* Drosophila. Vol. 3a. Academic Press, New York. pp. 375–429.

Askew RR. 1971. *Parasitic insects.* London: Heinemann.

Avidov Z, Balshin M, Gerson U. 1970. Studies on *Aphytis coheni*, a parasite of the California Red Scale, *Aonidiella aurantii*, in Israel. *Entomophaga* **15:** 191–207.

Baker HG, Baker I. 1983. A brief historical review of the chemistry of floral nectar. In: Bentley B, Elias T, eds. *The biology of nectaries.* New York: Columbia University Press, 126–152.

Barbier M. 1970. Chemistry and biochemistry of pollens. *Progress in Phytochemistry* **2:** 1–34.

Becher E. 1882. Zur Kenntnis der Mundtheile der Dipteren. [On the mouthparts of Diptera] *Denkschriften der Akademie für Wissenschaft, Wien* **45:** 123–162.

Bleicher E, Parra JRP. 1991. Efeito do hospedeiro de substituicao e da alimentacao na longevidade de *Trichogramma* sp. [Effect of host substitution on growth and longevity of *Trichogramma* sp.] *Pesquisa Agropecuaria Brasiliera, Brasilia* **26:** 1845–1850.

Bletchly JD. 1954. The mouthparts of the Dance Fly, *Empis livida* L. (Diptera, Empididae). *Proceedings of the Zoological Society of London* **124:** 317–334.

Boggs CL. 1997a. Reproductive allocation from reserves and income in butterfly species with differing adult diets. *Ecology* **78:** 181–191.

Boggs CL. 1997b. Dynamics of reproductive allocation from juvenile and adult feeding: radiotracer studies. *Ecology* **78:** 192–202.

Bouček Z. 1974. A revision of the Leucospidae (Hymenoptera: Chalcidoidea) of the world. *Bulletin of the British Museum (Natural History) (Entomology)* **23:** 1–241.

Briggs CJ, Nisbet RM, Murdoch WW, Collier TR, Metz JAJ. 1995. Dynamical effects of host-feeding in parasitoids. *Journal of Animal Ecology* **64:** 403–416.

Broadhead EC. 1984. Adaptations for fungal grazing in lauxaniid flies. *Journal of Natural History* **18:** 639–649.

Buckton GB. 1895. *The natural history of* Eristalis tenax *or the Drone Fly.* London: MacMillan and Co.

Casey TM, May ML, Morgan KR. 1985. Flight energetics of euglossine bees in relation to morphology and wing stroke frequency. *Journal of Experimental Biology* **116:** 271–289.

Cendaña SM. 1937. Studies on the biology of *Coccophagus* (Hymenoptera), a genus parasitic on non-diaspine Coccidae. *University of California Publications in Entomology* **6:** 337–400.

Collin JE. 1921. Description of a new genus and two new species of Cecidomyiidae, and six new species of acalypterate Muscidae (Ephydridae and Milichidae). *Transactions of the Entomological Society of London, January 1992*: 504–516.

Colyer CN, Hammond CO. 1951. *Flies of the British Isles.* London: Warne.

Dafni A. 1992. *Pollination ecology: a practical approach.* Oxford: IRL Press.

Delucchi V. 1953. *Aphidecta obliterata* L. (Coleoptera, Coccinellidae) als Rauber von *Dreyfusia (Adelges) piceae* Ratz. [*Ahpidecta obliterata* as a predator of *Dreyfusia piceae*]. *Pflanzenschutz Bericht* **11:** 73–83.

Dethier VG. 1976. *The hungry fly.* Harvard: Belknapp Press.

Deyrup MA. 1988. Pollen-feeding in *Poecilognathus punctipennis* (Diptera: Bombyliidae). *Florida Entomologist* **71:** 597–605.

Dimmock G. 1881. *The anatomy of the mouthparts and the sucking apparatus of some Diptera.* Boston: Inaugural Dissertation.

Disney RHL. 1994. *Scuttle flies: the Phoridae.* London: Chapman and Hall.

Disney RHL, Kochare NN, Godase SK. 1992. A new parasitoid (Diptera: Phoridae) of the mango shoot borer, *Chlumetia transversa* (Lepidoptera: Noctuidae), in India. *Bulletin of Entomological Research* **82:** 191–195.

Dobson HEM, Peng Y-S. 1997. Digestion of pollen components by larvae of the flower-specialist bee *Chelostoma florisomne* (Hymenoptera: Megachilidae). *Journal of Insect Physiology* **43:** 89–100.

Downes JA. 1955. The food habits and description of *Atrichopogon pollinivorus* n.sp. (Diptera: Ceratopogonidae). *Transactions of the Royal Entomological Society of London* **106:** 439–453.

Downes WL, Dahlem GA. 1987. Keys to the evolution of Diptera: the role of honeydew. *Environmental Entomology* **16:** 847–854.

Dyer LE, Landis DA, 1996. Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environmental Entomology* **25:** 1192–1201.

Eggleton P, Belshaw R. 1992. Insect parasitoids: an evolutionary overview. *Philosophical Transactions of the Royal Society of London* **337:** 1–20.

Ellers J. 1996. Fat and eggs: an alternative method to measure the trade-off between survival and reproduction in insect parasitoids. *Netherlands Journal of Zoology* **46:** 227–235.

Ellington CP. 1991. Limitations on animal flight performance. *Journal of Experimental Biology* **160:** 71–91.

Ellington CP, Machin KE, Casey TM. 1990. Oxygen consumption of bumblebees in forward flight. *Nature* **347:** 472–473.

Elton CS. 1966. *The pattern of animal communities.* London: Methuen and Co.

Elzinga RJ, Broce AB. 1986. Labellar modifications of Muscomorpha flies (Diptera). *Annals of the Entomological Society of America* **79:** 150–209.

Faegri K, van der Pijl L. 1979. *The principles of pollination ecology.* Oxford: Pergamon Press.

Ferrar P. 1987. *A guide to the breeding habits and immature stages of Diptera Cyclorrhapha. Entomonograph.* Leiden: E. J. Brill.

Finch S. 1971. Comparison of the nutritive values of proteins and related compounds to adult cabbage root fly, *Erioischia brassicae. Entomologia Experimentalis et Applicata* **14:** 115–124.

Finch S. 1974. Sugars available from flowers visited by the adult cabbage root fly, *Erioischia brassicae* (Bch.) (Diptera: Anthomyiidae). *Bulletin of Entomological Research* **64:** 257–263.

Finch S, Coaker TH. 1969. Comparison of the nutritive values of carbohydrates and related compounds to *Erioischia brassicae. Entomologia Expermentalis et Applicata* **12:** 441–453.

Flanders SE. 1950. Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Canadian Entomologist* **82:** 134–140.

Foster MA, Ruesink WG. 1984. Influence of flowering weeds associated with reduced tillage in corn on a black cutworm (Lepidoptera: Noctuidae) parasitoid, *Meteorus rubens* (Nees von Esenbeck). *Environmental Entomology* **13:** 664–668.

Frey R. 1921. Studien über den Bau des Mundes der niederen Diptera Schizophora nebst Bemerkungen über die Systematik dieser Dipteran Gruppe. [Studies on the structure of the mouth in the lower Diptera Schizophora, with remarks on the systematics of these dipteran groups]. *Acta Societatis pro Fauna et Flora Fennicae* **48:** 1–246.

Gaugler R, Schutz S. 1989. Environmental influences on hovering behaviour of *Tabanus nigrovittatus* and *T. conterminus* (Diptera: Tabanidae). *Journal of Insect Behaviour* **2:** 775–785.

Gerstfield G. 1853. *Mundtheile der saugenden insekten.* [Mouthparts of sucking insects]. Dorpat, Germany.

Gilbert F. 1981. Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecological Entomology* **6:** 245–262.

Gilbert F. 19855a. Diurnal activity patterns in hoverflies (Diptera, Syrphidae). *Ecological Entomology* **10:** 385–392.

Gilbert F. 1985b. Ecomorphological relationships in hoverflies (Diptera, Syrphidae). *Proceedings of the Royal Society of London B* **224:** 91–105.

Gilbert LE. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proceedings of the National Academy of Sciences of the United States of America* **69:** 1403–1407.

Godfray HCJ, 1994. *Parasitoids: behavioural and evolutionary ecology.* New Jersey: Princeton University Press.

Graenicher S. 1910. The bee-flies (Bombyliidae) in their relations to flowers. *Bulletin of the Wisconsin Natural History Society* **8:** 91–101.

Graham-Smith GS. 1930. Further observations on the anatomy and function of the proboscis of the blowfly *Calliphora erythrocephala* L. *Parasitology* **22:** 47–113.

Grant V, Grant KA. 1965. *Flower pollination in the Phlox family*. New York and London: Columbia University Press.

Grimaldi D. 1988. Bee flies and bluets: *Bombylius* (Diptera: Bombyliidae) flower-constant on the distylous species, *Heydotis caerulea* (Rubiaceae), and the manner of foraging. *Journal of Natural History* **22:** 1–10.

Györfi J. 1945. Beobachtungen über die Ernährung der Schlupfwespenimagos. [Observations on the nutrition of adult ichneumon wasps]. *Erdészeti Kisérletek* **45:** 100–112.

Hagley EAC, Barber DR. 1992. Effect of food source on the longevity and fecundity of *Pholetesor ornigis* (Weed) (Hymenoptera: Braconidae). *Canadian Entomologist* **124:** 341–346.

Hall JC. 1981. Bombyliidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 1*. Ottawa: Agriculture Canada, 589–602.

Harborne JB. 1988. *Introduction to ecological biochemistry*. London, Academic Press.

Harder LD. 1985. Morphology as a predictor of flower choice by bumble bees. *Ecology* **66:** 198–210.

Hardy DE. 1987. Pipunculidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 2*. Ottawa: Agriculture Canada, 745–748.

Haslett J. 1983. A photographic account of pollen digestion by adult hoverflies. *Physiological Entomology* **8:** 167–171.

Hassan E. 1967. Untersuchungen über die Bedeutung der Kraut- und Strauchschicht als Nahrungsquelle für Imagines entomophager Hymenopteren. [Studies on the significance of the herb- and shrub-layer as food sources for adult entomophagous Hymenoptera]. *Zeitschrift für angewandte Entomologie* **60:** 238–265.

Heimpel GE, Collier TR. 1996. The evolution of host-feeding behaviour in insect parasitoids. *Biological Reviews* **71:** 373–400.

Heimpel GE, Rosenheim JA, Kattari D. 1997a. Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus*. *Entomologia Experimentalis et Applicata*, **83:** 305–315.

Heimpel GE, Rosenheim JA, Rosenheim JA, Mangel M. 1997b. Predation on adult *Aphytis* parasitoids in the field. *Oecologia* **110:** 346–352.

Heinrich B. 1979. *Bumblebee economics*. Cambridge, Massachusetts and London: Harvard University Press.

Hendrichs J, Lauzon CR, Cooley SS, Prokopy RJ. 1993. Contribution of natural food sources to adult longevity and fecundity of *Rhagoletis pomonella* (Diptera: Tephritidae). *Annals of the Entomological Society of America* **86:** 250–264.

Hennig W. 1973. Ordnung Diptera (Zweiflugen). *Handbuch auf Zoologie* **4(2)2/31(20):** 1–337.

Hennig W. 1981. *Insect Phylogeny (translated by A. C. Pont)*. Chichester: John Wiley and Sons.

Herting, B. 1960. Biologie der westpalaärktischen Raupenfliegen (Diptera, Tachinidae). [Biology of west-palaearctic caterpillar flies (Tachinidae)]. *Monographien zur angewandte Entomologie* **16:** 1–202.

Hesse R, Doflein F. 1914. Tierbau und Tierleben in ihrem Zusammenhang betrachtet. [A consideration of the relationship between structure and natural history in animals]. Vol. 2. Das Tier als Glied des Naturganzen. [*The animal as a component of Nature*]. Leipzig-Berlin: Teubner Verlag.

Holloway BA, 1976. Pollen-feeding in hoverflies (Diptera: Syrphidae). *New Zealand Journal of Zoology* **3:** 339–350.

Hoyt CP. 1952. The evolution of the mouthparts of adult Diptera. *Microentomology* **17:** 61–125.

Huddleston T, Walker AK. 1988. *Cardiochiles* (Hymenoptera: Braconidae), a parasitoid of lepidopterous larvae, in the Sahel of Africa, with a review of the biology and host relationships of the genus. *Bulletin of Entomological Research* **78:** 435–461.

Idoine K, Ferro DN. 1988. Aphid honeydew as a carbohydrate source for *Edovum puttleri* (Hymenoptera: Eulophidae). *Environmental Entomology* **17:** 941–944.

Idris AB, Grafius E. 1995. Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Biological Control* **24:** 1726–1735.

Idris AB, Grafius E. 1996. Nectar collecting behaviour of *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth, *Plutella xylostella* (Lepidoptera; Plutellidae). *Environmental Entomology*, **26:** 114–120.

Jervis MA, Copland MJW. 1996. The life cycle. In: Jervis M, Kidd N, eds. *Insect natural enemies: practical approaches to their study and evaluation*. London, Chapman and Hall, 63–161.

Jervis MA, Kidd NAC. 1986. Host-feeding strategies in hymenopteran parasitoids. *Biological Reviews* **61:** 395–434.

Jervis MA, Kidd NAC. 1992. The dynamic significance of host-feeding by insect parasitoids: what modellers ought to consider. *Oikos* **62:** 97–99.

Jervis MA, Kidd NAC, 1995. Incorporating physiological realism into models of parasitoid feeding behaviour. *Trends in Ecology and Evolution* **10:** 434–436.

Jervis MA, Kidd NAC. 1996a. *Insect natural enemies: practical approaches to their study and evaluation.* London: Chapman Hall.

Jervis MA, Kidd NAC. 1996b. Phytophagy. In: Jervis M, Kidd N, eds. *Insect natural enemies: practical approaches to their study and evaluation.* London, Chapman and Hall, 375–394.

Jervis MA, Kidd NAC. 1998. Parasitoid adult feeding behaviour: implications for biological control. In: Hawkins BA, Cornell HV, eds. *Theoretical approaches to biological control.* Cambridge: Cambridge University Press, in press.

Jervis MA, Hawkins BA, Kidd NAC. 1996a. The usefulness of destructive host feeding parasitoids in classical biological control: theory and observation conflict. *Ecological Entomology* **21:** 41–46.

Jervis MA, Kidd NAC, Heimpel GE. 1996b. Parasitoid adult feeding behaviour and biocontrol – a review. *Biocontrol News and Information* **17:** 11N–26N.

Jervis MA, Kidd NAC, Walton MP. 1992. A review of methods for determining dietary range in adult parasitoids. *Entomophaga* **37:** 565–574.

Jervis MA, Kidd NAC, Fitton MG, Huddleston T, Dawah HA. 1993. Flower-visiting by hymenopteran parasitoids. *Journal of Natural History* **27:** 67–105.

Johnson SD, Steiner KE. 1997. Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). *Evolution* **51:** 45–53.

Kidd NAC, Jervis MA. 1989. The effects of host-feeding behaviour on the dynamics of parasitoid-host interactions, and the implications for biological control. *Researches on Population Ecology* **31:** 235–274.

Kidd NAC, Jervis MA. 1991. Host-feeding and oviposition strategies of parasitoids in relation to host stage. *Researches on Population Ecology* **33:** 13–28.

Kugler H. 1955. *Blütenokologie.* [*Flower ecology*]. Stuttgart: Gustav Fischer Verlag.

Künckel d'Herculais J. 1875. L'organisation et développement des Volucelles. [The organisation and development of *Volucella* (Diptera, Syrphidae)]. Paris: G. Masson.

Leatemia JA, Laing JE, Corrigan JE. 1995. Effects of adult nutrition on longevity, fecundity and offspring sex ratio of *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae). *Canadian Entomologist* **127:** 245–254.

Leius K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Canadian Entomologist* **92:** 369–376.

Leius K. 1961a. Influence of food on fecundity and longevity of adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Canadian Entomologist* **93:** 771–780.

Leius K. 1961b. Influence of various foods on fecundity and longevity of adults of *Scambus buolianae* (Htg) (Hymenoptera: Ichneumonidae). *Canadian Entomologist* **93:** 1079–1084.

Leius K. 1963. Effects of pollen on fecundity and longevity of adult *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Canadian Entomologist* **95:** 202–207.

Le Ralec A. 1995. Egg contents in relation to host-feeding in some parasitic Hymenoptera. *Entomophaga* **40:** 87–93.

Lewis DJ, Domoney CR. 1966. Sugar meals in Phlebotominae and Simuliidae (Diptera). *Proceedings of the Royal Entomological Society A* **41:** 175–179.

Lim GS. 1982. *The biology and effects of parasites of the diamond-back moth*, Plutella xylostella (L.). London: Unpublished Ph.D. thesis, University of London, Imperial College.

Lindner H. 1919. Über die Mundwerkzeuge einige Dipteren und ihre Beziehungen zur Ernährungsweise. [On the mouthparts of some Diptera and their relation to feeding]. *Zoologischer Anzeiger* **50:** 19–27.

Mackauer M. 1983. Quantitative assessment of *Aphidius smithi* (Hymenoptera: Aphidiidae): fecundity, intrinsic rate of increase and functional response. *Canadian Entomologist* **115:** 399–415.

Manning JC, Goldblatt P. 1996. The *Prosoeca peringueyi* (Diptera, Nemestrinidae) pollination guild in southern Africa – long-tongued flies and their tubular flowers. *Annals of the Missouri Botanical Garden* **83:** 67–86.

Maurizio A. 1975. How bees make honey. In: Crane E, ed. *Honey: a comprehensive survey*. London: Heinemann, 77–105.

McAlpine JF. 1965. Observations on anthophilous Diptera at Lake Hazen, Ellesmere Island. *Canadian Field Naturalist* **79:** 247–256.

McAlpine JF. 1981. Morphology and terminology – adults. In: McAlpine JF, Peterson BV, Sherwell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 2*. Ottawa: Agriculture Canada, 9–63.

McAlpine JF. 1989. Phylogeny and classification of the Muscomorpha. In: McAlpine JF, Wood DM, eds. *Manual of Nearctic Diptera Volume 3*. Ottawa: Agriculture Canada, 1397–1578.

McAlpine DK, de Keyzer RG. 1994. Generic classification of the fern flies (Diptera: Teratomyzidae) with a larval description. *Systematic Entomology* **19:** 305–326.

McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM. 1981. *Manual of Nearctic Diptera Volume 1*. Ottawa: Agriculture Canada.

McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM. 1987. *Manual of Nearctic Diptera Volume 2*. Ottawa: Agriculture Canada.

McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM. 1989. *Manual of Nearctic Diptera Volume 3*. Ottawa: Agriculture Canada.

Menzbier MA, 1880. Über das Kopfskelett und die Mundwerkzeuge der Zweiflugler. [On the head skeleton and the mouthparts in flies]. *Bulletin de la Société des Naturalistes de Moscou* **55:** 8–71.

Miller WE. 1996. Population behaviour and adult feeding capacity in Lepidoptera. *Environmental Entomology* **25:** 213–226.

Mitter JL. 1917. Note on the method of feeding of *Corizoneura (Pangonia) longirostris* Hardwick, with a description of the mouthparts. *Indian Journal of Medical Research* **5:** 523–528.

Morales-Ramos JA, Rojas MG, King EG. 1996. Significance of adult nutrition and oviposition experience on longevity and attainment of full fecundity of *Catolaccus grandis* (Hymenoptera: Pteromalidae). *Annals of the Entomological Society of America* **89:** 555–563.

Mühlenberg M. 1971. Phylogenetische-systematische Studien an Bombyliiden (Diptera). [Phylogenetic and systematic studies on bombyliids]. *Zeitschrift für Morphologie und Anatomie der Tiere* **70:** 73–102.

Müller H. 1883. *The fertilisation of flowers*. London: MacMillan and Co.

Nayar JL. 1964. External morphology of head capsule in *Syrphus balteatus* de Geer (Syrphidae, Diptera). *Indian Journal of Entomology* **26:** 135–151.

Nettles WC. 1987. *Eucelatoria bryani* (Diptera: Tachinidae): effect on fecundity of feeding on hosts. *Environmental Entomology* **16:** 437–440.

Nicolson SW. 1994. Pollen feeding in the eucalypt nectar fly, *Drosophila flavohirta*. *Physiological Entomology* **19:** 58–60.

Olson DL, Nechols JR. 1995. Effects of squash leaf trichome exudates and honey on adult feeding, survival and fecundity of the squash bug (Heteroptera: Coreidae) egg parasitoid *Gryon pennsylvanicum* (Hymenoptera; Scelionidae). *Environmental Entomology* **24:** 454–458.

Oosterbroek P, Courtney G. 1995. Phylogeny of the nematocerous families of Diptera (Insecta). *Zoological Journal of the Linnean Society* **115:** 267–311.

Owen J, Gilbert F. 1989. On the abundance of hoverflies. *Oikos* **55:** 183–193.

Parmenter L. 1953. The hoverflies (Syrphidae). *Entomologists' Record and Journal of Variation* **65:** 185–190.

Patt JM, Hamilton GC, Lashomb JH. 1997. Foraging success of parasitoid wasps on flowers: interplay of insect morphology, floral architecture and searching behaviour. *Entomologia Experimentalis et Appplicata* **83:** 21–30.

Percival M. 1965. *Floral biology*. Oxford: Pergamon Press.

Peterson A. 1916. The head capsule and mouthparts of Diptera. *Illinois Biological Monographs* **3:** 177–280.

Proctor M, Yeo PF, Lack A. 1996. *The natural history of pollination*. London: Collins New Naturalists.

Prys-Jones O, Corbet SA. 1983. *Bumblebees*. Cambridge: Cambridge University Press.

Pyke GH. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* **63:** 555–573.

Rathay E. 1883. Untersuchungen über die Spermogenien der Rostpilze. [Studies on the spermogonia of the rust fungi]. *Denkschrift Kais. Akad Wissensch.* **46:** 1–51.

Rice MJ. 1970. Cibarial stretch receptors in the tsetse fly (*Glossina austeni*) and the blowfly (*Calliphora erythrocephala*). *Journal of Insect Physiology* **16:** 277–289.

Richards OW. 1926. A note on a dipterous parasite of ladybirds. *Entomologist's Monthly Magazine* **62:** 99.

Rupp L. 1989. *Die mitteleuropäischen Arten der Gattung* Volucella *(Diptera, Syrphidae) als Kommensalen und parasitoide in den Nestern von Hummeln und sozialen wespen*. [The mid-european species of the genus *Volucella* as commensals and parasitoids in the nests of bees and social wasps]. Unpublished dissertation, Faculty of Biology, Albert-Ludwigs-University, Freiburg-im-Breisgau, Germany.

Sahragard A, Jervis MA, Kidd NAC. 1991. Influence of host availability on rates of oviposition and host-feeding, and on longevity in *Dicondylus indianus* Olmi (Hym., Dryinidae), a parasitoid of the Rice Brown Planthopper, *Nilaparvata lugens* Stål (Hem., Delphacidae). *Journal of Applied Entomology* **112:** 153–162.

Schiemenz H. 1957. Vergleichende funktionell-anatomische Untersuchungen der Kopfmuskulatur von *Theobaldia* und *Eristalis*. [Comparative functional and anatomical studies of the head musculature of *Theobaldia* and *Eristalis*]. *Deutsche entomologische Zeitschrift (N.F.)* **4:** 268–331.

Schlinger EL. 1960. A review of the genus *Eulonchus* Gerstaecker. Part I. The species of the *smaragdinus* groups (Diptera: Acroceridae). *Annals of the Entomological Society of America* **53:** 416–422.

Schlinger EI. 1981. Acroceridae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 1*. Ottawa: Agriculture Canada, 575–584.

Schmid-Hempel P, Kacelnik A, Houston AI 1985. Honeybees maximise efficiency by not filling their crop. *Behavioural Ecology and Sociobiology* **17:** 61–66.

Schmidt-Nielsen K. 1972. Locomotion: energy cost of swimming, flying and running. *Science* **177:** 222–228.

Schuhmacher H, Hoffman H. 1982. Zur Funktion der Mundwerkzeuge von Schwebfliegen bei der Nahrungsaufnahme (Diptera: Syrphidae). [On the function of the mouthparts of hoverflies in food uptake]. *Entomologia Generalis* **7:** 327–342.

Schutz SJ, Gaugler R. 1989. Honeydew-feeding behaviour of salt marsh horse flies (Diptera; Tabanidae). *Journal of Medical Entomology* **26:** 471–473.

Sirot E, Bernstein C. 1996. Time sharing between host searching and food searching in parasitoids: state-dependent optimal strategies. *Behavioural Ecology* **7:** 189–194.

Smith KGV. An introduction to the immature stages of British flies. *Handbooks for the Identification of British Insects* **10(14):** 1–280.

Smith KGV, Peterson BV. 1987. Conopidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 2*. Ottawa: Agriculture Canada, 749–756.

Ssymank A, Gilbert F. 1993. Anemophilous pollen in the diet of syrphid flies, with special reference to the leaf feeding strategy occurring in Xylotini (Diptera, Syrphidae). *Deutsche Entomologische Zeitung* **2:** 245–258.

Stanley G, Linskens HF. 1974. *Pollen: biology, biochemistry and management.* Berlin: Springer-Verlag.

Steyskal GC. 1987. Pyrgotidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 2*. Ottawa: Agriculture Canada, 813–816.

Stoffolano JG. 1995. Regulation of a carbohydrate meal in adult Diptera, Lepidoptera, and Hymenoptera. In: Chapman RF, de Boer G, eds. *Regulatory mechanisms in insect feeding*. London: Chapman and Hall, 210–247.

Stubbs AE, Chandler P. 1978. A Dipterist's handbook. *Amateur Entomologist* **15:** 1–255.

Teskey HJ. 1981. Nemestrinidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Necrotic Diptera Volume 1*. Ottawa: Agriculture Canada, 585–588.

Toft CA, 1983. Community patterns of nectivorous adult parasitoids (Diptera: Bombyliidae) on their resources. *Oecologia* **57:** 200–215.

Toft CA. 1984a. Activity budgets in two species of bee flies (*Lordotus*: Bombyliidae, Diptera): a comparison of species and sexes. *Behavioural Ecology and Sociobiology* **14**: 287–296.

Toft CA. 1984b. Resource shifts in bee flies (Bombyliidae): interactions among species determine choice of resources. *Oikos* **43:** 104–112.

Toft CA. 1989a. Population structure and mating system of a desert bee fly (*Lordotus pulchrissimus*) (Diptera: Bombyliidae). 1. Male demography and interactions. *Oikos* **54:** 345–358.

Toft CA. 1989b. Population structure and mating system of a desert bee fly (*Lordotus pulchrissimus*) (Diptera: Bombyliidae). 2. Female demography, copulations and characteristics of swarm sites. *Oikos* **54:** 359–369.

Townes H. 1958. Some biological characteristics of the Ichneumonidae (Hymenoptera) in relation to biological control. *Journal of Economic Entomology* **51:** 650–652.

Townes H. 1972. Ichneumonidae as biological control agents. *Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management* **3:** 235–248.

Tucker VA. 1969. The energetics of bird flight. *Scientific American* **220:** 70–78.

van den Assem J. 1996. Mating behaviour. In: Jervis M, Kidd N. eds. *Insect natural enemies: practical approaches to their study and evaluation*. London: Chapman and Hall, 163–221.

van Lenteren JC, van Vianen A, Gast HF, Kortenhoff A. 1987. The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae), XVI. Food effects on oogenesis, life span and fecundity of *Encarsia formosa* and other hymenopterous parasites. *Zeitschrift für Angewandte Entomologie* **103:** 69–84.

Vijaysegaran S, Walter GH, Drew RAL. 1997. Mouthpart structure, feeding mechanisms, and natural food sources of adult *Bactrocera* (Diptera: Tephritidae). *Annals of the Entomological Society of America* **90:** 184–201.

Vine HCF. 1895. Predacious and parasitic enemies of aphides, including a study of hyperparasites. Part II continued. *Journal of Microscopy and Natural Science* **5:** 33–43.

Wigglesworth VB. 1972. *The principles of insect physiology, 7th edition.* London: Chapman and Hall.

Willmer PG. 1983. Thermal constraints on activity patterns in nectar-feeding insects. *Ecological Entomology* **8:** 455–469.

Willmer PG. 1985. Size effects on the hygrothermal balance and foraging patterns of a sphecid wasp, *Cerceris arenaria. Ecological Entomology* **10:** 469–479.

Willmer PG. 1986. Foraging patterns and water balance: problems of optimization for a xerophilic bee, *Chalicodoma sicula. Journal of Animal Ecology* **55:** 941–962.

Wood DM. 1987. Tachinidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 2.* Ottawa: Agriculture Canada, 1193–1269.

Wood DM, Borkent A. 1989. Phylogeny and classification of the Nematocera. In: McAlpine JF, Wood DM, eds. *Manual of Nearctic Diptera Volume 3.* Ottawa: Agriculture Canada, 1333–1370.

Woodley NE. 1989. Phylogeny and classification of the "orthorrhaphous" Brachycera. In: McAlpine JF, Wood DM, eds. *Manual of Nearctic Diptera Volume 3.* Ottawa: Agriculture Canada, 1371–1395.

Woodring JP. 1985. Circulatory systems. In: Blum MS, ed. *Fundamentals of insect physiology.* New York; John Wiley and Sons.

Yamamura N, Yano E. 1988. A simple model of host-parasitoid interaction with host-feeding. *Researches on Population Ecology* **30:** 353–369.

Yeates DK. 1994. The cladistics and classification of the Bombyliidae (Diptera, Asiloidea). *Bulletin of the American Museum of Natural History* **219:** 1–191.

Yeates DK, Greathead D. 1997. The evolutionary pattern of host use in the Bombyliidae (Diptera): a diverse family of parasitoid flies. *Biological Journal of the Linnean Society* **60:** 149–185.

Yeates DK, Irwin ME. 1996. Apioceridae (Insecta: Diptera): cladistic reappraisal and biogeography. *Zoological Journal of the Linnean Society* **116:** 247–301.

Yuval B, Hollidayhanson ML, Washino RK. 1994. Energy budget of swarming mosquitoes. *Ecological Entomology* **19:** 74–78.

Zaitsev VF. 1982. Microstructure of the labella of the fly proboscis I. The structure of the pseudotracheal closing apparatus. *Entomological Review (Washington)* **61:** 61–69.

Zaitsev VF. 1984. [Anthophily and the structure of the labella of the proboscis of Diptera]. *Verhandlungen der SIEEC X, Budapest* 169–171.

Zaitsev VF. 1988. Family Bombyliidae. In: Bei-Bienko GY, ed. *Keys to the insects of the European part of the USSR.* Washington DC: Smithsonian Institute and National Science Foundation.

Zimina LV. 1957. [Structure and function of the intestine of *Syrphus* (Diptera, Syrphidae)]. *Zoologischeskii Zhurnal* **36:** 1039–1043.

Zoebelen G. 1955. Der honigtau als nahrung der Insekten. I. (Honeydew as food for insects] *Zeitschrift für angewandte Entomologie* **38:** 369–416.