CHAPTER

# 15

# The evolution of feeding strategies

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CONTENTS

**Keywords:** Morphology – specialization – predators – predatory behaviour – Syrphidae.

## *Abstract*

We analyse the evolution of feeding strategies in the Syrphidae (Diptera), an insect group containing phytophages, saprophages, carnivores and even ectoparasitoids. To consider their evolution, we first develop a generic phylogeny for the family based on larval characters, and discuss the evolution of larval ecomorphology. We then focus on the predators, choosing the aphidophagous Syrphinae for detailed study. From their generic phylogeny we see a trend from feeding in the herb layer to feeding on arboreal aphid colonies. A trend from plesiomorphic generalists to apomorphic specialists is suggested, but not supported by the admittedly poor-quality literature data.

Finally, we consider the evolution of species in two closely related plesiomorphic genera of predators. After estimating the phylogeny from adult characters, we use

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Lynch's comparative method to analyse the evolution of behavioural, ecological and morphological characters. There is evidence for a small phylogenetic component to ecological measures (prey range, number of generations per year, growth rates and abundance). Predictions about the directions of evolutionary change in behavioural characters were all supported by the evidence (for measures of casting rate, capture rate, capture efficiency, handling time, and response to starvation). Morphology is strongly constrained by phylogenetic relatedness: most evolutionary change is in size and its associated allometry.

## INTRODUCTION

Much of the work of community ecologists during the last 40 years has involved inferring causes of ecological differences between related species from morphological, ecological or behavioural data. This has been an attempt to explain the so-called 'problem of species coexistence'. The whole field of ecomorphology involves the mapping of morphological onto ecological differences (Karr & James, 1975), often for single variables, but increasingly using multivariate techniques (e.g. Miles & Ricklefs, 1984; Gilbert, 1985a). Implicit in most of these studies is the assumption of equilibrium, (that is that the observed patterns reflect the product of current measurable forces. The morphology of each species is assumed to be moulded independently so as to reflect the forces of natural selection, acting via ecological and behavioural features, with the main result of producing an integrated community. Throughout the early part of this research programme, explanations were dominated by the resource-based competition model of species packing, which provided an all-embracing theoretical framework (e.g. Pianka, 1975).

The collapse of this paradigm in the 1980s was in large part due to a re-emphasis of two factors: the advent and use of null hypotheses in ecology (Strong, 1980), and the insistent cry that evolutionary history cannot be ignored. Species are not ecologically less similar that we would expect from random expectation, but are more similar (Kikkawa, 1977), not necessarily because competition is a weak force in communities, but because species are related through their evolutionary history.

The historical perspective on these questions now adds a new dimension to Hutchinson's famous question "Why are there so many kinds of animals?", first posed while he gazed into the pool at the shrine of Santa Rosalia, looking for water boatmen. Hutchinson (1959) considered single morphological characters; we are now able to combine multivariate with phylogenetic techniques (e.g. Miles & Dunham, 1992). This is clearly a fruitful area of future research, as Losos' (1990a,b) elegant studies of ecomorphology and performance in lizards demonstrate. Valuable insights can also be gained into the process of diversification. In a beautiful study of *Phylloscopus* warblers, Richman & Price (1992) showed that there was rapid and extensive morphological change early in the diversification of the group, associated with differences in prey size and feeding method. Later, smaller morphological changes leading to differences between sister species were mainly associated with habitat differences. This is interesting in the light of Schoener's (1974) classic paper on differences between coexisting species with similar niches: his review indicated that such species differed mainly along habitat dimensions, less often on food dimensions, and rarely on a temporal dimension to the niche.

With the advent of all this renewed interest in the role of phylogeny have come new tools for the analysis of this role. For quantitative data, we can divide these methods according to the type of ecological question being asked. First, one can ask whether one trait is *influenced* by the phylogenetic relationships between species. The appropriate methods here are either the Mantel test for association between phylogenetic and ecological distance matrices (J.M. Cheverud, personal communication), or the phylogenetic autocorrelation (Cheverud, Dow & Leutenegger, 1985; Gittleman & Kot, 1990). A different sort of question is whether two traits *covary*, after having allowed for the fact that data are not independent, by *removing* the effect of phylogenetic relationships: the most popular method here is 'independent comparisons' (Harvey & Pagel, 1991; Harvey & Purvis, 1991).

Several authors have viewed the autocorrelation and independent comparisons methods as alternatives, only considering the second type of question. Following on from this, various workers have explored the accuracy with which these and other techniques remove phylogenetic effects (Martins & Garland, 1991; Gittleman & Luh, 1992, Chapter 5).

Using an extension of the maximum likelihood methods of quantitative genetics, both types of question are combined in the comparative method proposed by Lynch (1992). In this method, each quantitative trait is split into a grand mean value (shared by all members of the phylogeny), a phylogenetically inherited additive value (a deviation from the grand mean), and a residual. The residual contains all non-additive genetic components, environmental effects and sampling errors. The output consists of parameter estimates and their standard errors (S.E.), the variance–covariance matrices of both additive and residual values, estimates (with standard errors) of hypothetical ancestral values, and log-likelihood significance tests of a variety of hypotheses. Lynch argues that his method is an advance for three reasons: it uses the multivariate intercorrelated data in an efficient way to estimate the parameters; log-likelihood tests form a sound basis for hypothesis testing; and it uses only the additive evolutionary values to estimate ancestral phenotypes, minimizing bias.

In this paper, we use phylogeny to study the evolutionary ecology of insects, applying Lynch's technique where appropriate. We are principally interested in the evolution of morphology and ecology, and especially in the way in which larval and adult characters covary.

## The study group

Our chosen study group are the hoverflies (Syrphidae), one of the largest families of the Diptera with more than 5500 species already described world-wide. The adults are well known for their habit of hovering and of visiting flowers for nectar and pollen; these habits have resulted in natural selection for mimicry, since their other well-known feature is their wasp- and bee-like patterns, which have evolved independently several times within the family (Gilbert, unpublished data)..

In contrast to the fairly uniform feeding behaviour of adults, larvae have amazingly diverse feeding habits (Gilbert, 1986, 1990), with substantial proportion species being saprophages (44%), zoophages (40%) and phytophages (16%). Saprophages are exceedingly diverse, from aquatic filter-feeders to wood-borers. Whilst many of the zoophages are aphid (Rotheray & Gilbert, 1989) or ant-brood predators (Garnett, Akre & Sehlke, 1985), at least one species group consists of ectoparasitoids on wasp larvae (Rupp, 1989). This great diversity makes the family very suitable for testing ideas about the evolution of different feeding modes.

Some work has been carried out on the multivariate ecomorphology of adult syrphids (Gilbert, 1985a,b,c,d, 1990; Gilbert *et al.*, 1985; Owen & Gilbert, 1989; Gilbert & Owen, 1990). Synthesizing these results, and despite some dissenting voices (see Gilbert, 1991), the conclusion is that the quantitative relationships between feeding ecology, activity patterns, egg size/number and morphology are very strong. The strongest pattern, established by canonical correlation analysis, is the relationship between proboscis shape and the time spent feeding on nectar or on pollen (Gilbert, 1985a). These mappings between morphology and ecology do not, however, extend to detectable competitive effects between species close in morphological or ecological space (Gilbert & Owen, 1990).

Virtually none of this work was carried out in a phylogenetic context, however, because at the time there were no phylogenies of syrphids except for some very sketchy ideas based on rather crude data. Inspired by the comparative larval morphological work of the Czech dipterologist Pavel Laska, in 1986 we decided to develop phylogenies of syrphids (Rotheray & Gilbert, 1989, unpublished manuscript).

## THE PHYLOGENY OF THE FAMILY

We now have a fairly clear picture of the main features of the generic phylogeny of hoverflies. Full details will be published elsewhere (Rotheray & Gilbert, unpublished manuscript); briefly, more than 160 morphological characters were scored for more than 110 Holarctic genera, and these data subjected to analysis using the Hennig86 phylogenetic program (Farris, 1988). To obtain the final trees, we frequently used Farris' method of successive weighting to reduce the number of equally parsimonious trees. We used only larval structural features, and worked at a generic level. This is because of an interesting contrast that we believe has rarely been noted before, namely that although larval ecological differences are much wider than adult ecological differences, larval structure is much more conservative than adult morphology in the sense that it retains more phylogenetic information. We suggest this is a general feature of insect evolution.

Syrphids belong to the group Aschiza, assumed to be the sister-group of the higher flies, the Cyclorrhapha. One of us (G.E.R.) studied larvae of the other aschizan groups in order to establish the root of the tree. Over the last 100 years there has been a great deal of controversy over the exact relationships between aschizan taxa (see McAlpine, 1989), perhaps because assessments have always been made on the basis of adult characters. Adult characteristics may evolve too quickly to retain enough higher-level phylogenetic information: in larvae, in contrast, the result is very clear. The Lonchopteridae are the most plesiomorphic of the Aschiza, and the Syrphidae the most apomorphic. The sister-group of the syrphids is the Pipunculidae, and of the Syrphidae + Pipunculidae, the Phoridae (cf. Wada's, 1991 conclusions).

Lonchopterids and platypezids feed as larvae on fungi and other microorganisms, and the phorids also contain fungal-feeding larvae (although as larvae they are, like the syrphids, highly diverse: see Disney, 1990). Although the pipunculids are clearly the sister-group of the syrphids, as far as we know as larvae they are all endoparasitoids of Homoptera. According to our analysis, the most plesiomorphic syrphid is *Eumerus*, which feeds in wet semi-liquid rot pockets of plant roots infected with basal rot *Fusarium* (Creager & Sprujit, 1935). Feeding on micro-organisms must have bridged the gap between platypezids and syrphids, and therefore the original pipunculids must also have been microphagous. A further possibility is that predatory phorids gave rise to the parasitic pipunculids, and syrphids evolved from these via a return to saprophagy.

## THE EVOLUTION OF LARVAL ECOMORPHOLOGY

From the analysis of aschizan larvae, the key innovations of larval structure in the first syrphid were probably the following: large size; the development of 'new' structures around the mouth that help in gathering and filtering the food, as well as guiding it to the mouth; an enlarged prothorax with longitudinal grooves, increasing its contractile abilities and resulting in an increased food-gathering capability; a modified anal segment, especially in the fusion of the two posterior spiracles into the posterior respiratory process; and the development of a longer ventral than the dorsal surface, leading to a tilting upwards of the posterior respiratory process.

Most of these innovations are associated with living in a semi-liquid environment. An increased food-gathering ability was probably necessary because syrphid larvae are so much larger than their aschizan relatives, although comparable modifications are found in the small aquatic Phoridae (Disney, 1991).

Figure 1 shows our current best estimate for the phylogeny of the Syrphidae. Note that while all the predatory Syrphinae are lumped together (for clarity and because of the unity of their larval form), this group in fact represents one third of all species and many different genera. Five major features are notable from this tree: we sketch these features here, but they are described and analysed fully elsewhere (Rotheray & Gilbert, unpublished manuscript).

The greatest diversification of feeding habit occurs low down on the tree, and hence presumably early in the evolutionary history of the group. Above *Brachyopa* all genera are saprophages of one sort or another, the differences probably being caused by repeated transitions between the habitat sets of decaying vegetation *versus* tree sap or heartwood.

The transition between the ancestral form and phytophagous genera (mainly *Cheilosia*) is fairly easy to imagine, and few structural modifications were probably necessary. We do not know what the 'phytophages' actually digest; they do ingest plant tissue, but it is possible that they remain feeders on the bacteria and fungi of decay, vastly increased by comminution of the plant substrate during feeding. Diversification of these phytophages has given rise to leaf miners, stem/root tunnellers and the bizarre cambial feeders on conifers (Rotheray, 1988, 1990).

We can follow genera feeding on the bacteria and fungi of decay right up the spine of the tree, from *Cheilosia* (fungi) to *Rhingia* (dung) to sap runs on trees (*Ferdinandea*, *Brachyopa*) and on into the rest of the saprophages (see Fig. 1).

The evolution of the predatory habit probably occurred twice, possibly three times. One pathway gave rise to the sister-taxa (currently tribes) of the Syrphinae and Microdontinae. The Syrphinae are nearly all aphid predators of great agricultural

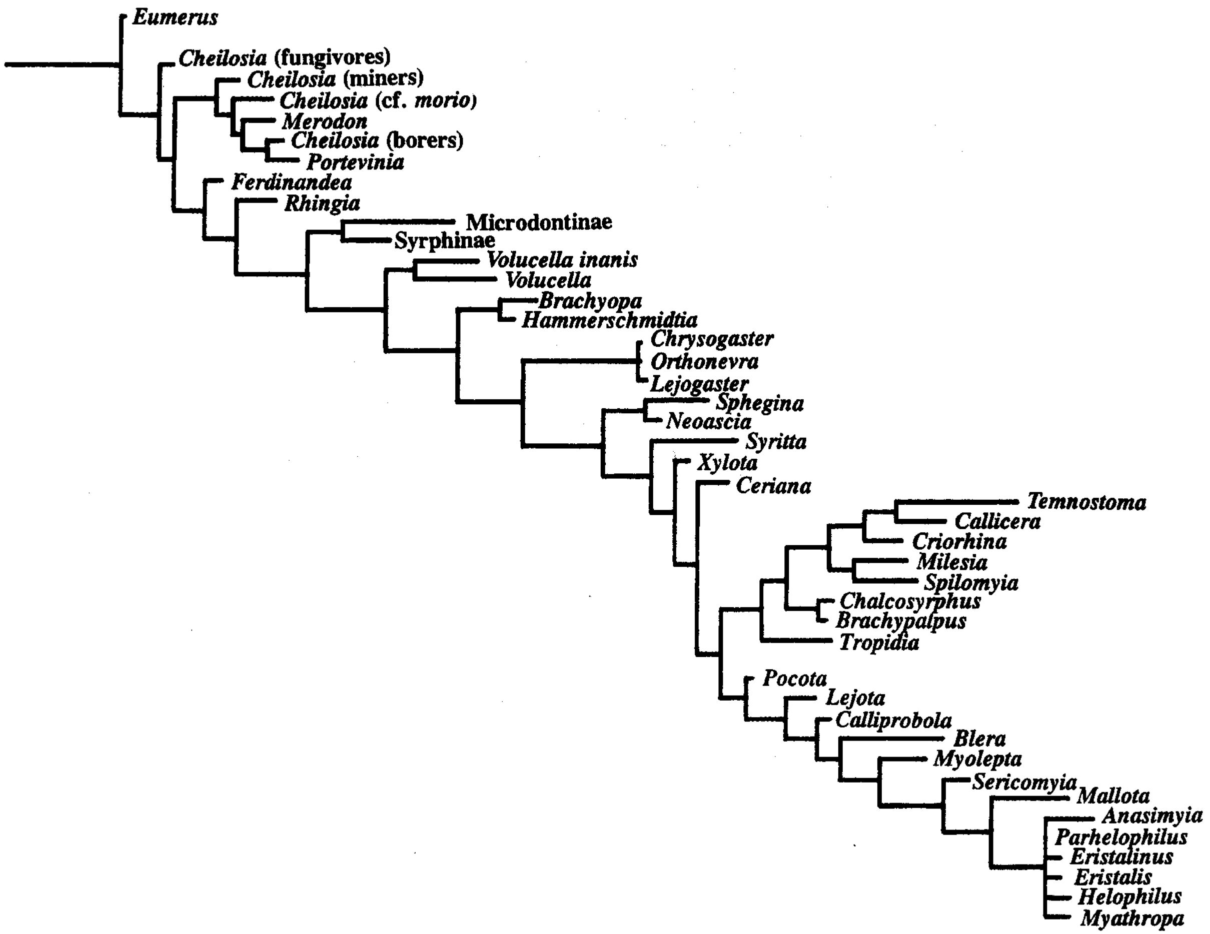

**Figure 1** Phylogeny of the genera of hoverflies (Syrphidae). This consensus tree was produced from larval and puparial characters by the Hennig86 program. Full details of the analysis are in Rotheray & Gilbert (unpublished manuscript).

importance, while microdons are predators of ant brood (although early and rather sketchy European work suggests that they might be saprophages). *Microdon* larvae are particularly odd, and were first described as a new taxon of mollusc, so different are they from the normal syrphid or even dipteran larval form (Donisthorpe, 1927). The differences are certainly connected with their myrmecophilous habits, since they resemble other insect myrmecophiles. Do these two taxa represent independently evolved predators? There is an intermediate form, currently classified as a *Platycheirus* (Syrphinae) on the basis of its adult characters, but having a very microdon-like larva. This is *P. milleri* from New Zealand, whose larva lives in ant nests (Thompson, 1972). It is almost certain that this apparent 'intermediate' is actually the product of convergent evolution (see Rotheray & Gilbert, unpublished manuscript).

The last feature we highlight here is the great diversity of saprophages. Three taxa have evolved independently to exploit more aquatic environments (chrysogasterines, spheginines and eristalines). Alternatively, there are those living in decaying cambium and heartwood, consisting mainly of the line leading from *Chalcosyrphus* to *Temnostoma*.

Associated with these ecological changes, there are three main morphological transitions. Again we do not have the space to describe these in detail here (see Rotheray & Gilbert, unpublished manuscript), but they are illustrated in Figs 2–4.

## **The larval thorax** (Fig. 2)

In *Eumerus* the thorax is broad and the head more or less absent, involuted as in the Cyclorrhapha. In the syrphine predators the thorax is strongly narrowed and elongated, probably in connection with their need to grasp small food items and suck out their contents. In *Volucella* there is a new development, the expansion of the anterior fold; this carries a new coating of spicules, and is possibly defensive in function.

The gradual enlargement of this anterior fold, and the appearance of additional longitudinal grooves, forms a transition series from *Syritta* to *Sericomyia* and the eristalines. We interpret this as allowing an enhanced rate of food-gathering and hence increased size. (The eristalines are the insect equivalents of baleen whales: giant, aquatic filter-feeders.) This transition series is associated with inhabiting more aquatic habitats, and a major problem is the ingress of water into the anterior spiracles. The chrysogasterines have lost their anterior spiracles completely in response to this problem, but the eristalines have developed an alternative: retractile spiracles, which are withdrawn into an invaginated pocket.

There has been an enormous development of the thorax along the other branch of the evolutionary tree, from *Tropidia* to *Temnostoma*, with the appearance of large hooks and spicules all over the thoracic surface. These were probably developed in response to the problem of preventing wear and of movement through particle-filled media, since these larvae occur under bark and in decaying heartwood. *Neoascia* species occur in similar material within decaying vegetation, and have independently evolved thoracic hooks, probably for much the same reason. From *Brachypalpus* to *Spilomyia* there is also an increase in the folding pattern because of the requirement for hook musculature. This culminates in the highly derived *Temnostoma*. This genus has all but lost the prothorax, and the meso- and metathorax are enlarged enormously and partly coalesced. On the anterior margin of the

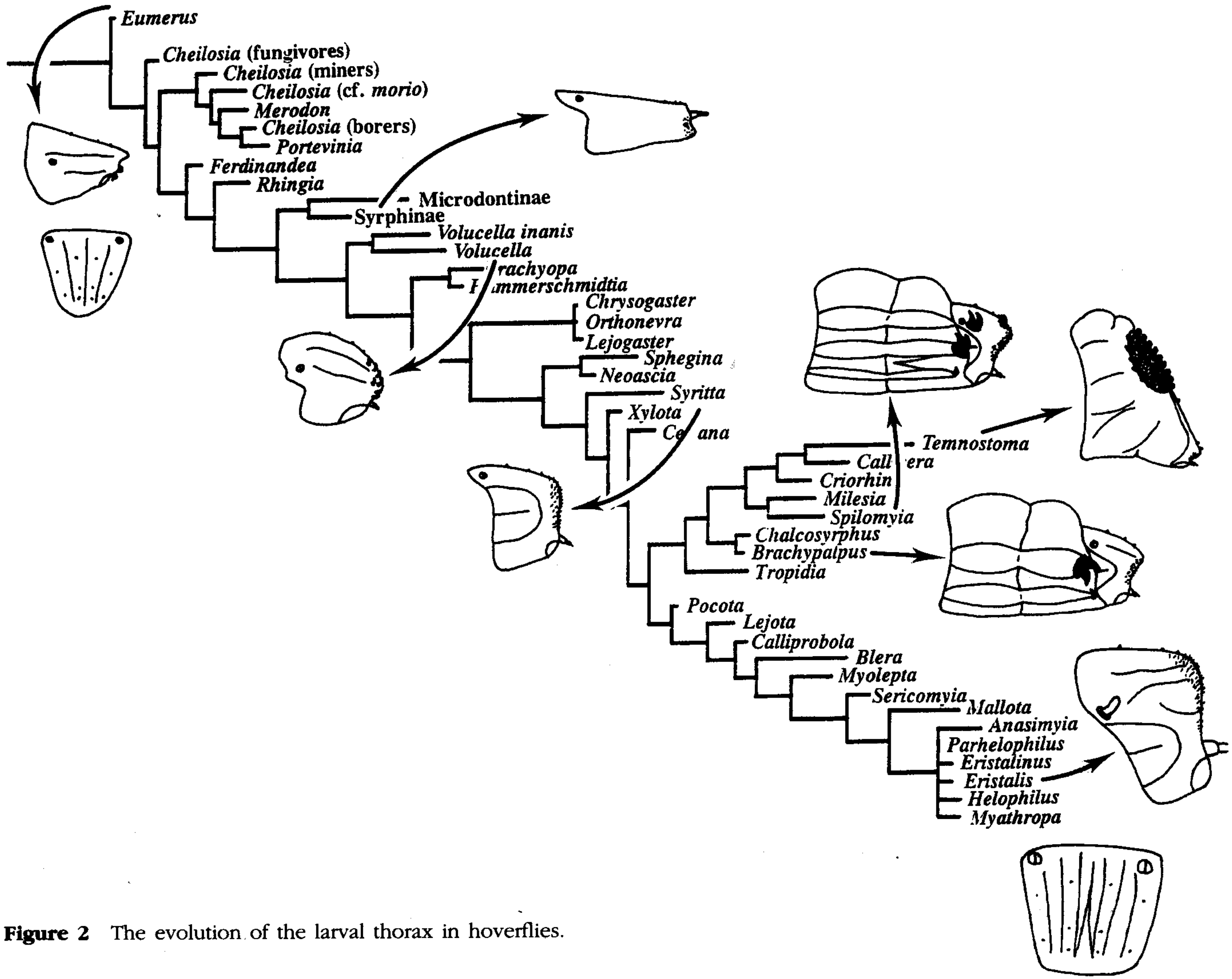

**Figure 2** The evolution of the larval thorax in hoverflies.

mesothorax are huge plate-like structures with massive hooks, used in tunnelling in wet wood.

## **Locomotory organs** (Fig. 3)

Locomotory organs are rudimentary in all plesiomorphic groups, consisting merely of pairs of bulges in the first six abdominal segments. These have no muscles, and work hydrostatically using the haemolymph.

The terrestrial predatory syrphines hunt aphids on plants, and this creates a severe problem of attachment to the plant (Rotheray, 1986, 1987). In response to this, they have developed a network of grooves on locomotory organs, around the anus and on the enlarged tip of the anal segment, all of which fill with saliva-like fluid from the anal segment. This sets up strong surface-tension forces that keep the larva on the plant. Different species have adapted to searching on different parts of plants (Rotheray, 1987): for example, *Epistrophe* is flattened and moves well on the leaf lamina, whereas *Scaeva* and *Eupeodes* have invented a U-shaped grasping organ that allows them to search much more efficiently on plant stems. All of this movement operates using haemolymph pressure, without musculature.

As in the case of the larval thorax, *Volucella* is a key taxon in the development of locomotory organs, for it is here that true prolegs, that is the locomotory organs with muscles, make their first appearance. In addition, the prolegs bear large hooked setae called crochets, that presumably help them to grip the wasp combs where they live.

The remaining evolution of the larval thorax merely involves increases or decreases in the relative sizes of the prolegs and/or crochets, both decreasing to almost complete absence in the line leading to *Temnostoma*, while increasing to very large sizes in the line leading to the eristalines.

## **The anal segment** (Fig. 4)

It is in the development of the anal segment that we see the true potential of the syrphid design realized. In the plesiomorphic groups there is only a single fold to the segment. In *Eumerus* this develops a further ring, and each has a pair of lappets, that is, fleshy protuberances. In the predatory syrphines these lappets have moved to the rear of the segment, and the whole segment is enlarged for gripping the substrate.

Once again there is significant innovation in *Volucella*, with the appearance of a third ring to the anal segment with its associated pair of lappets. Each ring then evolves semi-independently during the subsequent evolution of the family. There are increases in relative length when invading more aquatic habitats, and decreases in relative length when invading semi-solid habitats. Thus elongated anal segments are seen in the chrysogasterines, the spheginines and the eristalines, with the length of each ring extended approximately equally. In the line leading from *Pocota* to *Eristalis*, however, the third ring elongates (*Calliprobola*), then the first and second together also elongate (*Myolepta*), and finally the first ring narrows and extends enormously (eristalines).

What happened to adult form during this diversification of larval structure and feeding habits? We know little as yet of these patterns, but data uncorrected for

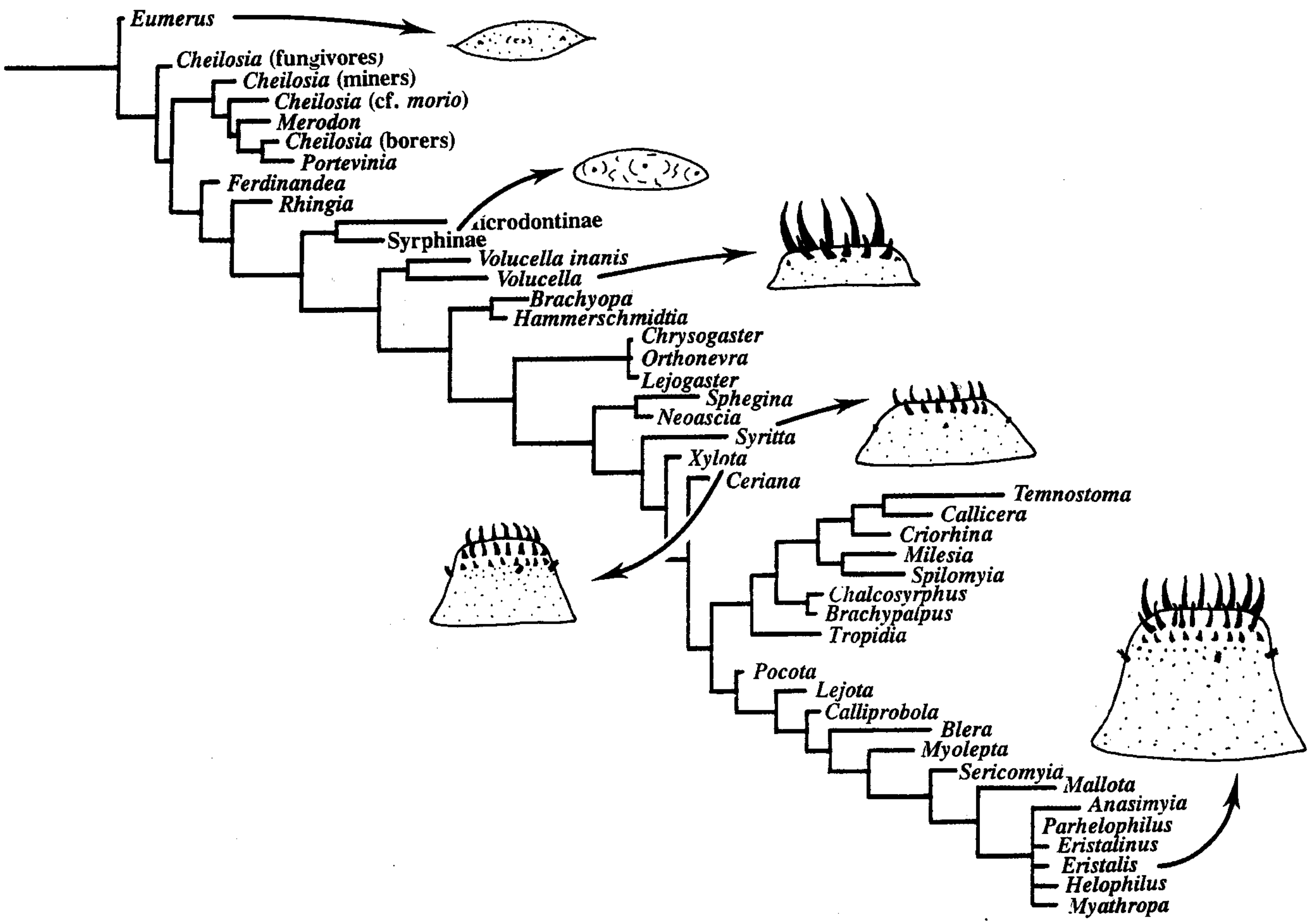

**Figure 3** The evolution of larval locomotory organs in hoverflies.

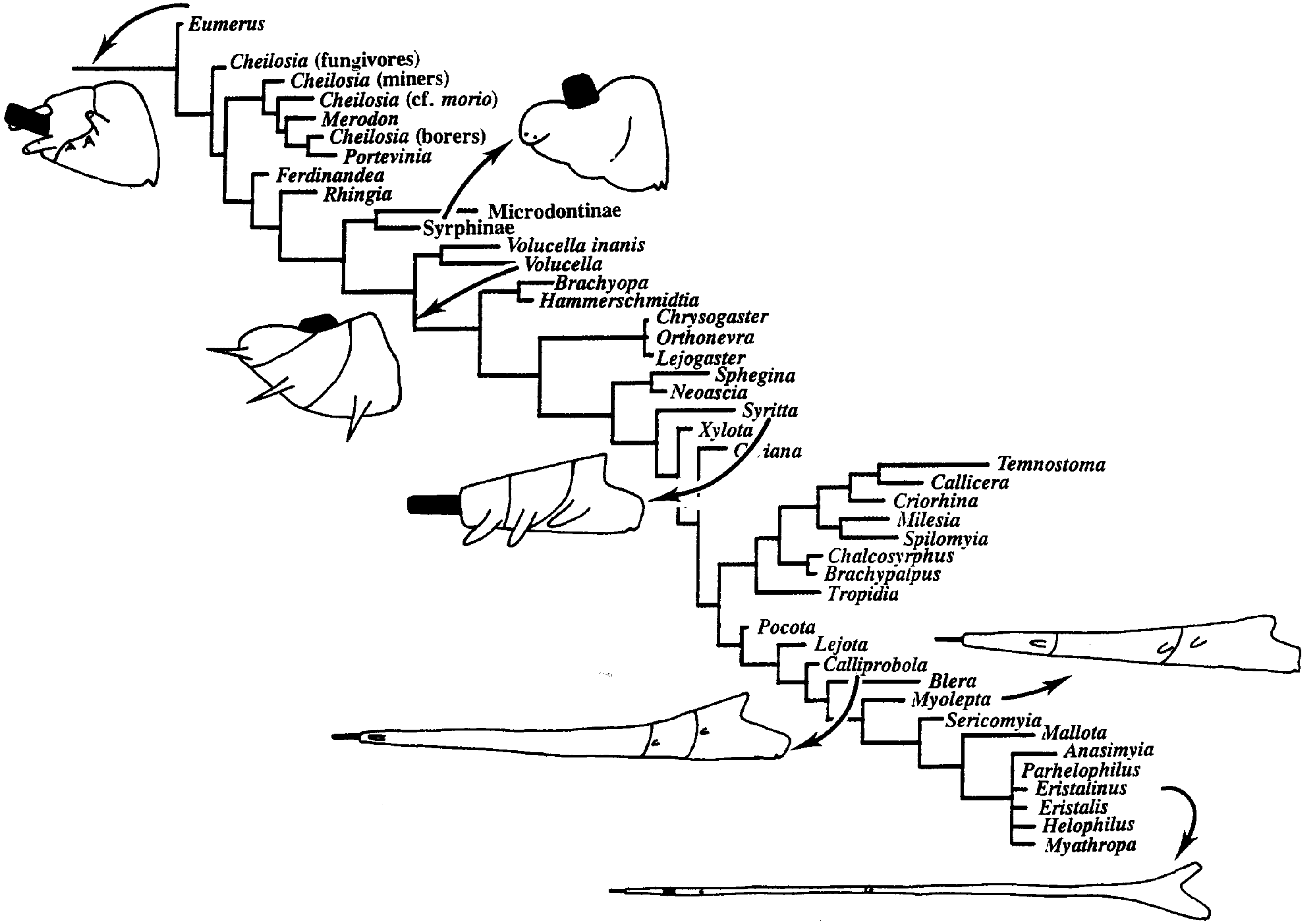

**Figure 4** The evolution of the anal segment in larval hoverflies.

phylogenetic relatedness show that predators are relatively small, and saprophages generally relatively large. In addition, phytophages lay few large eggs, whereas saprophages lay many small eggs (Gilbert, 1990). Now with an estimate of the phylogeny of the family, we can begin to assess the way in which larval and adult evolution are interlinked, as we look at the predatory syrphids, and in more detail within the genus *Platycheirus*.

## THE EVOLUTION OF PREDATORY GENERA

Our main current focus is on the evolution of predators, and in particular the evolution of specialized feeding habits (Owen & Gilbert, 1989; Rotheray & Gilbert, 1989; Gilbert, 1990; Gilbert & Owen, 1990). Very little is known about the selection pressures associated with predatory specialization (Bristowe, 1988; Gilbert, 1990).

Whilst there are three taxa of syrphid predators, we know very little about the microdons (mostly South American) or volucellines (relatively few species with rather poorly known behavioural ecology). Thus we concentrate on the aphid predators, the syrphines. They have an intrinsic interest since they are the only dipteran larvae with colours, used in crypsis (Rotheray, 1986), and they are economically important in aphid biocontrol (e.g. Chambers, 1986).

There are more than 1500 species of Syrphinae, covering very varied ecological types including feeding habits from extreme specialists to generalists. For example, *Triglyphus primus* larvae have only once been found feeding on any aphid other than in the galls of the aphid *Cryptosiphum artemisiae* on groundsel, *Artemisia vulgaris* (see Sedlag, 1966). In contrast, larvae of *Episyrphus balteatus* have been found on almost every aphid species that has been studied within its geographic range.

Again using larval characters, we have developed a generic phylogeny for this group (Rotheray & Gilbert, 1989: revised in Rotheray & Gilbert, unpublished manuscript). Figure 5 shows the resulting phylogeny. We used this in conjunction with two different types of data. The first is the type of aphid colony typically fed upon by members of the genus. There is a clear trend from genera feeding on aphids of the herb layer to genera feeding on arboreal aphids (see Gilbert, 1990). Interestingly the three genera furthest from the root of the tree (*Paragus*, *Scaeva*, *Eupeodes*) appear to have re-invaded herb-layer aphid colonies. In two of these, *Scaeva* and *Eupeodes*, a new U-shaped grasping organ allows greater efficiency in feeding on aphid colonies on stems: originally this organ may have evolved as an adaptation to feeding on aphids of conifer needles.

Is prey range influenced by phylogenetic relatedness? In an attempt to answer this we used the median number of prey species recorded for species in the genus, obtained from a comprehensive review of 20th-century literature on the family (Gilbert, unpublished). For these data to constitute an adequate test of whether there is an association between prey range and phylogeny, we would really need the prey range of the most plesiomorphic member of each genus. This we cannot estimate since we do not yet have species-level phylogenies of any but two to three syrphine genera.

In addition, these numbers may be especially biased for particular genera. For example, larvae of the plesiomorphic *Melanostoma* and some species of *Platycheirus* may be generalized predators in the leaf litter (Rotheray & Gilbert, 1989),

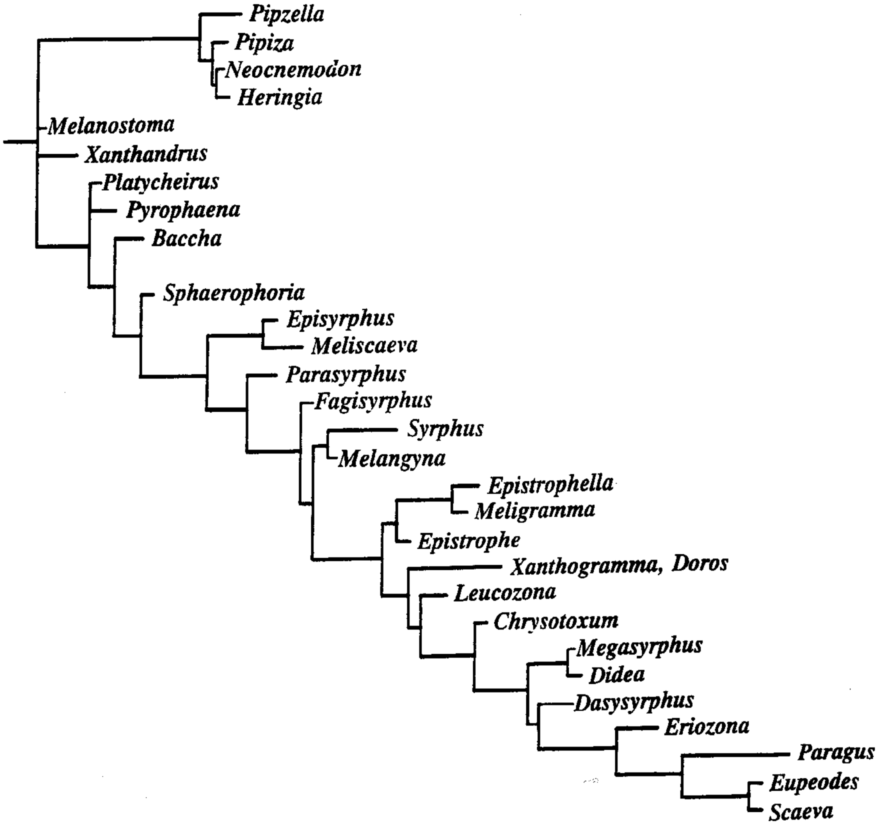

**Figure 5** The phylogeny of genera of the predatory hoverflies (the Syrphinae), based upon larval and puparial characters, and produced by the Hennig86 program.

rather than specific aphid predators. While the adults are enormously abundant, larvae are rarely found at all in aphid colonies in the field. It was believed at one time that these larvae fed largely on very small aphid colonies on grass, but could subsist on rotting plant material while they moved between aphid colonies (Davidson, 1922; Goeldlin, 1974). This is incorrect, since larvae cannot feed on autoclaved rotting leaf material (Zafar, 1987); they are more likely to be general zoophages feeding on arthropods in the leaf litter, but we really do not know.

A further problem is the misleadingly high number of hosts found for the genus *Eupeodes*, particularly the subgenus *Metasyrphus*. Here it is very probably true that the more plesiomorphic species have restricted prey ranges, since we suspect that many of these species are specialized on conifer aphids.

Testing these data with Lynch's phylogenetic heritability gives a value close to zero. This clearly does not support what seems to us to be a reasonably clear pattern, namely an increased degree of specialization in the more apomorphic genera. However, data quality at this generic level may be problematic: data at the species level are more promising (see below). There is even a suggested mechanism for a putative general drift towards specialization, namely escape from competition. Elsewhere it is shown that there is evidence that generalists compete, but no evidence that generalists compete with specialists, nor specialists with each other (Gilbert, 1990).

## THE GENERA *MELANOSTOMA* AND *PLATYCHEIRUS*

We now focus on one particular group of species in order to apply Lynch's methods to data at the species level. The genera we have chosen to use here are among the most plesiomorphic of the syrphines, and therefore may partly hold the key to the evolution of the predatory habit. *Melanostoma* and *Platycheirus* are overwhelmingly Holarctic genera with many species, especially *Platycheirus* (Vockeroth, 1990). All are small dark flies with a variable set of orange or white spots on the abdomen.

To generate the phylogeny, we need a set of characters that evolve reasonably quickly: larval characters may not be very useful because we suspect they evolve conservatively and, in any case, larvae are not available for many *Platycheirus* species. We therefore chose to use the remarkable forelegs of adult male *Platycheirus*. These have a great variety of extraordinarily modified hairs and tarsi (see Vockeroth, 1990); we suggest that these may be the result of a process of sexual selection similar to that which Eberhard (1985) hypothesized to be responsible for the remarkable variety of genitalic characters in animals. After careful examination of 83 species of *Platycheirus* (all the UK, three-quarters of the European and two-thirds of the Holarctic fauna), we settled upon 88 characters from the legs of the males. Male *Melanostoma* and *Xanthandrus* have unmodified legs, and we considered them to represent the outgroup. Full details of the character set and analysis will be published elsewhere (Emerson & Gilbert, in preparation).

The phylogeny of the 18 British species of *Platycheirus* (including the two species previously placed in the genus *Pyrophaena*, now a synonym: Vockeroth, 1990) shows three main branches (Fig. 6). The first leads to *P. manicatus*, and contains species where males have disc-like fore-tarsi and a thick brush of hairs along the fore-femur: although defined on the basis of non-metric adult leg characters, the

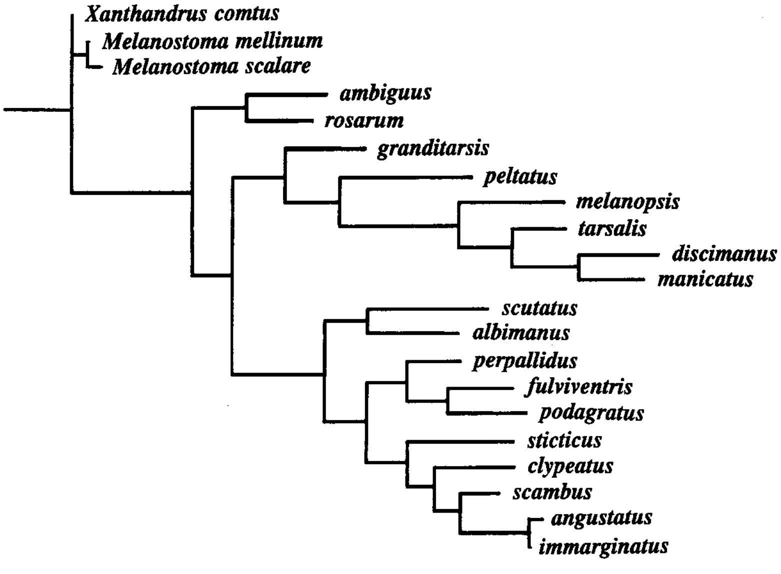

**Figure 6** The phylogeny of the genera *Xanthandrus*, *Melanostoma* and *Platycheirus*, based upon hairs and cuticular modifications of the legs of adult males, and produced using the Hennig86 program.

more apomorphic species of this line are also larger, and have increasingly long tongues. A second group has two species with peculiar hair clumps at the base of the fore-femur. The final branch leads to *P. immarginatus*, and the males of these species show a generalised flattening of the end of the foreleg: species of this line are also all specialist feeders on grass and other anemophilous pollens as adults, and have very short tongues. *Melanostoma* species also have these characteristics.

With this phylogeny, we can now explore the evolution of quantitative characters of morphology and ecology much more accurately than in the previous generic-level analyses.

## Morphological characters

Morphology is highly conserved during evolution: nearly all evolutionary change appears to represent size change with its associated allometry. We used data on head width, proboscis length and thorax volume: together these represent 'size' and 'proboscis shape', the two main determinants of foraging behaviour and activity (Gilbert, 1985a,b,d) and the major morphological differences between species (Gilbert, 1985c). All show high evolutionary heritabilities (thorax volume $h^2 = 0.35 \pm 0.13$; head width $h^2 = 0.64 \pm 0.13$; proboscis length $h^2 = 0.97 \pm 0.02$). It is interesting that the main food-niche determinant, proboscis length (Gilbert, 1981, 1985a), has the highest heritability.

Directional comparisons involve using the reconstructed ancestors at the nodes of the tree (Harvey & Pagel, 1991; Harvey & Purvis, 1991); such comparisons show a very tight covariance between evolution of size (thorax volume) and evolution in head width and proboscis length (Fig. 7). This in turn implies that the genetic links creating the allometry between size and shape have not changed during the evolution of the genus. Therefore the history of diversification in *Platycheirus* morphology is mainly one of size change.

## Ecological characters

For the 18 species of *Platycheirus* and the two *Melanostoma* we extracted from the literature (and from our own unpublished material) data on various ecological and morphological features, and tested whether they were associated with phylogenetic relatedness. These data were on the number of generations per year, the number of recorded prey species, morphology (head width, thorax volume, proboscis length: see Gilbert, 1985c), and abundance in one well-studied community (Owen, 1991).

Because the number of generations per year (1, 2 or 3) is not even approximately a continuous character, we used the non-parametric Mantel test (taken from Manly, 1985) to check for similarity between ecological and phylogenetic distance matrices. To generate distance matrices, we calculated a Euclidean distance between pairs of species using either the number of generations, or the number of character changes occurring on the tree (character states for nodes were taken from optimizations produced by the Hennig86 program). There is a significantly low value for the test statistic ($G = -2.64$, $P < 0.01$), indicating that the ecological and phylogenetic distance matrices are indeed related. This implies that the number of generations per year evolved conservatively during the evolution of the genus.

We also used the number of prey species per species, as recorded in the

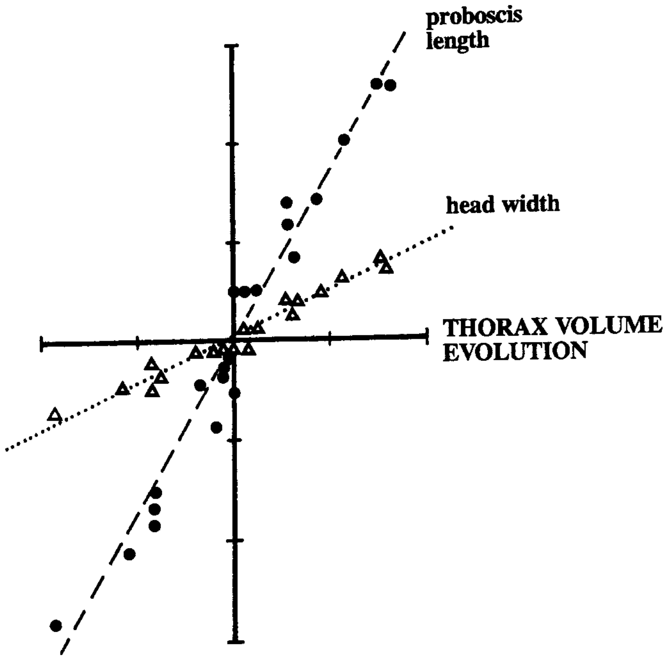

**Figure 7** Directional comparison (Harvey & Pagel, 1991; Harvey & Purvis, 1991) of the evolution of morphological characters in the genera *Melanostoma* and *Platycheirus*.

literature. Although these data are better than the generic-level data discussed above, there are major problems with these numbers, since *Melanostoma* and *Platycheirus* larvae are rarely found and even more rarely identified in field research work. Nevertheless, Lynch's phylogenetic heritability is low but significant ($h^2 = 0.09 \pm 0.038$, $P < 0.05$, $N = 20$), and its additive genetic covariance with size (head width) is negative. Thus in evolving to larger body sizes, there is an associated evolutionary decrease in prey range. This result is all the more remarkable because, with some notable exceptions, there is a very strong emphasis in the literature on ecological rather than historical forces explaining prey range (but see Futuyma & Moreno, 1988; Berenbaum, 1990a,b). Prey range has almost always been viewed as a product of current-day forces, at an equilibrium with natural selection. However, this result shows a historical component: prey range in one species is constrained by the prey range of its ancestors. These species-level data also support our contention that the evolution of prey range is a history of increasing specialization.

Even abundance is significantly associated with the phylogeny. Abundance measures are taken from Jennifer Owen's long-term study of insect populations in a suburban garden (Owen, 1981, 1991) which are correlated with abundances elsewhere in Europe (Owen & Gilbert, 1989). We used the sum of 20 years of trap catches as our estimate of abundance, and find that this measure contains a significant phylogenetically heritable additive component ($h^2 = 0.09 \pm 0.038$). Since abundance is measured at only one site, we expect only a crude relationship if any. The direction of change is that the more apomorphic species are rarer, and again there is a negative additive covariance with size evolution. Nee *et al.* (1991) have already demonstrated that there are taxonomic differences in the relationship between body size and abundance. Here we have shown explicitly an effect of phylogenetic relatedness on relative abundance.

### Behaviour and growth

Finally we focus on six species studied intensively in the laboratory under controlled conditions (Zafar, 1987). We are interested in the evolution of behavioural components of predation in the two *Melanostoma* species and four *Platycheirus*. The behavioural components of predation are exceptionally easily studied in syrphines (Rotheray, 1983, 1987, 1989), because the behavioural process of searching, attacking and feeding on aphids is so easily quantified. For each species under standardized conditions of age, starvation and temperature, we measured the average casting rate, capture rate, capture efficiency, handling time and the casting-rate response to a short period of starvation. In addition we fitted two-parameter growth curves (Koijman, 1986) of the form:

$$dW/dt = aW^{2/3} + 3bW \tag{1}$$

We fitted this equation to data for each species using the statistical program Statgraphics™, and tested the two fitted parameters, *a* and *b*, for the influence of phylogeny.

If increasing specialization involves becoming more efficient as a predator (Futuyma & Moreno, 1988), we predict that specialization will entail increases in the casting rate, capture rate and growth rate, whilst also involving decreases in handling time. We have used casting rate (the rate of making searching movements: see Rotheray, 1983, 1987, 1989) as a reference for directional comparisons because of our doubts about the quality of the data on prey range. The additive-value regression of casting rate on prey range is negative (-0.35 ± 0.15), as predicted. Because we have data for only six species, significance tests are of dubious validity (see the example used by Lynch, 1992). We are, however, able to consider the sign of the slope of the directional comparisons, and in every case the slope of evolutionary change is as predicted (Fig. 8). The additive-value regressions are strongly influenced by the large amount of evolutionary change occurring between the genera *Melanostoma* and *Platycheirus*: however, only one additive-value regression slope (handling time) changes when this point is removed.

## CONCLUSIONS

The new techniques now available constitute a significant advance for the comparative method. In conjunction with new multivariate methods, developed for relating environmental factors to species abundances (CANOCO, see ter Braak, 1986), we can now relate evolutionary change in a set of multivariate characters to environmental differences between the habitats in which they live. We have shown here that phylogenetic influence extends to all types of ecological, behavioural and morphological characters. This means that any sort of comparison between species must involve a phylogenetic component. The new techniques open up comparative analysis in an entirely new way. As Harvey & Pagel (1991: 203) discuss, the

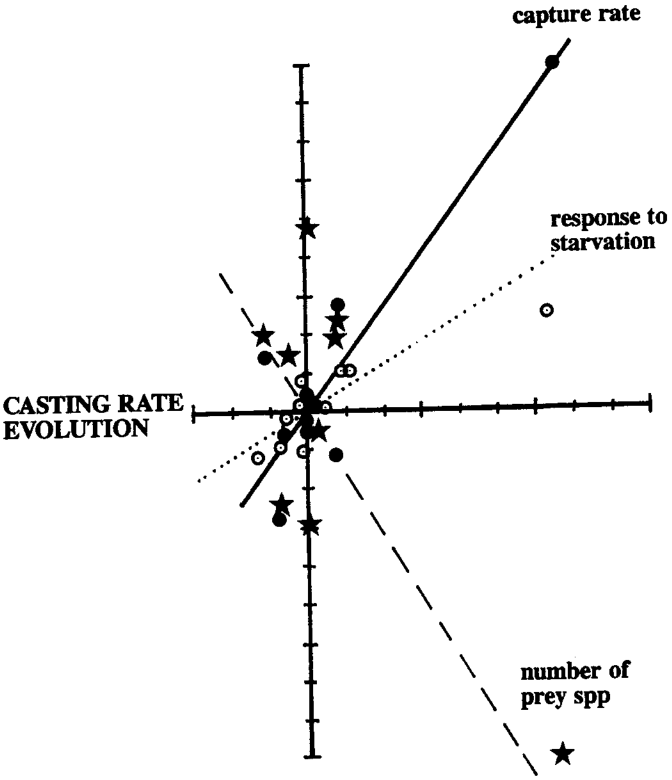

**Figure 8** Directional comparisons of the evolution of ecological and behavioural characters of the foraging behaviour of *Melanostoma* and *Platycheirus* larvae. The outlier points document the evolutionary change from *Melanostoma* to *Platycheirus*.

voluminous and accurate comparative data we have will soon be treated with just as much respect as experimental results on individual variation.

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