Improving knowledge of the cyclorrhaphan larva (Diptera)

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ABSTRACT
A significant factor in the evolution of the Cyclorrhapha (Diptera), the most biodiverse of higher dipteran taxa, is the larva. The larva also has wide-ranging trophic and environmental relationships, including positive and negative impacts on human health and wealth. Despite its importance, the larva is neglected and a low proportion of species are known in this stage. In this paper, factors contributing to larval neglect are reviewed, including: poor attitudes leading to cycles of neglect and shallow treatment; taxonomy that uses adult not larval stages; lack of material in collections; rearing barriers, and presumptions of morphological similarity suggesting that characters will be problematic to acquire and analyse. Neglect is pervasive and affects many subjects; those considered here are: species inventories and rarity assessments for biodiversity and conservation, in which larvae are usually ignored although they can be more cost-effective to sample and a richer source of environmental data; determining larval feeding modes where controversies due to conflicting evidence persist unresolved; and reliance on a limited pool of increasingly old publications whose data are repeated rather than tested and updated with new research. In an attempt to reinvigorate interest, which is the main aim of this paper, poorly assessed larval features possibly significant to cyclorrhaphan diversification are also considered. These include: change facilitated by independently evolvable modules; rapid change enabled by labile trophic morphology; shifts between saprophagy and phytophagy due to opportunities provided by angiosperm evolution; and enhanced adaptive potential resulting in derived more than basal taxa developing adaptations that enable access to new and little used resources. Apart from the need to rear more larvae, a major conclusion from this review is that knowledge will improve when the movement capabilities of larvae are used to inform morphological and taxonomic analyses.

Introduction
In 1863 the Viennese Dipterist Frederich Brauer proposed the taxon Cyclorrhapha for true fly species (Diptera) with a puparium, the dried, inflated, larval integument that shelters the pupa (Figure 1). Higher group analyses consistently recover and support this
taxon (Griffiths 1972; McAlpine 1989; Cumming et al. 1995; Wiegmann et al. 2011; Lambkin et al. 2013) and with 65,000+ named species and 91 families, the Cyclorrhapha includes the largest fraction of known dipteran diversity, more than 40% (Wiegmann et al. 2011).

The most comprehensive estimate of cyclorrhaphan relationships is by Wiegmann et al. (2011). In this estimate, families of the paraphyletic Aschiza (flat-footed flies, big-headed flies, hoverflies) are followed by the Schizophora. Within the Schizophora, the paraphyletic Acalyptrata (fruit flies, shoot flies, shore flies) is followed by the Calyptrata (blow flies, flesh flies, parasitic flies). Estimates of divergence times reveal that, compared to the Aschizan stem, the Schizophoran crown radiated rapidly, and the uncertain taxonomy and lack of features that apparently characterise many Schizophora are considered a consequence of rapid diversification.

A hallmark of Endopterygote insects, such as the Diptera, is independent evolution of life stages, and an evolvable larva has been put forward to explain, in part, the mega-diversity of the Cyclorrhapha (Hennig 1943; Rohdendorf 1974; Courtney et al. 2000; Wiegmann et al. 2011). Apart from high biodiversity, ecosystem roles of the cyclorrhaphan larva include re-cycling through saprophagy (McLean 2000; Martínez-Falcón et al. 2011); influences through mycophagy, phytophagy and zoophagy; and dependent natural enemies ranging from viruses to vertebrates (McLean 2000; Brown et al. 2009/10). Also extensive are impacts on humans, including both beneficial and harmful effects (Papp and Darvas 2000).

Despite their significance, a striking contradiction exists in that compared to the adults, cyclorrhaphan larvae are poorly sampled and most species are unknown in

Figure 1. Cyclorrhaphan third stage preserved larva and empty puparium, lateral views, head to the right. a, Coelopa frigida (Coleophidae), length 14 mm; b, Oecothea praecox Loew (Heleomyzidae), length 9 mm.
their larval stages (McAlpine et al. 1987; Papp and Darvas 1998, 2000, Brown et al. 2009/10). For such an important life form, the cyclorrhaphan larva is one of the most overlooked. Such neglect is not confined to the Cyclorrhapha, but is an entrenched feature affecting most Endopterygota (Emden 1957; Meier and Lim 2009).

In this paper, especially as they affect the fundamentals of character assessment, taxonomy and systematics, factors contributing to the neglect of the cyclorrhaphan larva and certain consequential effects are reviewed. Emphasis is given to the final-stage larva (Figure 1). Of larval stages, this is the most complex, has the greatest impact and is the stage most frequently described (Ferrar 1987). With the aim of reinvigorating interest, also considered are poorly assessed larval characteristics possibly contributing to cyclorrhaphan diversification, such as evolvable body modules that facilitate change, labile trophic morphology that facilitates rapid change, shifts between feeding modes such as saprophagy and phytophagy, and changes in adaptive potential.

**Causes of neglect**

**Attitudes**

Attitudes partly explain the ambiguity of a significant yet neglected cyclorrhaphan larva. Wheeler (2008) argued that in phylogenetic systematics, morphology and molecules should be equal partners, and many of the points made by Wheeler (2008) in support of morphology apply to the cyclorrhaphan larva relative to the adult. For instance, Wheeler (2008) discusses concerns that morphological characters are complex, difficult to analyse and less numerous than molecular ones. Such concerns seem to similarly discourage attempts to obtain larval data, and concerns are heightened by suspicions that larvae are especially difficult due to their supposed widespread morphological similarity (Ferrar 1987).

As a result, a self-reinforcing cycle of neglect and shallow treatment exists that inhibits the development of an improving state of knowledge. This is evident in chapters dealing with individual cyclorrhaphan families in Diptera monographs such as McAlpine et al. (1987), Papp and Darvas (1998, 2000) and Brown et al. (2009/10). Lack of data forces many authors to deal with larvae simplistically and they are introduced using stock phrases of the type ‘typical maggots with a smooth cuticle’, ‘larva whitish, tapered anteriorly, truncated posteriorly’, ‘standard muscomorph larva’, etc. Such generalised references are followed by character summaries of a similar nature, with the probable consequence that the potential significance of larval data is poorly perceived, which reinforces neglect and vice versa.

Furthermore, investigators tend to work with only one or a few related cyclorrhaphan families. The result is inward-looking attitudes and research agendas tied to particular taxa. While to some extent taxon-specific research is inevitable, it overlooks the value of comparing and integrating data across cyclorrhaphan families to recognise similarities and differences, expose errors and improve understanding. For example, in one of the few studies of its type, Roberts (1971) combined direct observation of larval behaviour with morphological analysis of preserved specimens to explain feeding mechanisms in calliphorid (Calliphoridae) and muscid (Muscidae) larvae (i.e. how food is transferred from an external source to the gut). Using a similar approach but supplementing
observed behaviour with films, Rotheray and Lyszkowski (2015) and Rotheray and Wilkinson (2015) investigated mechanisms of larval feeding and movement in 22 species from 10 cyclorrhaphan families. In these three studies, functions and movement capabilities were established for many components, new morphological and behavioural characters discovered and disparate morphology and behaviour integrated into holistic explanations of larval feeding and movement.

Using movement to inform morphological analysis is hardly new. Yet it is an approach rarely applied to cyclorrhaphan larvae, which, if they were larger animals, would probably be considered unusual and a priority for improving knowledge. Using film to record movement has many advantages; a permanent record is made and roles and details of rapidly moving components are resolvable and quantifiable. For instance, Rotheray and Lyszkowski (2015) filmed movement in mandibles and found that a species characteristic of schizophoran larvae was movement in either a parallel or a diverging plane. Furthermore, planes of movement and mandible shape appear to relate to food quality, in the direction of the harder the food the more parallel the movement and, usually, the shorter and wider the mandible hook. In gathering hard food, parallel movement concentrates scraping to a confined area, and a short, wide hook is a robust shape for withstanding the forces involved. In contrast, diverging mandibles and long, narrow hooks, often scalloped or flattened on the inside margin, optimise the amount of soft food scooped per feeding lunge. Mechanistically, planes of movement are governed by the angle of inclination of a linear, hinge joint which connects the mandible with the sclerite against which it articulates. Examples like these help counter the notion that larval morphology lacks potential and is difficult to analyse.

**Taxonomy**

A prosaic reason for neglect is that cyclorrhaphan taxonomy uses adult more than larval characters (Emden 1957; Meier 1995; Rotheray and Gilbert 2011). So, at the fundamental level of discovering, recognising and describing taxa, there is no reason to include the larva. This factor also explains the lack of preserved larvae in collections, another barrier to progress.

Finding and rearing larvae can, however, enhance discovery rates of new taxa (Rotheray et al. 2001, 2007). Larval morphology can also test taxonomic hierarchies derived from adults. Compared to adult morphology, larvae might appear featureless and impoverished; obviously they lack the character wealth found in, for example, wings and genitalia. Nonetheless, body size and shape, adornment or vestiture, and trophic, locomotory and respiratory structures have diversified greatly and are rich in features (Hennig 1952; Teskey 1981; Ferrar 1987; Courtney et al. 2000). At low taxonomic levels, such as congenerics, larvae might be difficult to distinguish, but with limited sampling and superficial assessment, this is not well tested (Meier 1995). For instance, British species of the genus *Lonchaea* (Lonchaeidae) are readily identified by larval and puparial characters, and species inventories are feasible based on sampling empty puparia left behind at development or breeding sites (MacGowan and Rotheray 2008), but how typical this example is among the Cyclorrhapha is uncertain. Lonchaeid larvae are also distinguished by feeding mechanism (Rotheray and Lyszkowski 2015) which does not
support Hennig (1952) who commented that in the Lonchaeidae, changes in larval feeding habit have been made without morphological adaptation.

Across the Endopterygota there are, however, opposing views as to the phylogenetic value of data from the larval stages. Meier and Lim (2009) assessed how well larval versus adult data supported nodes in published estimates of phylogeny across Endopterygote groups. Given the state of larval knowledge (i.e. usually less numerous larval characters and missing data), it is not surprising that the analysis found adult characters yielded higher support. Until larvae are better understood, the relative value of the two stages for taxonomy and phylogenetic systematics remains uncertain, although the question is really redundant under the approach of combining data from independent sources for inclusive analyses (Hennig 1943, 1966; Wheeler 2008).

**Collecting and rearing**

A deterrent to using larval data is the effort it takes to acquire them. With little preserved and identified material in collections, larvae have usually to be obtained from the field, and because few can be identified they must be reared (Meier and Lim 2009; Rotheray and Gilbert 2011). This means finding development sites, but for the majority of flies these are unknown or known imprecisely (Perry and Rotheray 2010). Even if found, rearing is risky due to mortality in cultures and the time it takes (often months and even years; Coe 1941), and unless exemplars are preserved, the larva is lost during metamorphosis.

An alternative method to collecting larvae from the field is inducing gravid females to oviposit under laboratory conditions. For example, Semelbauer and Kozánek (2012) obtained lauxaniid larvae (Lauxaniidae) using this method, which has the advantage of providing access to all life stages. A disadvantage is a lack of knowledge of natural development sites and breeding populations.

Rearing larvae can take time and effort, but the knowledge gained of bionomics, characters, development sites, distribution and abundance argues it is worth the attempt. Larval identification keys and DNA barcoding can bypass the difficulties of rearing, but few keys and barcodes are available. Even if available, just as with adults, they do not replace the need to have collections of preserved material for morphological study and re-study.

**Morphological similarity**

In an influential account of cyclorrhaphan breeding sites and immatures, Ferrar (1987) suggests that larval morphology is ‘functional’ with similarities according to diet, locomotion, respiration and protection. Finding characters and homologies will be difficult if larvae really are similar. Hinting that similarity is not a feature of larvae more than adults, in phylogeny estimates across endopterygote groups, Meier and Lim (2009) found no evidence that levels of homoplasy affect larvae more than adults. Nonetheless, for cyclorrhaphan larvae the magnitude of similarity is suspected to be high, and the idea alone is probably a deterrent.

For diet, comparing trophic structures (i.e. whole head skeletons) by feeding mode reveals no obvious similarity (Figures 2–4). Head skeletons may, nonetheless, possess
one or two characters indicative of diet. Attempts to find such characters have a long history (Keilin 1917; Keilin and Tate 1930; Dowding 1967; Roberts 1971; Skidmore 1985; Ferrar 1987). A similarity proposed for predation is a long, curved mandible which suits piercing prey (Figure 2g, h); for phytophagy mandibular teeth for rasping tissue (Figure 3b, c); and for saprophagy, cibarial or pharyngeal ridges for filtering food (Figure 5). These putative similarities are difficult to assess because of the uncertain frequency of exceptions (Ferrar 1987; Rotheray and Lyszkowski 2015). For example, not all predacious and phytophagous larvae possess curved mandibles (Figure 2b, k) and mandibular teeth (Figure 3d, e), respectively, and curved mandibles and mandibular teeth are also present in saprophagous larvae (Ferrar 1987; Semelbauer and Kozánek 2012; Rotheray and Lyszkowski 2015).

Cibarial ridges run along the floor of the head skeleton (Figure 5); Dowding (1967) demonstrated their role in filtering particulate food. Not all saprophagous larvae possess them, for example some or all Heleomyzidae (Skidmore 1966; Rotheray 2012), Muscidae

Figure 2. Head skeletons of exemplar zoophages, lateral view, mandible towards centre; figures in parentheses are lengths of the basal sclerites in mm. a, Protocalliphora azurea (Fallén) (Calliphoridae) (0.7); b, Leucopsis puncticornis Meigen (Chamaemyiidae) (0.3); c, Physoscephala sp. (Conopidae) (0.2); d, Neottiophilum praestum (Piophilidae) (0.9); e, Ilone albiseta (Sciomyzidae) (0.5); f, Chalarus sp. Walker (Pipunculidae) (0.1); g, image of Phaonia subventa (Harris) (0.6) and drawing of mandible (Muscidae); h, Megamerina dolium (Fabricius)(Megamerinidae) (0.5); i, Tachina grossa (L.) (Tachinidae) (1.3); j, Speccafrons halophila (Duda) (Chloropidae) (0.3).
In addition, some larvae possessing cibarial ridges combine saprophagy with phytophagy or zoophagy (Dowding 1967; Ferrar 1979). Mixed saprophagous/predacious muscid larvae (Muscidae) may bypass the ridges when feeding on prey (Ferrar 1979). This is achieved by opening the pharynx, so that food passes directly to the gut (Figure 5). Some larvae within the Syrphidae (Hartley 1963; Roberts 1969) and Tephritidae (Hagen 1966; Fitt and O’Brien 1985) are like phytophages in fragmenting and consuming plant tissue, but some of this comminuted tissue is not consumed and decays (Supplemental material 2.1). Like saprophages, these larvae ingest the decay and use the ridges to filter microbial food (Creager and Spruijt 1935; Roberts 1969; Ricarte et al. 2008). Mixed saprophagous/phytophagous feeding may be more common than realised and might be a means of overcoming digestion barriers presented by plant tissue.

(Ferrar 1979), Chryomyidae and Camillidae (Rotheray 2011), Piophilidae (Rotheray and Hancock 2012), Clusiidae (Rotheray and Horsfield 2013) and Calliphoridae, Lonchaeidae and Milichiidae (Rotheray and Lyszkowski 2015). In addition, some larvae possessing cibarial ridges combine saprophagy with phytophagy or zoophagy (Dowding 1967; Ferrar 1979). Mixed saprophagous/predacious muscid larvae (Muscidae) may bypass the ridges when feeding on prey (Ferrar 1979). This is achieved by opening the pharynx, so that food passes directly to the gut (Figure 5). Some larvae within the Syrphidae (Hartley 1963; Roberts 1969) and Tephritidae (Hagen 1966; Fitt and O’Brien 1985) are like phytophages in fragmenting and consuming plant tissue, but some of this comminuted tissue is not consumed and decays (Supplemental material 2.1). Like saprophages, these larvae ingest the decay and use the ridges to filter microbial food (Creager and Spruijt 1935; Roberts 1969; Ricarte et al. 2008). Mixed saprophagous/phytophagous feeding may be more common than realised and might be a means of overcoming digestion barriers presented by plant tissue.
Furthermore, in some saprophages ridges are reduced and vestigial, as in certain Heleomyzidae (Rotheray et al. 2016) (‘cibarial ridges’ in Supplemental material 1). Vestigial ridges are an intermediate step to their elimination altogether and these states could enhance performance, speeding the energy-efficient transfer of food to the gut (Rotheray and Lyszkowski 2015). Exceptions, mixed feeding modes and vestigial states complicate the idea that cibarial ridges make saprophagous larvae similar.

If diet has a weak relationship with trophic morphology, a stronger one might be with food quality. Food quality affects trophic morphology through the diversity of biomechanical challenges presented by food that varies from hard solids to watery liquids (Rotheray and Lyszkowski 2015). For example, in phytophagous Cheilosia larvae (Syrphidae), mandibular teeth correlate to food quality. At extremes of hard and soft food, larvae adapted to these qualities are indicated by the size and number of mandibular teeth, in the direction of the harder the food, the fewer and larger the teeth (Rotheray 1990). A similar continuum is apparent in the functionally similar but morphologically distinct labial teeth of platypezid larvae (Platypezidae) (Rotheray et al. 2004).
Figure 5. Cibarial ridges and head skeleton pump in the basal sclerites of cyclorrhaphan larvae, mandibles to the left. a, head skeleton in situ, third stage larva of *Alipumilio femoratus* Shannon (Diptera, Syrphidae), ventro-lateral view, 1 = mandibles, 2 = cibarial ridges on the floor of the basal sclerite; b, *Eumerus* sp. Meigen (Syrphidae), lateral view, 3 = pharynx running along the floor of the basal sclerite, 4 = valve at the rear of the upturned ventral cornu, 5 = bands of muscle originating on the dorsal cornu and inserting on the roof of the pharynx and the ventral cornu that operate the pump, specimen prepared and donated by C.J. Hartley to the National Museums, Scotland.
Larvae ingesting hard food tend to have large, heavily sclerotised head skeletons (Figures 2j, 3g, 4g), while those ingesting watery food are smaller and lightly sclerotised (Figure 4a, e, f) (Rotheray and Lyszkowski 2015). Behind this superficial similarity many differences exist; for example, the mandibles of larvae feeding on hard food tend to be one of two inexact types. One has a hook of variable length with a rectangular base (Figure 4g, k) and, during food gathering, a narrow range of movement. The other has a mandible with a short hook, a lozenge-shaped base (Figures 2g, 3b, 4b) and wider movement. In both types, as noted above, the mandibles do not diverge on lowering, dental sclerites are often replaced by oral plates (Figure 6b) and intermediate sclerites tend to be short, block shaped or fused or closely aligned to the basal sclerite (Figures 2j, 3e, 4b, g). In larvae ingesting watery food, mandibles are of variable shape, dental sclerites present or absent, intermediate sclerites bar-shaped (Figure 4a, e, f) and the mandibles diverge on lowering (Rotheray and Lyszkowski 2015).

In larvae ingesting watery food, the intermediate and basal sclerites are often fused to support a nozzle-shaped pharynx (Figures 2b, 3j, 4a), but in larvae ingesting hard food, various alignments occur. With mandibular muscles originating on the basal sclerite (Miller 1932; Hartley 1963; Roberts 1970), alignment buttresses the head skeleton against distortion from the greater forces required to gather hard food (Rotheray and Lyszkowski 2015). Alignment varies from little (Lonchaea sylvatica Beling (Lonchaeidae) Figure 4k) to some (Dasiops latifrons (Meigen) Figure 3e), to more (Stegana coleoptrata (Scopoli) Figure 4g) to complete alignment and fusion (Loxocera sylvatica Meigen Figure 3g). In some larvae that ingest hard food, such as S. coleoptrata, the mandibles are fused, which adds even more structural strength. Food quality may better predict trophic structures than diet does, but nonetheless the similarities in the species considered here are superficial; detailed study reveals that beneath them, trophic morphology is disparate and variable.

Body shape modified for locomotion is another proposed similarity (Ferrar 1987). For instance, larvae may be flattened for movement in narrow spaces, such as between decaying leaves in Lonchoptera larvae (Lonchopteridae) (de Meijere 1901; Hennig 1976); between the gills of lignicolous fungi in larvae of the platypezid genera Calotarsa, Paraplatypeza, Platypeza and Protoclythia (Rotheray et al. 2004); and between adpressed leaves in water tanks of bromeliads (Bromeliaceae) in certain Copestylum larvae (Syrphidae) (Rotheray et al. 2007) (Supplemental material 2.2). Taxonomic affinities are retained in these larvae, and beyond being flattened, little else is similar.

Syrphine larvae (Syrphidae) living on plants can also be flattened (Supplemental material 2.3), but this correlates to a different functional role: that of reducing shadow as part of crypsis (Rotheray 1986). A number of species are involved and their larvae are flattened to varying degrees, and some not at all (Dixon 1960; Rotheray 1986). Some Leucopis larvae (Chamaemyiidae) live on plants and are flattened but not cryptic. Flattening also occurs in larvae not necessarily living in narrow places or exposed on plants, such as those of the Fannidae and Periscelididae (Ferrar 1987). Flattening in these larvae increases the amount of body surface in contact with a substrate and, in another functional role, appears to enhance gripping and holding on.

Other shapes exist. Certain larvae of the Anthomyiidae and Tephritidae have short, broad bodies fitting space at their development sites, Asteraceae flowerheads, but not all larvae found in these flowerheads have shortened bodies – for example, Pallopteridae
In contrast, leaf-mining larvae in the former two families are long and thin, enabling them to fit inside leaves (Rotheray and Lyszkowski 2015). Again, not all leaf-mining larvae are elongate – those of the genus *Cheilosia* (Syrphidae), for example, are not (Rotheray 1988; Schmid 2000). Extreme shape modifications also occur, such as

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(Figure 6. Morphological features of the schizophoran head skeleton, pseudocephalon and prothorax, lateral view, mandible to the left. a, *Palloptera trimacula* (Pallopteridae) head skeleton extracted from a puparium, 1 = dental sclerite, 2 = cirri coating sides of the oral cavity, 3 = mandibles, 4 = apodeme on postero-dorsal apex of mandible base on to which elevator muscles insert, 5 = parastomal bars, 6 = dorsal bridge, 7 = dorsal cornu of basal sclerite, 8 = dorsal apodeme of ventral cornu, on or near to which mandibular elevator and depressor muscles originate, 9 = ventral cornu, in life apex upturned, 10 = basal sclerite, 11 = ventral bridge of the intermediate sclerite, 12 = labial sclerite; b, *Palloptera scutellata* (Macquart) (Pallopteridae), third stage preserved larva, in situ head skeleton, head cleared in potassium hydroxide (KOH), length = 1 mm, 1 = oral cavity, 2 = antennomaxillary organs, 3 = pseudocephalon, 4 = prothorax, 5 = anterior spiracles, 6 = mesothorax, 7 = muscles that insert on the apex of the oral plate, 8 = oral plate, a translucent sclerite appearing under the head skeleton, attached at apical end to the posterior margin of the oral cavity.)
the extraordinary length (more than 30 times as long as wide) of cambium-mining Phytobia larvae (Agromyzidae) (Ferrar 1987; Ylioja et al. 1998), and the leaf-mining larva of Pegomya solennis (Meigen) (Anthomyiidae) which has a remarkable asymmetrical pseudocephalon, flattened more on one side than the other. This enables the head to fit against the face of the mine in the exceptionally narrow leaf of the food plant. Furthermore, the mandibles overlap, with the result that teeth from each mandible are at the same height, enabling both to rasp tissue (Rotheray and Lyszkowski 2015).

Some larvae have flexible shapes, such as those of Meiosimyza Hendel (Lauxaniidae) and Pipiza Fallén (Syrphidae) which flatten themselves to overcome spatial restrictions in leaf litter and aphid galls, respectively (Rotheray and Lyszkowski 2015). Also, certain Copestylum larvae (Syrphidae) are able to extend or retract body length, to match available space in flowers (Ricarte et al. 2015). Again, in all these larvae, body shape appears not to be associated with similarities in other features, and they retain their taxonomic affinities (i.e. similarities are superficial).

Adornment for protection is also a proposed similarity (Ferrar 1987). Protective roles of adornment are varied and, apart from protecting against abrasion, include protection against desiccation, blockage of respiratory structures and natural enemies. For instance, sap runs can start and stop in an unpredictable fashion and to cope with periods when they stop and dry up, larvae developing in them often have thick, blotchy integuments that resist desiccation (e.g. Periscelididae, some Syrphidae). Posterior spiracles are protected by various adornments, including interspiracular setae, sclerotised projections of the spiracular plate and surrounding membranous projections. Adornment that protects against natural enemies is less clear. Some larvae have tapering projections, many bearing tactile sensilla that might warn of an approaching enemy; or they are sacrificed in predator mouthparts and, with the predator so distracted, the larva escapes [e.g. Microdon and Volucella larvae (Syrphidae) in ant and wasp nests, respectively (Rotheray and Gilbert 2011)]. They may also act as foci for material from the development site to encrust and thereby disguise larvae, or deflect predator bites and parasitoid ovipositors. Sclerotised plates may similarly deflect bites and ovipositors. Plates most obviously protect against abrasion, such as those of disparate size, shape and arrangement found on certain burrowing larvae (e.g. Platpezidae, Syrphidae). That larvae require protection from abrasion in other circumstances is suggested by cuts and wounds, whose healing is revealed by black marks on the integument (Rotheray and Lyszkowski 2015). Marks like these are frequent, especially in saprophagous larvae.

The typical adornment is a spicule (Figure 7). These micro-hooks usually coat the front of the prothorax and the locomotory pads that straddle segment borders, and surround the anus. They sometimes coat other areas of the body, such as forming rings on body segments (Figure 7). At all these locations, they not only protect against wear and tear but also prevent slippage during movement (Roberts 1970; Rotheray and Lyszkowski 2015). Spicules are diverse. On locomotory pads, for instance, they appear to correlate to degree of confinement in the direction of the tighter the space, the more reduced the spicules (Rotheray 2014). This is because, in confined spaces, the larva is able to hold on with the lateral and dorsal aspects of the body, rather than just the ventral surface. Examples are the larvae of Palloptera modesta (Meigen) (Pallopteridae) which develops in the confined space of seed-filled Asteraceae flowerheads, and Palloptera usta (Meigen) which develops under bark,
where space is actually not as confined. The former species has three rows of soft, blunt-tipped, locomotory spicules; the latter several rows of variable, sclerotised, thorn-like spicules (Rotheray 2014). Similarly, the larva of *Suillia laevifrons* (Loew) (Heleomyzidae) excavates a tunnel through compact tissue in stems of its food plant, *Luzula pilosa* (L.) Willd. (Juncaceae), and has relatively few spicules compared to *Suillia ustulata* (Meigen) which excavates a tunnel in relatively loose tissue in stems of its food plant, *Sambucus nigra* L. (Adoxaceae) and which has many more spicules (Rotheray 2012).

Spicules vary in size, shape, arrangement, distribution, colour and degree of sclerotisation. They are a source of taxonomic characters in all groups where they have been assessed, such as the Syrphidae (Rotheray and Gilbert 1999), Lonchaeidae (MacGowan and Rotheray 2008), Heleomyzidae (Rotheray 2012), Clusiidae (Rotheray and Horsfield 2013) and Pallopteridae (Rotheray 2014). With diversity in protective roles and types of adornment, similarities between larvae are limited.

Indeed, across the character systems referred to by Ferrar (1987) as similar and the examples considered here, apparent similarity is rarely more than superficial. Underlying it are the signatures of taxonomic groundplans modified in diverse ways, with the potential to extract from them a wealth of phylogenetically informative character data. Morphological similarity is known, however (i.e. the same features changing almost identically, yet independently, in response to environmental variables). Parallel evolution of this type was identified by Chapman et al. (2006) in a detailed molecular and morphological analysis of habitat shifts in snail-killing larvae of the genus *Tetanocera* (Sciomyzidae). Three independent shifts from aquatic to terrestrial habitats were found, each accompanied by the same sets of morphological change. Genetic architecture and developmental pathways are likely to be shared among these *Tetanocera* species, so it is not surprising that in response to similar environmental variables, similar change occurs. The corollary is that in more distantly related taxa, such high levels of correspondence are less likely.
Consequences

Inventory and status

Species inventories and status or rarity assessments are typically based on adults. Inventories are sometimes more effective if larvae are included. In northern forests, for instance, adults can be problematic to sample because they stay close to development sites – for example Syrphidae at sap runs (Rotheray 1996) and Clusiidae on fallen wood (Rotheray and Horsfield 2013) – or they fly in places difficult to sample, such as high in the canopy (Lonchaeidae: McAlpine and Munroe 1968) or low to the ground (Pallopteridae: Rotheray 2014). Inventories based on sampling larvae have often, for flies such as these, proved successful, cost-effective and a source of new taxa (Rotheray et al. 2001; Smith et al. 2006; Marcos-Garcia et al. 2012).

For tropical forest Syrphidae, Marcos-Garcia et al. (2012) quantified the effectiveness of Malaise trapping, hand netting and sampling larvae. Sampling larvae was the most productive method, Malaise trapping the least. A particular advantage of sampling larvae was the quality and quantity of associated biological data, such as information about development sites. Nonetheless, in habitats where development sites are patchy, over-dispersed or difficult to access, such as in Mediterranean forests, levels of effort required for larval sampling may not be cost-effective relative to sampling adults. Hence, in designing a species inventory, larval sampling should be included and, along with other survey techniques, each one tested per habitat to identify those most effective.

Terms such as ‘rare’, ‘common’ and ‘widespread’ are part of the common lore of biology. In the Cyclorrhapha, status approximations like these are based almost exclusively on adults. They are widely used in key works, taxonomic monographs and environmental reports, and form the evidential basis behind lists of threatened and endangered species (Falk 1979; Shirt 1987). These, in turn, inform the development of conservation policies, plans and priorities, such as the UK Biodiversity Action Plan. Rarity is, however, likely to be overestimated if adults are difficult to sample. On adult data, for instance, the syrphid Callicera rufa Schummel (Syrphidae) was included as a UK red data book category one endangered species (Shirt 1987). In contrast, early stage sampling revealed that C. rufa was frequent in Scotland, where it chiefly occurs in the UK (MacGowan and Rotheray 2006). Adult C. rufa are poorly sampled probably because they fly high in the forest canopy. Another example is European Pallopteridae (Diptera) which, based on adults, have enigmatic appearances and secretive, crepuscular habits (Lewis and Taylor 1965; Martinek 1977). Yet pallopterids are common and widespread when sampled in their larval stages. From one locality and just four host plants, for example, more larvae were found of Palloptera trimacula (Meigen) than had been collected as adults in Scotland over a 100-year period (Rotheray 2014).

Status based on adult captures is rarely checked or verified by larval sampling. The examples of C. rufa and pallopterans point to the value of doing so, although verification is often limited by a lack of knowledge about where to find larvae. Facilitating larval sampling, many temperate cyclorrhaphan species have overlapping larval generations, overwinter as larvae or develop during the winter, meaning they can be sampled over longer periods than adult flight periods (Perry and Rotheray 2010). Across wet and dry seasons, similar features may characterise tropical flies.
Larvae are better indicators than adults of habitats suitable for breeding, and there is unrealised potential in monitoring environmental change using larvae. For instance, among many possibilities, larvae developing in water-filled pockets, such as bromeliad water tanks and tree holes, are probably sensitive to the desiccating effects of climate warming. In Scotland, populations of the endangered saproxylic aspen hoverfly, *Hammerschmidtia ferruginea* Fallén (Syrphidae), fluctuate in response to the amount of dead wood, created primarily by winter storms (Rotheray et al. 2009). Fallen wood takes up to 2 years to become suitable for breeding. By monitoring inputs of fallen wood following storms, allowing for the time it takes to become suitable and supplementing amounts when necessary, the critical breeding resource for this species has been managed for more than 15 years (Rotheray et al. 2009, 2014).

**Determining feeding mode**

An ecological feature prone to misunderstanding is larval feeding mode. As noted in the section on ‘Morphological similarity’, morphological indicators of feeding mode are unreliable due to exceptions, vestigial structures and larvae with mixed diets. Even feeding observations can be misleading. For instance, Lonchaeidae and Pallopteridae are often described as having predatory larvae (Morge 1967; Ferrar 1987; Smith 1989; Chandler 1991; Merz 1998). Evidence supporting predation includes records of feeding on bark weevil larvae (Coleoptera, Scolytinae) and, as a result, they are considered agents of biocontrol for harmful species (Taylor 1929; Morge 1967; McAlpine and Morge 1970; Harman and Wallace 1971; Martinek 1977). Furthermore, Morge (1956) described an encounter between a larva of *Palloptera usta* (Pallopteridae) and one of *Stegana coleoptrata* (Drosophilidae) in which they twisted together until *P. usta* pierced *S. coleoptrata* and fed. Taylor (1929) enclosed larvae of *Lonchaea corticis* Taylor (Lonchaeidae) with weevil larvae and monitoring survival, found that healthy mature weevil larvae were definitely attacked by the lonchaeid larvae. Interestingly, he states that attacks only took place a few days after they were placed together.

Complicating the idea of predation is the frequent discovery of lonchaeid and pallopterid larvae in such large numbers that if other insect larvae are present, they are too scarce to provide enough prey, and, on such evidence, many species must be viewed as capable of saprophagy (Morge 1956; Ferrar 1987). Using similar techniques to those of Taylor (1929), Johnsey et al. (1965) investigated predation in *Lonchaea furnissi* McAlpine (Lonchaeidae) and did not record it, concluding that this larva is not a predator. Following Ferrar’s (1987) review of the subject, uncertainty persists about the nature of larval feeding in these and other families. Remarkably, in his chapter on Lonchaeidae in the Nearctic Diptera Manual, McAlpine (1987) does not refer to this basic issue.

What can be made of the conflicting evidence? Kishi (1972) provided a clue when attempting to observe predation by placing lonchaeid and weevil larvae together and recording that weevil larvae defended by biting and wriggling. Similar observations were made for *L. corticis* (Alfaro and Borden 1980). These lonchaeids fed chiefly on dead or dying weevil larvae.
Rotheray (2014) reported similar results with pallopterid larvae. Contacts between these and other larvae co-occurring at development sites usually resulted in them separating unharmed (Rotheray 2014). Zoophagy did occur, but rarely and only when the mouthhooks that are characteristically exposed and lowered at the end of waves of movement coincidentally landed on and penetrated another larva, usually a dead one because they were easier to pierce (Rotheray 2014). This may explain the observations of Taylor (1929) and Kishi (1972) that only after a few days did feeding occur on weevil larvae, by which time they were probably weak and less effective in defence (Ferrar 1987).

Under bark, lonchaeid and pallopterid larvae often move along tunnels excavated by weevil larvae, which increases the probability of encounters (Rotheray 2014). With their thin integuments, weevil larvae are susceptible to being pierced and, following feeding, fly larvae usually become immobile. These behaviours probably explain the zoophagy and co-occurrence noted in the literature (Rotheray 2014). Accidental predation and necrophagy are probably widespread among saprophagous larvae, and could also be a route to predation. This may have occurred in *L. corticis* which, in the Nearctic, develops on larvae of the weevil *Pissodes strobi* Peck (Coleoptera, Curculionidae) (Alfaro and Borden 1980). Alfaro and Borden (1980) found characteristics of larval behaviour to suggest that, unlike most lonchaeids, it has adapted to predation. It responds, for instance, to defending larvae by backing off and becoming still before resuming the attack. Nonetheless, *L. corticis* is most successful when attacking small larvae and those weakened or dead through starvation. Providing an exploitable resource, dead and weakened larvae are characteristically present at infestations of *P. strobi* because competition between larvae for food is part of the ecology of this species (Alfaro and Borden 1980). These examples reveal that within the Lonchaeidae and Pallopteridae, species exist with various zoophagous feeding habits: from obligatory to facultative predation, necrophagy to accidental predation, and its absence altogether. When attempting to evaluate the control potential of larvae from these and related families for programmes of pest management, variability in feeding habits should be recognised and investigation may be required to identify appropriate predatory species. These examples also demonstrate the value of observing individual larvae when determining feeding habits.

**Ideas and data**

In a neglected subject, ideas and data from a limited number of publications are repeated rather than tested and improved with new research. For example, Rotheray and Gilbert (2011) refer to an idea that became established in the syrphid literature of certain predatory larvae (Syrphinae) being able to switch to feeding on plant tissue if unable to find prey. This idea originates from a suggestion made in the 1920s and was repeated as if an established or highly probable fact. It was even used to underpin a theory explaining characteristics of these larvae (Chandler 1968). Eventually, Zafar (see Gilbert et al. 1994) demonstrated that, despite presenting starved and hungry syrphine larvae of the relevant species with plant tissue under a variety of conditions, no feeding was ever recorded.

Another example is the lonchopterid larva (Lonchopteridae). This larva could be informative due to the basal position of the Lonchopteridae, although just how basal
is unresolved (de Meijere 1901; Hennig 1952, 1976; Sinclair 1992; Zatwarnicki 1996; Collins and Wiegmann 2002; Rotheray and Gilbert 2008; Wiegmann et al. 2011; Lambkin et al. 2013). The lonchopterid larva is described as ‘primitive’ due to similarities to outgroups (de Meijere 1901; Hennig 1952, 1976). Both de Meijere (1901) and Hennig (1952, 1973) tackled the head skeleton, but morphological hypotheses and homology assessments from these works are repeated rather than re-examined. For instance, Hennig (1973) states that the lonchopterid larva carries a remnant of the head capsule of lower Diptera and is the only cyclorrhaphan to possess such a feature. This remnant appears as a dark, sclerotised, square-shaped structure on the antero-dorsal margin of the basal sclerite (de Meijere 1901, fig. 7; Hennig 1952, fig. 84; both reproduced in Ferrar 1987) and is referred to by various authors including Ferrar (1987) and Courtney et al. (2000).

The remnant is similar in shape and position to the dorsal bridge of other cyclorrhaphan larvae. The dorsal bridge is a sclerotised area where the two halves of the basal sclerite fuse (Figure 6), and the basal sclerite originates from the tentorial phragmata of outgroups, not the head capsule (Courtney et al. 2000). In lonchopterid larvae, the reason why this structure may be confusing is that it is highly conspicuous due to the unique box shape of the basal sclerite (fig. 12 in de Meijere 1901). In other cyclorrhaphans, the basal sclerite is narrower and the dorsal bridge less sclerotised and conspicuous.

Until recently, the feeding mode of this larva and the role of the mandible have been uncertain. Gut analyses record algal cells, bacteria, testate amoebae and fungal hyphae and spores (Healey and Russell-Smith 1971; Jones 1979). From these data and the places where larvae develop, Ferrar (1987) concluded that the larva scrapes micro-organisms from the surface of dead leaves and similar substrates. Analysing the head, Rotheray and Gilbert (2008) found that it consisted of a membranous trough or furrow onto which food, in the form of liquid biofilm, was probably shovelled. This was confirmed when feeding was filmed (Rotheray and Lyszkowski 2015), although less viscous biofilm might be ingested by pressing the head against it and using the pump in the head skeleton to suck it up.

On the basis of similarity to outgroups, the lonchopterid mandible appears to consist of at least two components, an apical hook and an oval-shaped sclerite. These components connect via a sclerotised bar to one of the paired labial rods in the floor of the trough (Figure 8) (Rotheray and Lyszkowski 2015). Articulation of the mandible with the labium is a synapomorphy proposed for the Cyclorrhapha (Krivosheina 1969; McAlpine 1989; Rotheray and Gilbert 2008). A single-component mandible was proposed by Hennig (1973) as a synapomorphy for the Cyclorrhapha which included the Lonchopteridae. The latter synapomorphy is repeated by many authors, including Teskey (1981), McAlpine (1989), Sinclair (1992), Courtney et al. (2000) and Lambkin et al. (2013), but it is not supported by the Lonchopteridae.

From the labial rods each mandible extends up the side margins of the trough, just in front of the pharynx, with the hook-like sclerites overlapping it dorsally (Rotheray and Gilbert 2008). The place where the mandibles articulate with the labial rods is strengthened by a sclerotised plate connecting them, the ventral bridge of other cyclorrhaphans (Figure 8). de Meijere (1901) illustrates the hook-like sclerite encased in membrane, a state confirmed by Rotheray and Gilbert (2008). By outgroup comparison, this membrane is the maxilla (Roberts 1969; Sinclair 1992). The lonchopterid maxilla also forms
the side margins of the trough, as revealed by the landmark maxillary palpus at each apex (de Meijere 1901; Hennig 1952; Roberts 1970; Rotheray and Gilbert 2008). Although mandibular muscles have not been investigated, filmed movement reveals a single, coordinated action in which the oval sclerite, the apical hook and the side margin of the trough, from the mandible to the maxillary palpus, all tilt up. At the end of scooping, this tips biofilm towards the pharynx (Rotheray and Lyszkowski 2015).

Significantly, the base of the trough bearing on each side a landmark for the pseudocephalon (an antenna) does not move during scooping, even though it is joined seamlessly to the distal maxillary section. This basal section is inflexible due to a pair of internal, sclerotised rods that extend from the basal sclerite through this part of the trough. These are, by similar position, the maxillary sclerites of outgroups and are referred to in other cyclorrhaphans as parastomal bars (Supplemental material 1). At the junction between the mobile and immobile parts of the trough is the probable border between the pseudocephalon and the membranous part of the maxilla. In other cyclorrhaphan larvae, connection between the maxilla and mandible is lost (Courtney et al. 2000; Rotheray and Gilbert 2008). In the lonchopterid larva, morphological connections between the maxilla, pseudocephalon and mandible are congruent with relationships between these structures in outgroups.

**Figure 8.** Lonchoptera sp. (Lonchopteridae), third stage larva, mandible and attachment to the labium, posterior view, 1 = apical hook, 2 = oval sclerite, 3 = labial ventral bridge, 4 = labial rod.
Lonchopterid features such as these make it the type of intermediate envisaged by Teskey (1981) as necessary to homologise the otherwise difficult to understand cyclorrhaphan – really, the schizophoran – larval head. Without films to supplement and inform morphological re-assessment of this larva, the amount of information recoverable from preserved material alone would fall well below that which is potentially available. This example is unlikely to be exceptional and demonstrates the value of incorporating movement in analyses, even for relatively well-studied larvae.

**Homologies and names**

Teskey (1981) stated that homologising the schizophoran head was difficult because intermediates were unrecognisable. Without intermediates, structures sharing an origin that can be referred to by the same name are difficult to recognise. For example, compared to outgroups, the schizophoran ‘mandible’ is so different in appearance and relationships, it seems more like a de novo structure. Consequently, ‘mouthhook’ is sometimes preferred over ‘mandible’, because the former term is descriptive of position and shape yet carries no implication of homology (Headrick and Goeden 1996). The schizophoran mandible has been the focus of conflicting views: Ludwig (1949) considered it mandibular in origin; Menees (1962) and Matsuda (1965) that it was derived from the maxilla; Cook (1949) that it contained both; and Snodgrass (1953) that it was a new structure. Recent embryological evidence has not helped, prompting Courtney et al. (2000) to suggest that the base is derived from the mandible and the hook from the maxilla. Related difficulties concern the antennomaxillary organs (Figure 6) (Sinclair 1992; Headrick and Goeden 1996; Courtney et al. 2000). Lack of agreement over such basic issues as naming structures contributes to ad hoc terminology and a sense of uncertainty concerning larvae.

A potential source of intermediates that might resolve the homology of the schizophoran head is aschizans (Courtney et al. 2000). Based on better knowledge of these larvae [Lonchopteridae, see previous section; Platypezidae, see Sinclair (1992), Rotheray et al. (2004); and Syrphoidea, see Albrecht (1990), Rotheray and Gilbert (1999), Koenig and Young (2007)] and standard criteria for character assessment, general resemblance, spatial similarity, landmarks and parsimony, intermediates have been found (Rotheray and Gilbert 2008). These intermediates substantiate morphological homologies for the cyclorrhaphan larva (Supplemental material 1) and suggest that the schizophoran head developed from processes of modification and integration of precursor components originating in cyclorrhaphan outgroups and the Aschiza.

The most conspicuous of these integrations include the labial rods (Figure 8), the pseudocephalon (Figure 6b) and the largest component of the cyclorrhaphan head skeleton, the basal sclerite (Figure 6a). Functionally, the basal sclerite is a pump (Figure 5) and a synapomorphy for the Cyclorrhapha (Roberts 1970; Hennig 1973; McAlpine 1989; Courtney et al. 2000). Compared to outgroups, the labial rods are elongate in the Lonchopteridae and bifurcate in other Cyclorrhapha. In the Platypoidea, the dorsal arm articulates with the mandible, and at the apex of the ventral arm is a hook or teeth appearing freely at the front of the head. This is the main food-gathering structure in platypezoids (Rotheray et al. 2004). Bifurcation is retained in the Syrphoidea, but the ventral arm is excised (the labial plate and sclerites of Hartley 1963). This excision retains a plesiomorphic free state and is a synapomorphy for the Eumuscomorpha (Syrphoidea + Schizophora). Another
eumuscomorphan synapomorphy is elongation of the dorsal arms, resulting in the mandibles they support being at the front of the head skeleton, and replacing the labial hook or teeth as the main food-gathering structures. In the Schizophora, the labial plate and sclerites (the subhypostomal and ligulate sclerites of Ferrar 1987) are reduced, vestigial and fused into the floor of an extension to the atrium, which is supported laterally by the dorsal arms (the intermediate sclerite of Hennig 1973) (Rotheray and Gilbert 2008). A third integration is the development of the pseudocephalon which in the Lonchopteridae is open anteriorly, in the Platypezoidea roofed over, and in the Eumuscomorpha overlaps the head skeleton which projects the antennomaxillary organs to the apex of the larva. Finally, in the Schizophora, the pseudocephalon ensheathes the mandibles resulting in the formation between them of a new food-gathering structure, the oral cavity (Rotheray and Gilbert 2008) (Figure 6).

Incorporating aschizan intermediates enables homologies of the schizophoran larval head to be proposed (Supplemental material 1). For example, by resemblance, similar position and landmarks, the schizophoran mandible is traceable from outgroup states, with the chief cyclorrhaphan changes being articulation with the labium, loss or fusion to become one component, separation from the maxilla, projection to the front of the head skeleton and ensheathment by the pseudocephalon.

By similar position and landmark muscle attachment, the schizophoran dental sclerite (Figure 6a) is the reduced and excised mandibular apodeme first appearing in the Syrphoidea. Occasionally it secondarily fuses with the mandible, as in certain Muscidae and Heleomyzidae (Rotheray and Wilkinson 2015, Rotheray et al. 2016). Despite excision, the plesiomorphic insertion of mandibular muscles is retained (Roberts 1971).

Aschizan states also suggest why the origin of the schizophoran antennomaxillary organs is problematic. Embryological evidence suggests that sensory elements from the maxillary palpus and the antenna are mixed, thus confusing origins (Courtney et al. 2000). In outgroups, the antenna and maxillary palpus belong to different structures (Roberts 1969). In the Lonchopteridae they appear to be part of the same structure, the side margin of the trough, but are separate at either end of it and are distinguishable by the greater length of the antennae. In the Eumuscomorpha, they are similarly distinguished by length, but are approximated with an intermediate state in the Platypezoidea. Proximity and possible incorporation of outlying antennal sensilla with the maxillary palpus during processes of approximation might affect the embryological results.

Data transforming these interpretations may come from the larva of the apparent sister to the Cyclorrhapha, the Apystomyiidae (Wiegmann et al. 2011), and basal, aschizan taxa currently unknown in their larval stages, the Opethiidae (Yeates and Wiegmann 1999; Collins and Wiegmann 2002) and the Melanderomyinae and Microsaniinae of the Platypezidae (Chandler 2001).

Significance

Evolvability

Compared to the impacts of larval feeding, feeding mechanisms (i.e. the morphology and behaviour involved in transferring food from an external source to the gut) are rarely studied (Roberts 1971). Reasons for this include the practical difficulties of
assessing movement that is too rapid to resolve, and the small size and concealment of some components (Roberts 1971; Tinkeu and Hance 1998). Digital filming overcomes these problems, and feeding mechanisms can be determined when films of movement are combined with morphological analysis of preserved material (Rotheray and Lyszkowski 2015). A general feature of cyclorrhaphan larvae revealed by such an approach is a compartmentalised body. The rear compartment, from the anal segment to between abdominal segment two and the metathorax, grips the substrate enabling the following compartment, forward to the anterior spiracles, to move sideways and up and down and alter direction during locomotion. The next compartment, from the anterior spiracles to the front of the prothorax, inclines down and remains stationary or twists and turns while the front compartments, comprising the pseudocephalon and the head skeleton, gather food or grip the substrate.

The feeding mechanism of the lonchopterid larva is shovelling liquid food using a membranous trough (see section on ‘Ideas and data’). In this larva, the head skeleton retains the outgroup state of being fixed in the thorax, and the two structures do not move independently of each other. Pumping in the head skeleton and mandible movement are also co-ordinated and these components do not move independently of each other. Platypezoid larvae use the sclerotised, hooked or toothed labial apex to tear and fragment relatively hard food. Soft and liquid food is simply sucked up by pressing the prothorax into it. The mandibles barely depress or elevate, but move apart slightly to guide food towards the pharynx. The head skeleton, as in the Lonchopteridae, has little or no movement independent of the thorax. Pumping is, however, independent of the mandibles, which enhances the efficacy of ingestion (Rotheray and Lyszkowski 2015).

Pumping in eumuscomorphan larvae is, like in the Platypezoidea, independent of mandible movement and, in addition, the head skeleton moves independently of the thorax, extending and retracting from it. Furthermore, with mandibles at the front of the head skeleton, their range of movement is greater. In basal eumuscomorphan taxa, such as the predacious larva of the Microdontinae (Syrphidae) (Stahls et al. 2003; Rotheray and Gilbert 2008), the pseudocephalon supports and guides the direction in which the head skeleton extends from the thorax, while the mandibles and labial plate depress to grab and tear into prey (Rotheray and Lyszkowski 2015).

Compared to those of the Syrphoidea, mandibles in the Schizophora have greater movement and, due to a structural and functional partnership with the pseudocephalon, a greater role in feeding (Rotheray and Lyszkowski 2015). The pseudocephalon ensheathes each mandible except for an apical gap through which the mandible extends. The roofed-over space between the ensheathed mandibles is the oral cavity, an upside-down, cup-shaped space at the back of which is the opening to the pharynx. To feed, the prothorax moves towards the food and the head skeleton extends from it. The mandibles protract from their sheaths, which opens the oral cavity. With continued protraction, food is gathered into the oral cavity and sucked in via the atrium (Rotheray and Lyszkowski 2015).

Wiegmann et al. (2011) refer to the imperviousness of the puparium, which, with a reduced larva for feeding in almost any nutrient-rich substrate, enabled cyclorrhaphan flies to diversify into a broad range of niches. The idea of a reduced larva feeding on almost any nutrient-rich substrate was not explained by Wiegmann et al. (2011). In any case, reduction is a poor way to characterise the changes outlined above. Larval feeding
mechanisms reveal that across the aschizan stem, particular components have novel states that integrate with others less modified, leading to new functional arrangements with increasing amounts of mobility. Although the oral cavity is an innovation in food gathering, across the schizophoran crown change in trophic morphology, particularly among saprophages and phytophages, is characterised less by rearrangement and innovation than by lability – that is, change in the size, shape and movement range of mobile components (Rotheray and Lyszkowski 2015). Lability explains the relative lack of qualitative characters and the superficial similarity of schizophoran larvae. Lability, however, probably facilitates rapid change, and it is this attribute that is the likely larval feature contributing most to the outstanding Schizophoran radiation.

Another important element is compartmentalisation or modularity, which enables independent change per module (Yang 2001). Modular evolution explains larval compartments and their disparate functional morphologies noted above. Furthermore, compared to outgroups, modules are more distinct in cyclorrhaphan larvae and are most diverse in the head (Rotheray and Lyszkowski 2015). Compared to other Diptera, the so-called ‘acephalic’ cyclorrhaphan larval head has reached developed states of desclerotisation and inversion, and these changes are viewed as among the most remarkable in the Diptera (Cook 1949; Teskey 1981; Courtney et al. 2000). The result is a head comprising two modules, the pseudocephalon and the head skeleton. In addition, these two modules are linked with the next module, the prothorax posterior to the spiracles. In the Schizophora, with characters evolving together (Rotheray and Lyszkowski 2015), these modules act like an adaptive complex (Cheverud 1996; Yang 2001), and enhanced performance (i.e. the fit of morphology and behaviour to environmental variables) may be the outcome. Possible support for this comes from one of the few studies measuring performance in species with and without this adaptive complex. Harrison and Cooper (2003) found slower growth and feeding movements in the aschizan larva of Megaselia scalaris (Loew) (Phoridae) compared to the schizophoran larva of Drosophila melanogaster Meigen (Drosophilidae).

**Feeding modes**

The rapid radiation of the Schizophora, 65–40 mya (Wiegmann et al. 2011), occurred at a time when most angiosperm families had diversified (Wikström et al. 2001). If they presented ecological opportunities for adult food (pollen and nectar) and development sites for phytophagy, opportunities will also have been created for saprophagy.

This probably explains why the most frequent schizophoran larval feeding modes are associated with plants (Ferrar 1987), and shifts between saprophagy and phytophagy must have played an important role in schizophoran diversification. As a route between these feeding modes, larvae with mixed saprophagous and phytophagous feeding characteristics were discussed in the section on ‘Morphological similarity’. For these larvae, plant tissue is, possibly, less of a barrier to digestion because of mutualistic microbes and, probably, gut symbionts (Mahmoud et al. 1999; Dillon and Dillon 2004; Behar et al. 2008; Martínez-Falcón et al. 2011).

Zoophagy is more frequent in later evolved Schizophora (Wiegmann et al. 2011). Perhaps opportunities were less frequent or zoophagy involves more difficult barriers. Mixed saprophagous and zoophagous larvae are a possible route to zoophagy; see
section on ‘Morphological similarity’. Predatory and ectoparasitic larvae must pierce prey/hosts and usually possess mechanisms to prevent food being lost through wounds, at least while feeding (Rotheray and Lyszkowski 2015; Rotheray and Wilkinson 2015). Suggesting independent acquisition of predation and ectoparasitism, disparate functional morphology achieves this. In syrphine larvae, loss of food is prevented by inverting the prothorax into a cup shape into which prey are drawn and held by a pair of opposing, tapered sclerites and sticky saliva. In contrast, the bird-brood, ectoparasitic Neottiophilum praeustum (Meigen) (Piophilidae) pierces host skin with sickle-shaped mandible hooks and seals round the wound by pressing the apex of the prothorax against it, and may use toothed combs to fragment blood clots (Rotheray and Hancock 2012). Predacious Phaonia Robineau-Desvoidy larvae (Muscidae) are different again. They possess a plethora of accessory mandibular sclerites, some of which pull a section of prey integument tight enabling the mandible hooks to disengage and pierce it, while others keep the oral cavity open. To trap prey fluids, the prothorax is initially held against the wound. After, to remove residual fluids and tissue, the prothorax is pushed into prey and the exceptionally narrow, cylindrical and spicule-coated apex engages the torn integument to help maintain a seal (Rotheray and Wilkinson 2015).

Feeding mechanisms in endoparasitic larvae are in need of study, but larvae with this feeding mode also have disparate trophic morphologies (Figure 2c, f, j). Nonetheless, a similarity is spines associated with the mandible, which probably hold or help macerate prey tissue. A spiniose labial plate occurs in the Pipunculidae. In Conopidae, spines project from the mandible base (Figure 2c), and in the Sciomyzidae, the dental sclerites are fused and this structure (the ventral arch in Ferrar 1987) is spinose (Figure 2e). Spines are apparently absent in endoparasitic larvae of the Tachinidae. Relative to saprophagous and phytophagous larvae that feed on hard food (see section on ‘Morphological similarity’), head skeletons in tachinids share features and they appear adapted for coping with firm prey tissue. The head skeleton is well sclerotised, the mandible hook short, the intermediate sclerite block shaped and aligned and sometimes fused to the basal sclerite (Figure 2j). The elevator muscle apodeme is greatly extended, more than in any other cyclorrhaphan larva (Figure 2j), indicating development of these muscles, which probably facilitates working with the depressor muscles to maintain the mandible in one position during head skeleton pivots, and thereby enhance cutting power.

**Co-existence**

A method of evaluating interaction between species at shared development sites is to compare larval feeding mechanisms. For instance, rich communities of cyclorrhaphan larvae can be found under bark of fallen trees and branches, but little is known of how larvae affect one another (Ferrar 1987; Rotheray et al. 2001). The feeding mechanisms of a few of these species have been investigated (Rotheray and Lyszkowski 2015). The drosophilid S. coleoptrata and the lonchaeid L. sylvatica, for example, feed on relatively dry material under bark, and they have the trophic features associated with gathering hard food (see section on ‘Morphological similarity’). In contrast, the drosophilid Chymomyza costata (Zetterstedt) and the lonchaeid Lonchaea nitens (Bigot) feed on more viscous states, and are closer in characteristics to larvae that feed on soft food. Further differences distinguish each species. S. coleoptrata seems to be more completely
adapted to feeding on hard food than *L. sylvatica* is. For instance, it has fully aligned intermediate and basal sclerites, and the mandibles are fused (Figure 4h, k). In the other pair, *L. nitens* has a more tapered, flexible prothorax and a head skeleton that can twist and turn, features that enable this larva to extract food from more confined spaces than *C. costata* can.

In fallen trees and branches with wet, decaying sapwood and heartwood, clusiid larvae are frequent, and feed by spot-sucking wet biofilm that coats the annual layers between which they squeeze. They move slowly and have a flattened apex to the prothorax and an inverted head, features that facilitate spot-sucking (Rotheray and Horsfield 2013). In contrast, the milichiid *Neophyllomyza acyglossa* (Villeneuve) develops in the same habitat, but has a highly tapered and manoeuvrable thorax and head skeleton, including a uniquely long and bendable intermediate sclerite. These features enable this larva to extract biofilm from narrow gaps and crevices (Rotheray and Lyszkowski 2015).

Each of these six taxa is distinguished by a feeding mechanism that is suited to gathering food of a particular quality and/or from a particular place. The part played by diverse feeding mechanisms in the biodiversity of larval communities is indicated but requires further analysis and confirmation from a wider range of examples.

Feeding mechanism differences even occur at low taxonomic levels, such as between the two *Lonchaea* species noted above. An evolutionary mechanism generating such differences is suggested in the Syrphidae where, within phylogenetic sequences, adaptive potential may be greater in derived than in basal taxa. For example, within the Syrphinae, larvae of the derived *Eupeodes* and *Scaeva* lineages (Stahls et al. 2003) possess a specialised searching mechanism for locating aphid prey on narrow, cylindrical substrates. It comprises a grasping organ at the anal end and an ability to spiral round and move up and down cylindrical substrates while holding on at the head end using suction from the head skeleton pump (Rotheray and Gilbert 2011). The mechanism was probably acquired on conifer foliage where many species of the group are found (Dušek and Láska 1976; Vockeroth 1992). Early evolved syrphines are mainly in the herb layer, and some *Eupeodes* and *Scaeva* species appear to have invaded this habitat where their searching mechanism is an advantage for exploiting aphids on narrow stems, which less derived larvae without such a mechanism cannot exploit as effectively (Rotheray and Gilbert 2011).

Another example is colonisation of bromeliads (Bromeliaceae) by the genus *Copestylum* (Syrphidae) (Rotheray et al. 2007). Live and dead bromeliads have been colonised by distinctive species groups within this remarkable and highly diverse New World lineage. *Copestylum* larvae are saprophages and in the characteristic water tank of live bromeliads, larvae feed on biofilm coating the smooth, adpressed and overlapping leaves (Supplemental material 2.2). In dead bromeliads, larvae feed on wet, decayed tissue.

Three *Copestylum* species groups have colonised bromeliad biofilm and, facilitating access to the narrow space between leaves, they exhibit four types of flattening. Two types occur among larvae belonging to the relatively basal *Tank* species group, one being less flattened than the other. An extreme level of flattening is represented by species of the more derived *Otongaensis* species group. In these larvae, not only is the whole body flattened, but so is the tube-like, posterior breathing process and the head
skeleton. Furthermore, uniquely, the anterior margin of the prothorax is notched, enabling the larva to reach, with its head skeleton, biofilm on leaf surfaces above and below it (Supplemental material 2.2). Flattening in Tank and Otongaensis larvae is fixed, but in intermediately derived larvae of the Macquarti species group, the larva is able to flatten and lengthen to squeeze between bromeliad leaves. Space between leaves reduces towards the base of the water tank and, with their greater levels of flattening and associated changes in feeding and movement, the more derived taxa are probably able to penetrate deeper than the basal taxa are.

Dead bromeliads do not impose the same spatial restraints and have been colonised by at least three Copestylum species groups. Two of these are represented by species with relatively small, unspecialised larvae that are confined to places where decayed tissue is soft and wet. Much larger larvae possessing thoracic spicules and hooks belong to the more derived Boqueronense species group. Using spicules and hooks, these larvae burrow through leaf bases and the stem-like, central scape, helping to spread and encourage decay, and thereby create food.

Across phylogenetic sequences of both predatory syrphines and Copestylum, it is suggested here that adaptive potential (genetic architecture and developmental pathways) accumulates and thereby facilitates the development of innovative functional morphologies that enable derived taxa to exploit resources less available or unavailable to basal taxa. Enhanced adaptive potential may be characteristic of phylogenetic sequences in the Cyclorrhapha. If so, this deserves further investigation.

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