Zoological Journal of the Linnean Society (1999), *127:* 1–112. With 27 figures

Article ID: zjls.1998.0156, available online at http://www.idealibrary.com on IDEAL®

Phylogeny of Palaearctic Syrphidae (Diptera): evidence from larval stages

GRAHAM ROTHERAY*

National Museums of Scotland, Chambers Street, Edinburgh, EHI 1JF

FRANCIS GILBERT

Department of Life Science, University of Nottingham, Nottingham NG7 2RD

Received April 1996; accepted for publication February 1998

We estimated the phylogeny of Palaearctic Syrphidae using 187 larval morphological characters obtained from about 65% of the fauna (85 supraspecific taxa represented by 118 species) and based the analysis at the generic level. The root of the syrphid tree was established from an outgroup consisting of other Aschizan families: the Platypezidae, Phoridae and Pipunculidae, with the tree rooted on the Lonchopteridae. The Syrphidae was the most derived Aschizan family. The Pipunculidae was the sister group to the Syrphidae. *Eumerus* was basal within Syrphidae. A trend exists towards increasing complexity of integumental folds and grooves across the Aschiza. In movement, the integument collapses along the line of these grooves. Grooves are evidence of muscles forming functional groups. Elaboration of independent groups of muscles appears to underlie much of the evolution of larval form within Aschiza. The basal feeding modes of syrphid larvae are mycophagy and phytophagy. Above these feeding modes, all remaining syrphids fall into one of two lineages comprising entomophages and saprophages, each of which has a single origin within the apparently polyphyletic *Volucella*. Major morphological innovation is associated with shifts between feeding modes; within feeding modes, change is gradual and tends towards increasing complexity. Change is mostly in structures associated with the mouthparts, thorax, anal segment and locomotory organs. Generic diagnoses with biological and taxonomic notes and a key to genera using larval characters are provided.

ADDITIONAL KEY WORDS:—cladistics – Aschiza – morphology – behaviour – evolution.

CONTENTS

---

* Email ger@nms.ac.uk

0024–4082/99/090001 + 112 $30.00

INTRODUCTION

> "The incredible error of some entomographers, that the larvae of insects have no importance in classification."
>
> Brauer (1891)

About 5400 species of Syrphidae are known from all regions of the world except Antarctica (Vockeroth & Thompson, 1987). They inhabit most terrestrial ecosystems including coasts, mountains, deserts and urban and agricultural situations. All or virtually all adults feed on nectar and pollen from flowers, and are important plant pollinators (see Gilbert, 1993); in addition, many adults have colour patterns that mimic noxious Hymenoptera (Dittrich *et al.*, 1994). In contrast, larvae are unusually diverse (Metcalf, 1916; Vockeroth & Thompson, 1987). They include: phytophages of numerous plant families; mycophages of fungal fruiting bodies; saprophages in media as diverse as dung, nests of social Hymenoptera, decaying wood and freshwater bodies of numerous types; and predators of a range of other insects. Characteristic larval morphologies are associated with feeding modes (Fig. 1). Metcalf (1916) describes five such feeding mode/morphological associations. Diversification of larval stages is rarely as substantial as it is in Syrphidae, being rivalled only by those of the related Aschizan family Phoridae (Disney, 1994) or perhaps larvae of the Drosophilidae (Diptera) (see Ferrar, 1987).

Despite such diversity, larval characters are little used in the numerous attempts to classify Syrphidae. Lioy (1864) was perhaps the first classification to include larval feeding modes. Brauer (1883) thought that, when properly studied, syrphid larvae would be useful in determining natural groups within the family, and Metcalf (1916) was also of this view. However a barrier to using larvae is that, compared with adults, few are available for study and published descriptions often lack detail. For example Thompson (1990) estimates that larvae of only 7% of nearctic syrphids are known. Where enough are known, larval characters have helped resolve problems that were proving intractable using adult characters alone (Rotheray & Gilbert, 1989).

Recently, after much effort in the field, many more syrphid larvae have been

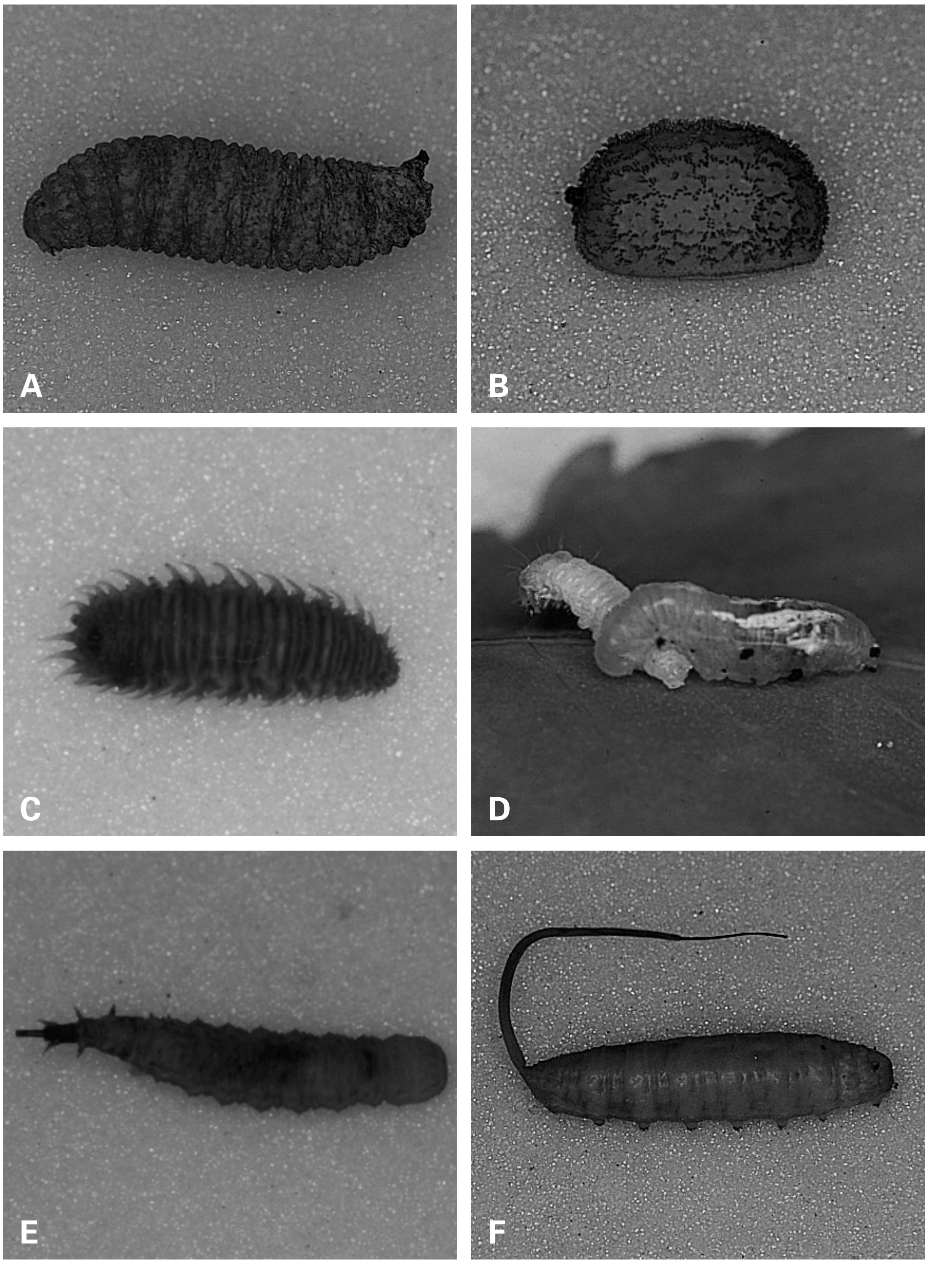

Figure 1. Third stage syrphid larvae, whole views. A, *Cheilosia grossa*, head to the left, a phytophage of *Cirsium* (Compositae). B, *Microdon mutabilis*, head to the right, an entomophage of formicid (Formicidae, Hymenoptera) eggs, larvae and cocoons. C, *Volucella pellucens*, head to the right, a saprophage/entomophage in vespid (Vespidae, Hymenoptera) nests. D, *Xanthandrus comtus*, head to the left, actively feeding an entomophage of various gregarious lepidopteran caterpillars (Lepidoptera). E, *Xylota sylvarum*, head to the right, a saprophage in decaying heartwood of deciduous and conifer trees. F, *Myathropa florea*, head to the right, a saprophage in various saproxylic microhabitats including tree-holes and sap-runs.

located (Maier, 1982, 1987; Rotheray, 1993) which, together with other material we obtained, makes a broader study feasible, the aims of which are:

(1) To analyse and compare the external morphology of syrphid larvae with larvae from other Aschiza families which constitute an outgroup. Aschiza larvae have, in general, been superficially treated and often misunderstood. In this paper many new characters are described.

(2) To construct a cladogram at the generic level for all the syrphid taxa we have obtained that occur within the Palaearctic region, based on larval characters. When larvae are studied, it is usually sclerotized structures like the head skeleton and respiratory organs that receive most attention. However, even a cursory study of larvae within Aschiza reveals high levels of variation in integumental features. In this analysis we use these characters extensively, finding in them a rich source of new information (Appendix 1). Part of this cladistic analysis involves re-analysing our previous data for predatory larvae (Rotheray & Gilbert, 1989; Gilbert *et al.*, 1994).

(3) To provide generic diagnoses and an identification key. Generic diagnoses based on larval characters should assist future systematic study. At present, too few larvae are known to provide a key to species.

PREVIOUS ESTIMATES OF SYRPHID PHYLOGENY

Only overall schemes of syrphid phylogeny, or those that deal with reasonably large sections of the family are considered here. There are relatively few such reconstructions of the phylogeny of higher taxa within the Syrphidae, or even of any opinions about the evolutionary tree. The few authors trying to reconstruct phylogeny (e.g. Goffe, 1952; Glumac, 1960; Thompson, 1972; Hippa 1978, 1990; Borisova, 1984; Kuznetsov, 1987; Vujic & Glumac, 1993) generally do not use cladistics, or if they do, they do not use parsimony methods, restricting themselves to subjective definitions of monophyletic groups usually based on single characters. There have been several different ways in which the family has been classified into subfamilies and tribes, but over the last 25 years there has been a consensus in a system of three subfamilies, each with a number of tribes: the Microdontinae (tribe Microdontini), the Syrphinae (tribes Bacchini, Melanostomini, Syrphini, Toxomerini, etc) and the Eristalinae (tribes Callicerini, Cerioidini, Cheilosini, Chrysogasterini, Eristalini, Eumerini, Milesini, Pipizini, Sericomyiini, Volucellini, Xylotini, etc).

Metcalf (1913) included a tree-like diagram in his monograph, placing the phytophagous species as the most primitive type. He followed this with a subjective sequence of transformations to derive all the feeding types in the family, and his scheme has nothing but historical interest. Following on from Metcalf's (1921) subsequent and pioneering work on the structure of the male terminalia, a number of authors (Glumac, 1958, 1960; Dušek & Láska, 1967; Hippa, 1968; Vockeroth, 1969) began the process of redefining the large polyphyletic groupings into monophyletic genera and higher categories. While the recognition of monophyletic genera occurred very quickly, the higher classification of the Syrphidae has always been problematic.

A very general phylogenetic outline of the family was given by Thompson (1972). He thought that the Microdontidae were the sister-group of the Syrphidae, and (presumably) that the first dichotomy gave rise to the predatory Syrphinae and the rest, the Milesiinae. Within the Milesiinae, he considered the tribes Cheilosini, Pipizini, Volucellini and Callicerini to be basal; Sericomyiini and Eumerini to be intermediate; and Eristalini to be derived, together with Ceriodini and Milesiini as the most derived groups. The classification of the Pipizini has been a long-standing problem, since members have a syrphine-like larva, but a milesiine-like adult (see Thompson, 1972).

From his detailed study of the genitalic structures of adult males, and other adult morphological characters, Hippa (1978) considered the Cheilosini (in the Milesiinae) and the Melanostomini (in the Syrphinae) to be closely related, as also stressed by Glumac (1960). Glumac and his co-worker Vujic (Glumac, 1958, 1960, 1980; Glumac & Vujic, 1990; Vujic & Glumac, 1993) derive a series of vague hypotheses about phylogeny based on genitalia and larval feeding mode. Glumac's initial work corrected many of the then current mistakes in syrphid classification; for example, he stated that *Eumerus* and *Merodon* must be closely related, a view now generally accepted. However, he also made a number of simplistic assumptions. Based on the male genitalia of a very large number of genera, he proposed that the eristaline groups were the most basic because they were the 'simplest'. From the saprophagous larvae, he derived the predators via the phytophagous species, citing as a fact (as do many other syrphid workers) the speculative musings of Davidson (1922) about the ability of some melanostomine larvae to feed on rotting plant matter. There is no correspondence at all between Glumac's early (Glumac, 1960) or more recent (Glumac & Vujic, 1990; Vujic & Glumac, 1993) schemes of relationships, and ours presented here. In particular Glumac's body of work relies on the weak assumption that genitalic structures become more complex through evolutionary time.

A more recent assessment of syrphid evolution was made by Borisova (1984). She combined information from Shatalkin (1975a, b), Hull (1949), Hartley (1961), Rohdendorf (1974), and Thompson (1972) with her own unique work on female ovipositors and ovarioles to predict the characters of the ancestral syrphid: in the male, five pre-genital segments and the dichoptic condition; in the female, a short ovipositor composed of complete sclerites, and a relatively large number of ovarioles that mature eggs synchronously, ovipositing them in a single batch; and a saprophagous larva with a short telescopic posterior respiratory process that lived in liquid or semi-liquid media. Although no extant syrphid combines all these characters, she thought that the chrysogasterines were the closest and therefore likely to be the most basal group. From the chrysogasterines, she traced two lines of syrphid evolution. The first elaborated and improved traits adaptive to aquatic conditions, leading to a longer posterior respiratory process in the larva, and an increase in female reproductive potential with up to a few hundred ovarioles, retaining synchronous egg development and batch laying. The second line was the transformation of the larvae to a terrestrial habitat in phytophagous, and eventually to predatory lifestyles. This entailed a great reduction in the length of the posterior respiratory process in the larva, and a reduction in the potential fecundity to only a few tens of ovarioles, coupled with asynchronous egg development and oviposition in small batches, often only single eggs.

The first person to compare larval structure in any detail was Krüger (1926). On the basis of an amazingly detailed anatomical and structural study, he suggested that *Rhingia* and *Brachyopa* were the most primitive of the 15 species he looked at. He constructed a morphological series connecting the various types, which placed

Brachyopa, *Xylota* and *Syritta* as the connecting links between *Rhingia* and *Eristalis*, with *Volucella* as a side branch from *Rhingia* or nearby. *Microdon* was also derived from a *Rhingia*-like form, and from *Microdon* he subsequently derived the predatory syrphines. In a very simplified form, this scheme is very like our eventual phylogeny.

Also by studying syrphid larval structure in great detail (but not in any outgroups), Hartley (1961, 1963) came to the conclusion that the eristaline larval type was the most primitive; he based this view largely on the great diversity of the saprophagous forms. He thought that it was fairly easy to derive other types of larval cephalopharyngeal apparatus from the saprophagous type, but not *vice versa*. Roberts (1971) also studied larval cephalopharyngeal structures, but came to the opposite conclusion, namely that the 'phytophagous' *Eumerus* was primitive, and the eristaline type was in fact highly specialized. He based this on a comparison with a rhagionid larva, which he labelled a 'primitive brachyceran' and which therefore could be regarded as an outgroup.

Kuznetsov (1987) studied the first-instar larvae of Pipizini, Syrphini and Eristalinae. He thought that he had discovered a key character in the form of the posterior respiratory process in these first instars. He described three states: the posterior respiratory process consisting of separate tubes positioned on small non-sclerotized papillae (the condition in the Syrphinae); consisting of separate tubes positioned on two more or less strongly sclerotized processes (in the Pipizini); and consisting of a single, fused, well-developed, highly sclerotized tube, on the top of which are the spiracular openings of both tracheae (in the Eristalinae). On various criteria, not including outgroup comparison, he concluded that the primitive condition must be that of the Syrphinae, with the most advanced state in the Eristalinae.

Internal characters can also help in elucidating relationships between syrphid taxa. Melzer & Paulus (1989) studied the fine structure of the larval eye in three genera (*Episyrphus, Volucella* and *Eristalis*), and discovered that all three possessed a tracheolar tapetum, but with differing degrees of development. Based on their study of a number of dipteran taxa, they tentatively suggested that this might be a defining synapomorphy for the family. The number of tracheoles and the number of layers creating the tapetum increased in the order *Episyrphus* < *Volucella* < *Eristalis*. In *Episyrphus* the rhabdomeres are at right angles to the depression of the tentorial phragmata, whilst in *Eristalis* they run parallel to it; *Volucella* is intermediate. *Eristalis* and *Volucella* have what the authors consider to be the ancestral number of retinula cells making up the organ (i.e. 35–40), whereas there are about three times as many in *Episyrphus*. Since the authors were unable to study the larvae of any phytophagous syrphids, they could not resolve the cladogram of these types, but there were strong evolutionary developments in both predatory (number of retinula cells) and saprophagous forms (tapetum).

King (1991) chose two syrphines (*Allograpta, Toxomerus*) and two saprophages (*Syritta, Eristalis*) in his study of the evolution of the adult cardia. All four possessed gastric caeca; Maki (1935) had already drawn attention to remarkable differences in the form of the gastric caeca in the adult alimentary canal of various syrphids—it is very likely therefore that all syrphids possess these organs, and that they may have useful characters. Development of the anterior midgut cells was much more pronounced in *Syritta* and *Eristalis* than in the two syrphines, similar in fact to muscoid flies.

Finally, another way of assessing phylogeny might be from karyotypes. However,

Table 1. Aschiza larvae included in outgroup

Family	Species	Habitat
Lonchopteridae	*Lonchoptera bifurcata*	leaf litter
Lonchopteridae	*Lonchoptera lutea*	leaf litter
Platypezidae	*Bolopus furcatus*	fungi
Platypezidae	*Polyporivora omata*	fungi
Platypezidae	*Lindneromyia* sp.	fungi
Phoridae	*Aenigmatias lubbocki*	ex *Formica* ant
Phoridae	*Megaselia altifrons*	decayed wood
Phoridae	*Megaselia pygmaea*	fungi
Phoridae	*Megaselia rufipes*	ex *Helix* snail
Phoridae	*Triphleba minuta*	fungi
Phoridae	*Spiniphora bergenstammi*	ex milk bottle
Pipunculidae	*Chalarus* sp.	ex typhlocybine leafhopper
Pipunculidae	*Verrallia* sp.	ex *Philaenus* sp. froghopper

an incredibly extensive work on syrphid karyotypes (see Boyes *et al.*, 1980) unfortunately sheds little light on syrphid phylogeny. The authors considered the Eristalini to be primitive, and the Pipizini to be derived, but they based this conclusion on the very flimsy grounds that 12 chromosomes were commonly found in some other families of Diptera. Since the Eristalini have the highest proportion of species (79 out of 110 species) with 12 chromosomes, this must mean that they are 'primitive'; chromosomal reduction they regarded as a derived feature, and hence since virtually all Pipizini show this state (23 of 24 species), they must be 'advanced'. In view of the variability of chromosomal numbers they report (intraspecific, intrageneric, intratribal) coupled with the small range of possibilities (6, 8, 10, 12 or 14), it is unlikely that these views reflect the true pattern of relationships.

METHODS

Obtaining larvae

Larval stages are more difficult to work with than adults because few collections exist, and for many species larval stages are unknown. For this study many larvae were collected from the field, often being obtained for the first time (Rotheray, 1988a, 1991, 1993; Rotheray & Gilbert, 1989). Details on finding syrphid larvae are given by Rotheray (1993). Many additional larvae were borrowed from individuals and institutions (noted in the Acknowledgements).

Cladistic analysis

Field collected larvae were reared to the third stage, then fixed in boiling water and preserved in 70% alcohol. To score characters, preserved final stage larvae were dried on tissue paper and examined using light microscopy (Rotheray, 1993). Head skeletons were studied by either soaking puparia or the anterior end of preserved larvae in 10% KOH for several hours. The head skeleton was removed from the puparium or dissected from the preserved larva and examined under light microscopy. A set of 187 characters were obtained from all over the body of the larva (Appendix 1), and scored on an outgroup consisting of 13 non-syrphid Aschiza species (Table 1) and 118 syrphid species in 85 supraspecific taxa (Appendix 2).

This set of larval characters incorporates those previously analysed for aphid predators (Rotheray & Gilbert, 1989). The syrphid species analysed are given in the section on generic diagnoses. In four taxa, *Spilomyia* Meigen, *Milesia* Latreille, *Lejota* Rondani and *Blera* Billberg, all of which are rare in northern Europe, we used Nearctic species because these were the only ones available. In other taxa we included extra Nearctic species depending on availability of material, as detailed in the generic diagnoses section.

We obtained the set of shortest trees from the character-state matrix using standard cladistic methods implemented by the program Hennig86, with all characters set as unordered. We rooted the tree on the Lonchopteridae, generally considered to be the basal group of the Aschiza (McAlpine, 1989). Given the large number of taxa involved, we were forced to obtain trees using the command sequence *mh**; *bb**, rather than the preferred *ie-; bb**. There were always multiple equally parsimonious trees (whose consensus is shown in Fig. 5), which were reduced to three very similar trees by using the successive weighting option (*xs w; bb**;), and then to a single tree by secondary analyses on large subsections of the tree. We randomized the order of the taxa in the input file, and always obtained the same three trees. The secondary analyses were done also to make sure that the relationships were stable (which they were), and in all cases we included reference taxa from other parts of the tree to indicate any instability. Character-state changes in the tree were assessed by transferring the tree and character matrix to PAUP version 2.4.1; we used ROOT = ANCESTOR and OPT = DELTRAN for the optimization (Appendix 3). The final fully resolved tree with its numbered nodes (Fig. 6) is used to refer to all the changes that we discuss.

To investigate functional morphology, a range of larvae were observed feeding, moving and breathing. Larvae of *Eumerus, Cheilosia, Ferdinandea, Microdon, Pipiza, Platycheirus, Syrphus, Brachyopa, Sphegina, Xylota, Criorhina, Callicera, Temnostoma, Caliprobola, Mallota* and *Myathropa* were observed by placing them next to, or within, the breeding medium. The ventral surface was observed during feeding and moving by placing larvae on sheets of glass.

Where size and proportion are mentioned in morphological descriptions, they are relative to the first abdominal segment for mouthpart and thoracic features, and relative to the 6th abdominal segment for features of the 7th abdominal and anal segments. For convenience, we refer to the compounded posterior segment as the ‘anal segment’.

RESULTS AND DISCUSSION

General features of final-stage Aschiza larvae

All Aschiza larvae have three instars except those of Pipunculidae which have two (Jervis, 1980). In cross-section, final-stage Aschiza larvae are dorso-ventrally flattened or subcylindrical. Larvae usually taper anteriorly and posteriorly, and vary in length from 2 to 25 mm (Fig. 2). In relation to Nematocera larvae, the head is reduced to a membranous cephalic segment and sclerotized mouthparts (Teskey, 1981). There are three thoracic segments and eight abdominal segments. The anus is on the ventral surface of the compounded, eighth abdominal segment (= anal segment). A pair of anterior spiracles usually protrude from the dorsal surface of

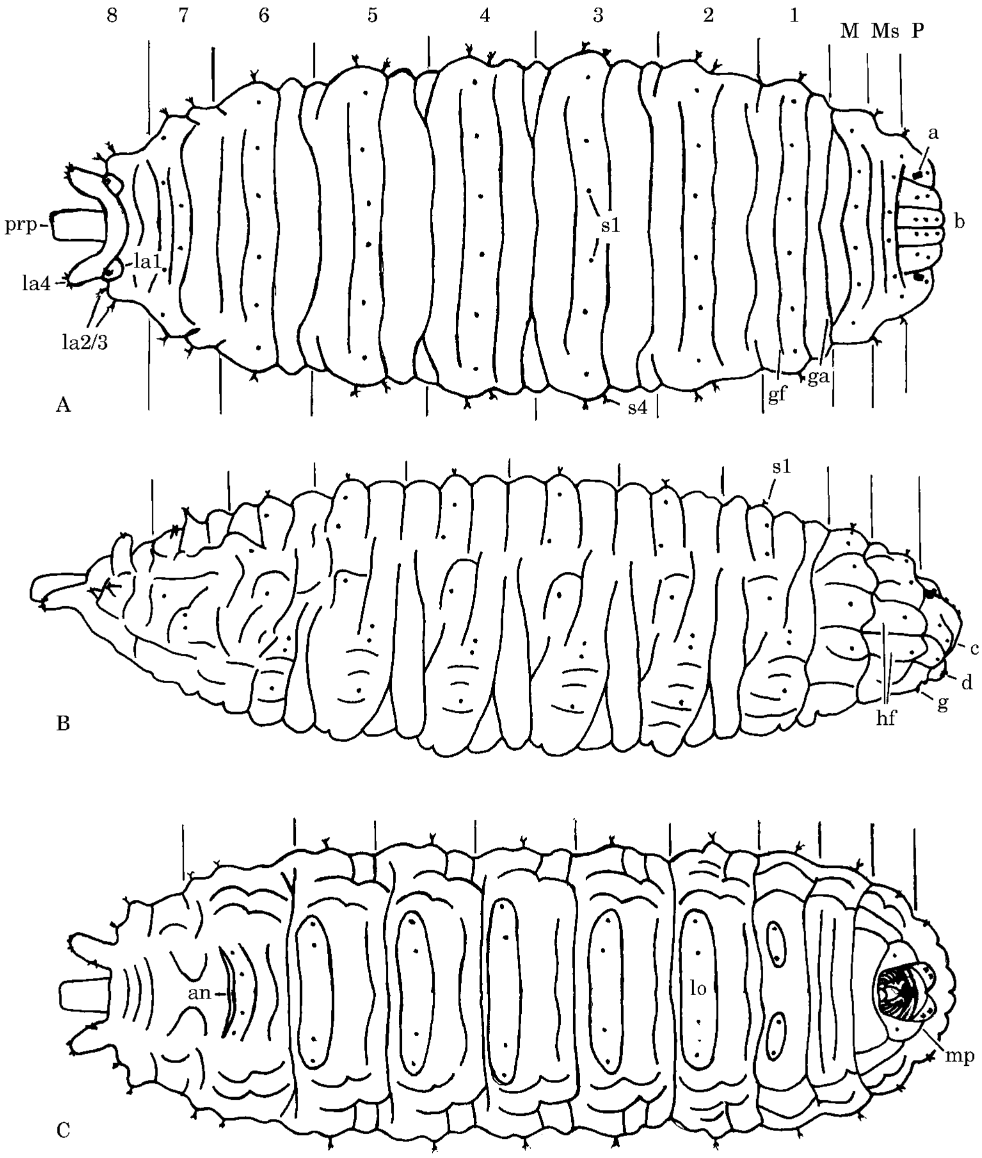

Figure 2. *Eumerus tuberculatus*, third stage larva. Length 14 mm. A, dorsal view. B, lateral view. C, ventral view. 1–8 = abdominal segments; P = prothorax; Ms = mesothorax; M = metathorax a = anterior spiracle; b = longitudinal folds on the prothorax; ga = groove between metathorax and first abdominal segment; gf = groove between folds on the first abdominal segment; s1 = sensilla pair one; s4 = sensilla 4; la1 = lappet 1; la2/3 = lappets 2a & 2b; la4 = lappet 3; prp = posterior respiratory process; c = anterior fold; d = antennomaxillary organs; g = mandible; hf = horizontal folds of the thorax bearing sensilla 4 and 5; lo = locomotory organ; an = anus; mp = mouthparts, see Fig. 8b

the prothorax and posterior spiracles from the anal segment. Abdominal segments 2–7 are similar to each other in structure, shape and form. However, the thorax and particularly the prothorax, the anal segment and sometimes abdominal segments 1 and 7 are modified in various ways.

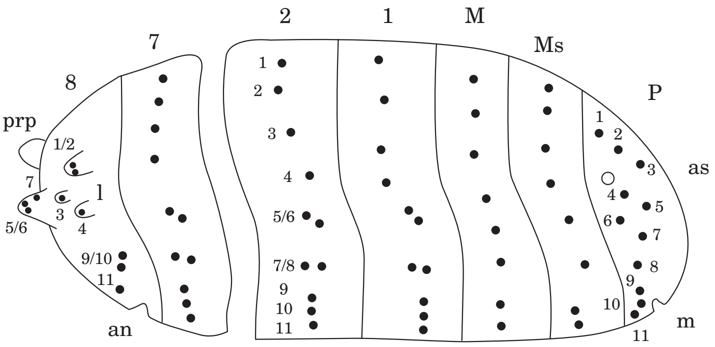

Figure 3. Morphological map of *Eumerus tuberculatus* showing position and numbering of segmental sensilla of one half of the body. Dorsal side uppermost; segments 3–6 not shown but similar to segment 2; P = prothorax, Ms = mesothorax, M = metathorax, numbers 1–11 = sensilla, as = anterior spiracle, m = mouth, prp = posterior respiratory process, l = lappets, an = anus, mesothorax and metathorax with 8 sensilla each, and sensilla 7 and 8 apparently fused on the 8th abdominal segment.

TABLE 2. Sensilla locations in relation to morphology in larval Syrphidae

Segment	Sensilla number	Location	Fig
prothorax	1,2,3	longitudinal folds	8
	4,5	fold anterior to anterior spiracle	8
	6,7,8	U-shaped fold on the lateral margin	8
	9,10	lateral lips	8
	11	posterior to ventral lip	8
mesothorax and metathorax	1,2,3	dorsal folds	
	4,5	horizontal folds of lateral margin	8
	6	ventro-lateral margin	8
	7,8	ventral folds	8
7th abdominal segment	2	fold behind fold with sensilla 1 in larvae with extended posterior ends	27
	9,10,11	fold anterior to anus	
anal segment	1,2	tip of lappet 1	3
	3,4	tip of lappet 2	
	5,6	tip of lappet 3	
	7,8	base of lappet 3 in *Eumerus-Brachyopa*	2,3,19
	7,8	fold at base of lappet 3, some entomophagous *Volucella*	19
	7,8	lateral margin of anal segment	19
	9	fold lateral to anus	2
	10,11	fold posterior to anus	2
	10,11	base of tail in long-tailed larvae	27

Boundaries between segments appear as shallow grooves, but in many Aschiza they are obscured by secondary grooves and folds in the integument. A groove is an impressed line on the integument, and a fold is a region of the integument delimited by grooves. The ventral surface is often flattened with locomotory organs on the metathorax and abdominal segments 1–6/7. In most Aschiza, locomotory organs appear as segmental pairs of oval-shaped protuberances bearing sensilla. Each segment bears a pattern of sensilla (*sensu* Hartley, 1961). Few analyses have been made of sensilla distribution patterns within Aschiza. The most complete descriptions are for Syrphidae (Hartley, 1961; Rotheray & Gilbert, 1989). Kessel *et*

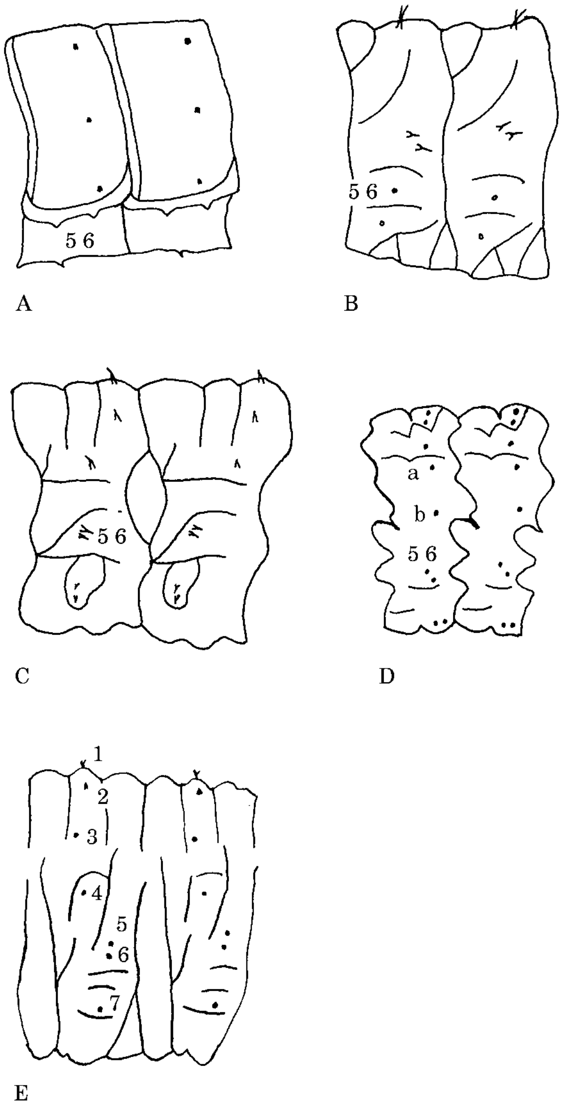

Figure 4. Variation in abdominal segments 2 and 3, lateral views, dorsal side uppermost. A, *Lonchoptera bifurcata* (Lonchopteridae), dorso-ventral height = 1.0 mm. B, *Bolopus furcatus* (Platypezidae), height 1.2 mm. C, *Triphleba minuta* (Phoridae), height 0.8 mm; D, *Chalarus* sp., (Pipunculidae), height 0.8 mm; E, *Eumerus tuberculatus* (Syrphidae) height 2.5 mm. 1–7 = sensilla numbers; a, b = sensilla 4 apparently divided into two sensilla.

al. (1973) do not mention them in their descriptions of platypezid larvae, nor does Jervis (1980) deal with them in his study of pipunculid larvae. However, Albrecht (1990) describes them (as papillae) for the pipunculid genus *Dorylomorpha.* Descriptions of phorid larvae (see Ferrar, 1987) rarely include sensilla. Where sensilla are mentioned, the lateral and ventral sensilla are often neglected.

Sensilla are present on every body segment and are useful ‘markers’ for determining positions on the body (Fig. 3, Table 2). Dorsal and some lateral sensilla are usually

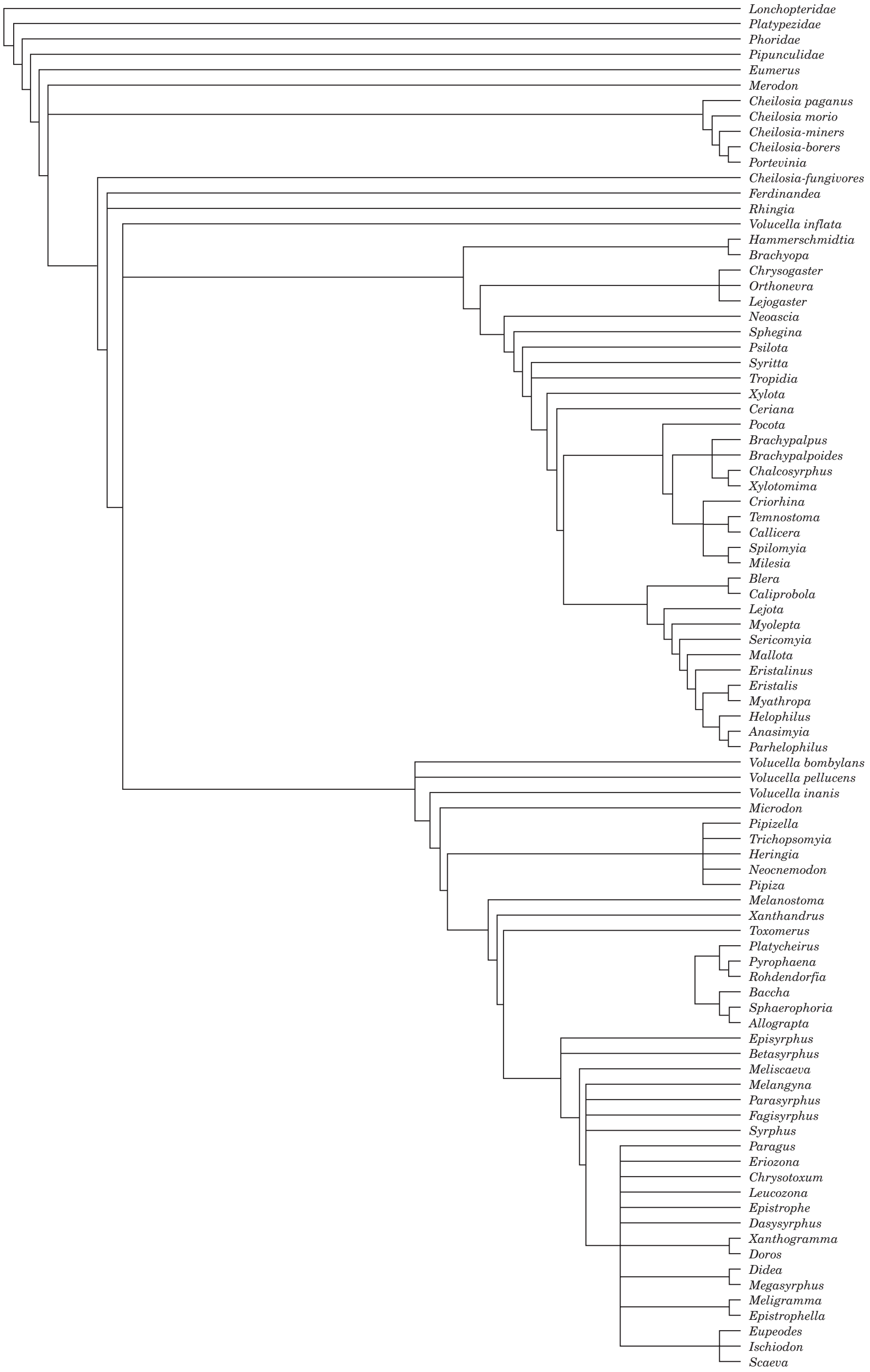

Figure 5. Consensus tree. This consensus tree was produced by the '*nelson*' command of Hennig86, working upon the multiple equally short trees that resulted from the command '*bb**' operating on all available taxa and unweighted characters.

accompanied by setae, or are borne on fleshy projections (papillae). Under light microscopy, lower lateral and ventral sensilla are often inconspicuous, appearing as spot-like indentations on small, oval folds. A pattern in sensilla distribution is present which is similar across Aschiza. Reading from a mid-dorsal to a mid-ventral line down one half of abdominal segments 1–7, there are up to four pairs of evenly-spaced sensilla followed by two pairs of approximated sensilla and up to three on the ventral surface (Fig. 4).

In the Syrphidae there are up to 11 sensilla present on each segment. The mesothorax and metathorax have 8 sensilla. One sensillum each appears to have been lost at positions 5/6 and 7/8 and 9/10/11 (Fig. 3). On abdominal segments 1–7, sensilla 10 or 11 are sometimes lost. On the anal segment one sensillum has been lost from 7/8. The sensilla of the prothorax and anal segment are characteristically located on particular folds of these segments (Table 2).

Cladistic analysis

The final tree based on the Lonchopteridae shows that the Platypezidae are plesiomorphic, with Syrphidae the most derived (Figs 5, 6). The Pipunculidae is the sister group to the Syrphidae (Fig. 6).

Syrphidae can be diagnosed on the following larval characters. Body length variable from 5 to 25 mm. Segmental boundaries obscured by intrasegmental grooves (Fig. 4). Head skeleton with ridged mandibular lobes attached to the mandibles (character number 6, Appendix 1) or, in some entomophagous taxa, head skeleton developed anteriorly without mandibular lobes (character 2). Head with dorsal lip, a projection between the mouth and the antennomaxillary organs, often coated in setae (character 14). Prothorax with longitudinal folds on the dorsum of the prothorax (character 18). Either side of the mouth, the anterior margin of the prothorax with a pair of ovoid projections, the lateral lips, each bearing sensilla 9 and 10 (character 59). Front part of the prothorax with an extended region, the anterior fold, which curves down to meet the base of the antennomaxillary organs and is often coated in sclerotized vestiture (character 66). Posterior spiracles fused into a single elongate structure, the posterior respiratory process, (character 166). Anus sited at the anterior margin of the anal segment (character 176).

The final tree (Figs 5, 6) shows that *Eumerus* is the most plesiomorphic taxon within the Syrphidae. Traditional suprageneric groups are not indicated, with higher categories such as the Syrphinae and Eristalinae of Vockeroth & Thompson (1987) either corresponding to paraphyletic groups, since they do not include all taxa at particular nodes, or polyphyletic, since they are spread over several nodes. While traditional higher categories are not supported, the analysis of species validated all of the genera examined with two exceptions, *Cheilosia* and *Volucella*, which appear to be polyphyletic (Fig. 6). These genera are unusual among syrphids in having more than one larval feeding mode and, unlike other genera, larval morphology is variable. Within *Cheilosia*, some species are mycophagous, either feeding on fungi and their breakdown products in pockets of decay in live or dead plants (*Cheilosia pagana*) or feeding on the fruiting bodies of macro-fungi (*Cheilosia* fungivores), while others are phytophagous (*Cheilosia morio* to *Cheilosia* borers) (Table 3). However, *Cheilosia* may not be truly polyphyletic. With less than 5% of larvae available for study, our

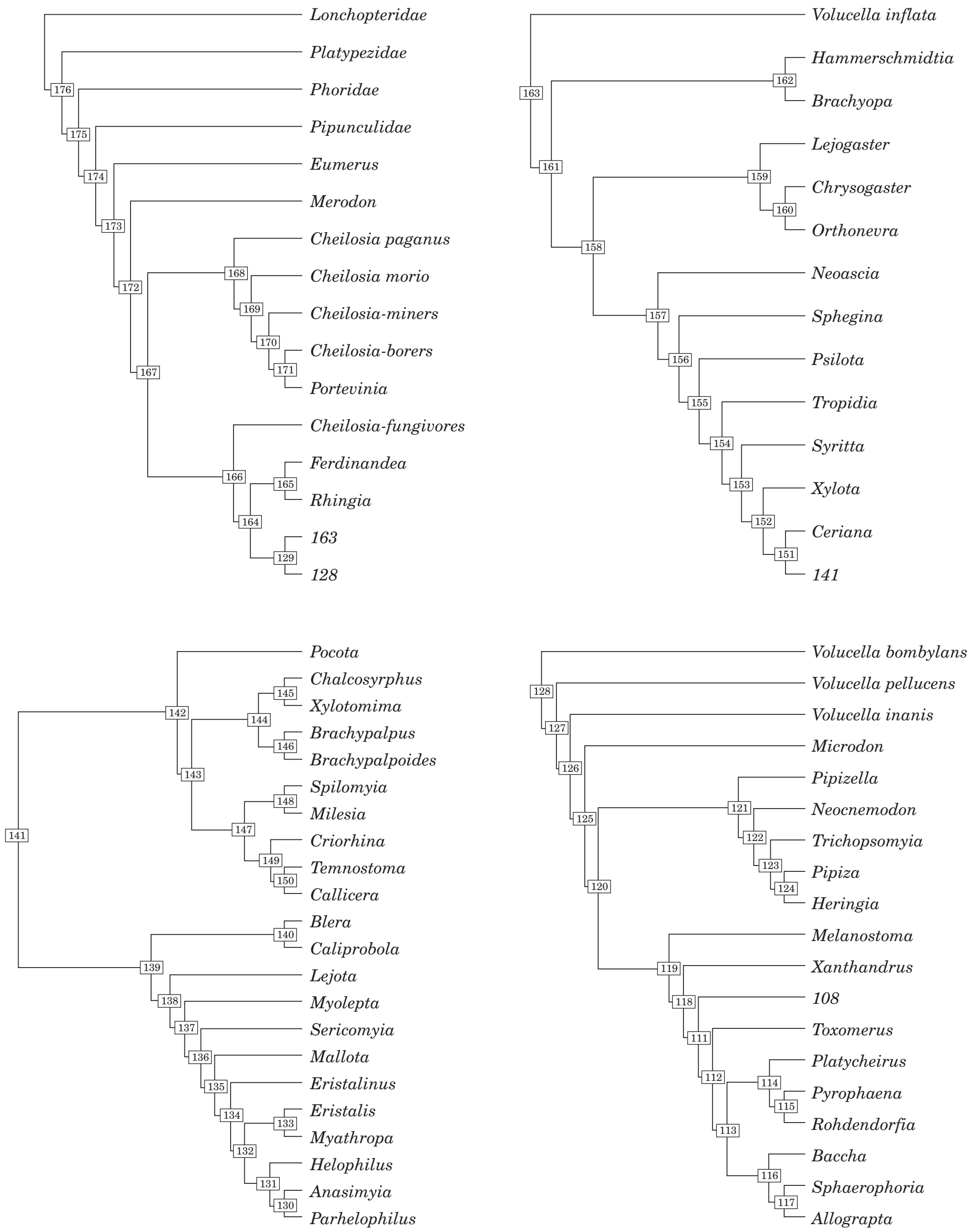

Figure 6. Fully resolved tree. This fully resolved tree (length 571, consistency index 0.45, retention index 0.87) was produced by: (a) successive weighting (the '*xs w*' command of Hennig86) of the multiple equally short trees of Fig. 5 (quoted tree statistics, however, use unweighted characters); (b) separate secondary analyses of large clades of the tree.

analysis probably over-emphasizes derived elements. When more larvae are studied, synapomorphies are likely to be found.

Within *Volucella*, one species has saprophagous feeding habits (*Volucella inflata*), while others are either facultative or obligatory entomophages (*Volucella inanis*, *pellucens*

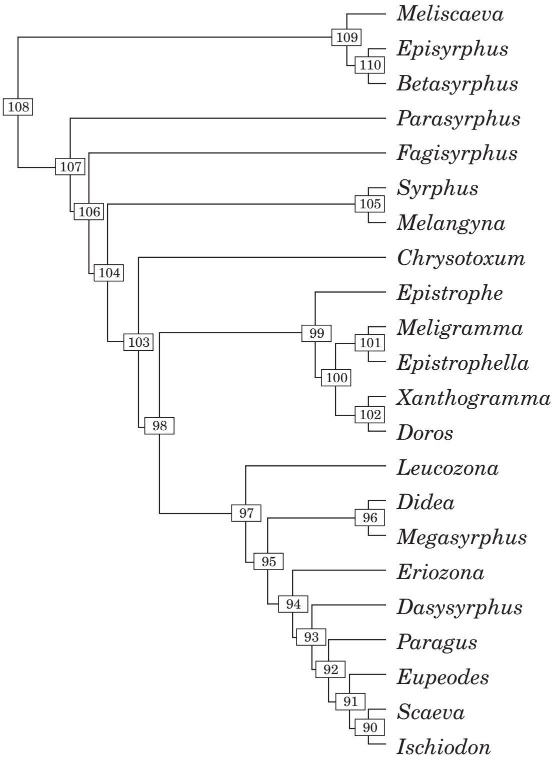

Figure 6. *continued.*

and *bombylans*). *Volucella* apparently contains within its current boundaries the origins of two branches comprising most of the remaining syrphid taxa (Fig. 6).

In general, the analysis of clade **120** (i.e. the Pipizini + Syrphinae, *sensu* Thompson & Vockeroth, 1987) produced similar results to our previous study (Rotheray & Gilbert, 1989), but it is now attached to the tree of the whole family (Fig. 6). *Microdon* is the sister group to clade **120**. *Paragus* is in a different position from our former estimate, and is now close to *Scaeva* and *Eupeodes* (Fig. 6). Previously, *Paragus* was problematic, but its position is now unequivocal in the sense that it took this position in all the equally parsimonious trees. The taxonomic position of the Pipizini (*sensu* Vockeroth & Thompson, 1987) has been considered uncertain, with some adult characters suggesting a close relationship with taxa other than predacious Syrphidae. Its basal position may explain the transitional nature of some of these adult characters.

Diversification of feeding modes and habitats

A sequence was revealed by superimposing larval feeding modes and habitats on the cladogram of Fig. 6 (Table 3). Lonchopteridae, Platypezidae and Pipunculidae each have one feeding mode. Lonchopteridae feed by scraping micro-organisms, fungal hyphae and spores from the surface of fallen vegetation in moist leaf litter (Ferrar, 1987). Platypezid larvae are also associated with fungi and feed on hyphae, fruiting bodies and fungal breakdown products (Ferrar, 1987). Larval form in Platypezidae

TABLE 3. Summary of larval habitats for outgroup and syrphid taxa following the sequence in Fig. 6

Taxon	Feeding mode	Larval habitat
Lonchopteridae	mycophagy	fungal hyphae & micro-organisms from surface of fallen vegetation
Platypezidae	mycophagy	surface of encrusting fungi; fungal fruiting bodies
Phoridae	mycophagy, saprophagy, parasitism and predation	fungi; decaying organic media; predators & parasites of invertebrates
Pipunculidae	entomophagy	endoparasitoids of Cicidellidae, Delphacidae & Cercopidae (Homoptera)
Eumerus	mycophagy/?phytophagy	underground parts of non-woody plants; pockets of decay in live non-woody plants above ground
Merodon	mycophagy/?phytophagy	underground parts of non-woody plants
Cheilosia paganus	mycophagy	pockets of wet fungal decay in live and dead non-woody plants
Cheilosia morio	phytophagy	cambial tissues of pine trees
Cheilosia miners	phytophagy	leaf mines in herbaceous plants
Cheilosia borers	phytophagy	bores in stems and roots of herbaceous plants
Portevinia	phytophagy	underground parts of non-woody plants
Cheilosia fungivores	mycophagy	fungal fruiting bodies
Ferdinandea	mycophagy/saprophagy	exuding tree sap & wet fungal decay in plant roots
Rhingia	mycophagy/saprophagy	wet fungal decay in bovine dung
Volucella inflata	saprophagy	exuding tree sap
Volucella bombylans	saprophagy/entomophagy	dead, dying and live larvae of social aculeates
Volucella pellucens	saprophagy/entomophagy	dead, dying and live larvae of social aculeates
Volucella inanis	entomophagy	larvae of social aculeates
Microdon	entomophagy	eggs, larvae & puparia of ants
Pipizella^{+}**	entomophagy	soft-bodied homoptera, particularly Aphididae
Hammerschmidtia	saprophagy	exuding tree sap and decaying sap under bark
Brachyopa	saprophagy	exuding tree sap and decaying sap under bark
Lejogaster^{+}	saprophagy	decaying vegetation in freshwater bodies
Neoascia	saprophagy	decaying vegetation and dung in wet conditions including freshwater bodies
Sphegina	saprophagy	exuding tree sap and decaying sap under bark

continued

TABLE 3. *continued*

Taxon	Feeding mode	Larval habitat
Psilota	saprophagy	decaying sap under bark
Tropidia	saprophagy	decaying vegetation and dung in freshwater bodies
Syritta	saprophagy	decaying vegetation in wet conditions
Xylota	saprophagy	wet decaying vegetation, decaying sap under bark, wet decaying heartwood
Ceriana	saprophagy	exuding tree sap and decaying sap under bark
Pocota	saprophagy	wet decaying heartwood in rot-holes
Chalcosyrphus	saprophagy	decaying sap under bark
Brachypalpus	saprophagy	decaying sap under bark
Brachypalpoides	saprophagy	wet decaying heartwood at base of trees and tree roots
Spilomyia	saprophagy	wet decaying heartwood in rot-holes
Milesia	saprophagy	wet decaying heartwood in rot-holes
Criorhina	saprophagy	wet decaying heartwood in rot-holes and tree roots
Callicera	saprophagy	wet decaying heartwood in rot-holes and trees roots
Temnostoma	saprophagy	boring in moist, soft decayed heartwood in fallen wood
Blera	saprophagy	wet decaying heartwood in rot-holes and tree roots
Caliprobola	saprophagy	wet decaying heartwood in tree roots
Lejota	saprophagy	wet decaying heartwood in tree roots
Myolepta	saprophagy	wet decaying heartwood in rot-holes
Sericomyia	saprophagy	decaying vegetation in freshwater bodies
Mallota	saprophagy	wet decaying heartwood in rot-holes
Eristalinus	saprophagy	decaying vegetation in freshwater bodies
Eristalis	saprophagy	decaying vegetation in freshwater bodies
Myathropa	saprophagy	wet decaying vegetation in water pockets on trees; wet decaying heartwood, exuding tree sap
Helophilus	saprophagy	decaying vegetation in freshwater bodies
Anasimyia	saprophagy	decaying vegetation in freshwater bodies
Parhelophilus	saprophagy	decaying vegetation in freshwater bodies

** The '+' means 'including all taxa above in the tree'.

varies from dorso-ventrally flattened species feeding between gills in fungi, to subcylindrical forms tunnelling into them (Ferrar, 1987). A third larval form occurs in *Callomyia*, which is dorso-ventrally flattened and feeds on the surface of encrusting fungi (Lundbeck, 1927; Chandler, 1978). Like lonchopterids, it has the metathorax fused with the first abdominal segment. The Pipunculidae are endoparasitoids of various Homoptera, particularly Cicadellidae, Delphacidae and Cercopidae (Ferrar, 1987).

In contrast, Phoridae and Syrphidae have multiple feeding modes involving mycophagy, saprophagy, predation and parasitism. Phytophagy is additionally present in the Syrphidae (Table 3).

Except for *Cheilosia* and *Volucella*, all genera were true to particular feeding modes, and species within genera often occur in the same microhabitat. Taxa in the basal syrphid sequence, *Eumerus* to node **129**, are mycophagous, except for *Portevinia* and some *Cheilosia* which are phytophagous (with possible additions in *Merodon*). Basal taxa either feed on fungi and bacteria associated with areas of decay in live and dead plants, or on fungal fruiting bodies. Mycophagous taxa use mouth-hooks to scrape food together and soft mandibular lobes to scoop it up. Phytophagous taxa use their mouth-hooks to fragment plant tissues. Mycophagous and phytophagous larvae live in fluids and prevent the breathing tubes from becoming blocked by various means, but morphology in relation to locomotion is little developed.

At node **129** in the tree, syrphid evolution diverges, with both branches originating within the genus *Volucella*, as currently defined. One branch (to clade **163** and *V. inflata*) is saprophagous, while the other (to clade **128** and *V. bombylans*) is entomophagous (Fig. 6; Table 3).

Syrphid entomophages exploit two main groups of prey. The prey of basal entomophages are larvae of social Hymenoptera (*Volucella* and *Microdon*): the prey of the most derived group (clade **120**) are soft-bodied Homoptera. The shift between them may have occurred in ant nests (Formicidae), in which are found larvae of both *Microdon* and *Pipizella*. Entomophages feed by piercing or tearing their prey and sucking up the contents. *Volucella, Microdon* and clade **120** each have different but related means of gripping and piercing prey. Syrphid entomophages frequently live exposed on relatively dry substrates such as plant surfaces. They possess a variety of mechanisms for holding on and gripping the substrate, but their breathing organs are relatively little developed in comparison with the saprophages.

Syrphid saprophages have large mouths and a mechanism to filter bacteria suspended in fluids of varying viscosity; unlike the entomophages, their mouthparts are very uniform. Saprophages exploit three main habitats: wet decaying vegetation, decaying tree sap and wet decaying heartwood. Shifts between them are frequent (Table 3). Trees falling into water bodies are the likely route which facilitated these shifts. Saprophages are immersed in fluids, and have prolegs with crochets to hold on and grip the substrate. Air exchange frequently involves extensions of the anal segment.

High levels of morphological innovation are associated with shifts between syrphid feeding modes. Diversification within feeding modes is characterized by less innovation and a trend towards morphological complexity i.e. succeeding nodes appear to incorporate and/or elaborate on change from previous nodes, with few reversals or losses.

Morphological and behavioural evolution

Larval form is very varied across the Aschiza. A particular trend is increasing numbers of intra-segmental grooves (Fig. 4). The trend towards higher numbers of

Table 4. Comparison of larvae of Pipunculidae (*Chalarus* and *Verrallia*) with Syrphidae (*Eumerus*)

Character	Pipunculid	Syrphid	Fig.
intrasegmental folds and grooves	few	many	4
dorsal, lateral and ventral lips	not developed	well developed	7, 8
mandibular lobes	absent	present	7, 8
flexible collar surrounding mouth	not developed	well developed	7, 8
dorsum of prothorax	no grooves	grooves present	7, 8
lateral folds on thorax	no folds	2 parallel folds	7, 8
posterior breathing tubes	short and separate	elongate and fused	2
position of breathing tubes	high on anal segment	at tip of segment	2
shape of anal segment	rounded at tip	elongate and tapered with longer ventral than dorsal aspect	2
dorsum of anal segment	no transverse grooves	grooves present	2
position of anus	not on anterior margin	on anterior margin	2
lappets	absent	present	2

grooves is not related to changes in body size because phorids and pipunculids are often smaller, and syrphids larger, than the more basal platypezids. Nor are grooves related to changes in body shape: subcylindrical platypezids have simpler patterns of grooves than subcylindrical phorids, which are in turn simpler than those in similarly shaped pipunculids and syrphids.

When muscles contract, the integument collapses along the intra-segmental grooves. Such muscles are easily visible using transmitted light on recently moulted, final-stage larvae. Grooves signify discrete areas of the integument controlled by particular groups of muscles. Diversification of these muscles and related integumental characters apparently underlies much of the variation of larval form across the Aschiza.

Mycophagy and phytophagy in Syrphidae

The basal sequence in Syrphidae consists of mycophagous and phytophagous taxa (Fig. 6; Table 3). The most basal syrphid taxon is *Eumerus*. *Eumerus* larvae often occur in pockets of semi-liquid decay in live or dead plants, particularly bulbs and roots (Hodson, 1932; Creager & Spruijt, 1935). Larvae of the syrphid sister group, the Pipunculidae, are endoparasitoids within the abdomens of leafhoppers (Ferrar, 1987). Young pipunculid larvae feed on haemolymph and older larvae also on body tissues (M.A. Jervis, pers. comm.). Although both groups are immersed in food, pipunculid larvae probably imbibe food passively since it is under pressure within the host. This is not the case for mycophagous syrphids, where imbibing food is an active process.

Comparing *Eumerus* (Syrphidae) with *Chalarus* (Pipunculidae), a number of innovations are apparent, particularly in the structure of the mouthparts, thorax and anal segment (Table 4). Briefly, although mouthparts in both taxa bear hooked

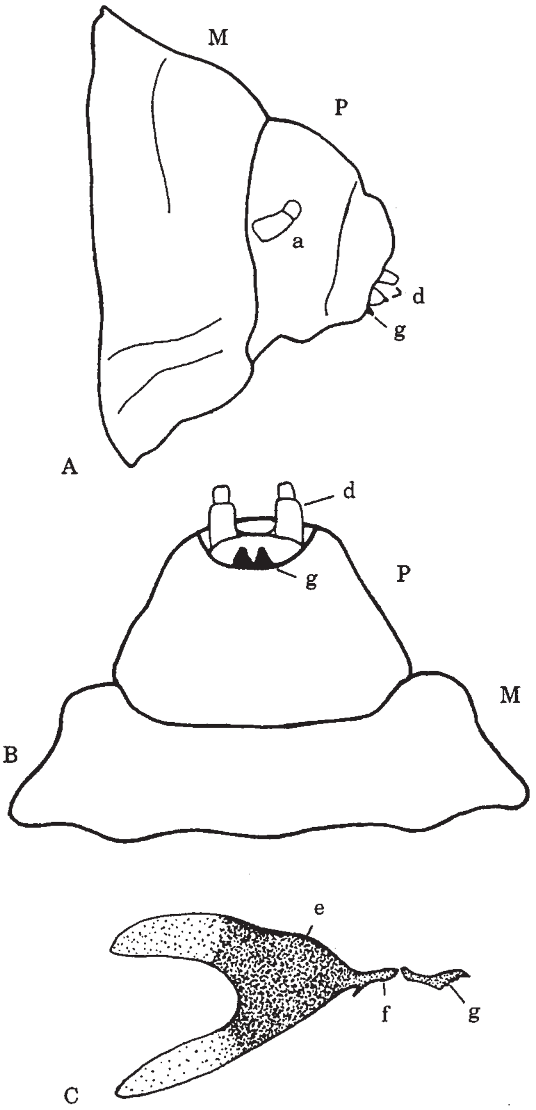

Figure 7. *Chalarus* sp. (Pipunculidae), final stage larva, length 4 mm. A, prothorax and mesothorax, lateral view. B, prothorax and mesothorax, ventral view. C, head skeleton. P = prothorax; M = mesothorax; a = anterior spiracle; g = mandible; d = antennomaxillary organs; e = labrum; f = tentorial bar; g = mandible.

mandibles and imbibe semi-liquid food, those of *Eumerus* are relatively larger and more complex (Figs 7, 8).

Feeding in *Eumerus* is facilitated by four groups of apomorphic structures which together confer a high degree of manoeuvrability in comparison with pipunculids. First, there are bands of muscle along the lateral margins of the mesothorax and metathorax. Externally these muscles are indicated by two pairs of parallel, horizontal folds at the level of sensilla 4 and 5 on the mesothorax and metathorax. At their proximal end these folds fuse together, forming a U-shape on the prothorax bearing

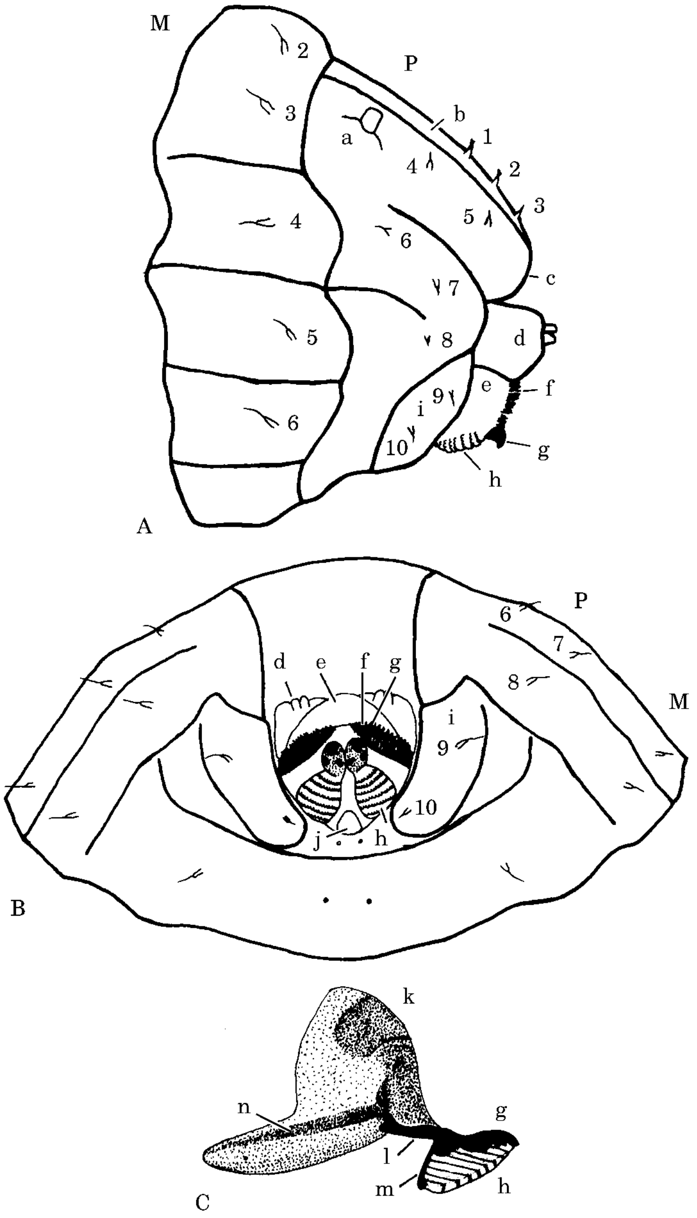

Figure 8. *Eumerus tuberculatus*, third stage larva. A, prothorax and mesothorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. 1–10 = sensilla; P = prothorax; M = mesothorax; a = anterior spiracle; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; e = flexible collar; f = dorsal lip; g = mandibular hook; h = mandibular lobe; i = lateral lip; j = ventral lip; k = labrum; l = tentorial bar; m = mandibular apodeme; n = tentorial arm.

sensilla 6–8 (Fig. 8). The presence of these muscles was confirmed by examination of transverse sections of syrphid larvae. These muscles enable the thorax to move independently from the abdomen, and extend the thorax into the food. Second, the prothorax can move independently of the rest of the thorax using muscles which are indicated by longitudinal grooves on the dorsum (Fig. 2, character b). The prothorax moves up and down to immerse the flexible collar into the food. Third, the flexible collar surrounding the mouth can expand; and fourth, the mouth-hooks project forward and the mandibular lobes press into the food. The food can then be scooped into the mouth by muscular contractions which close the mandibular lobes together. Feeding scoops usually occur rapidly, in sequences of repeated movements. Ridges from the mandibular lobes extend over the lateral margins of the mouth and assist in scooping food into the mouth.

There are also innovations to the anal segment (Table 4). Summarizing, in *Eumerus* the breathing tubes are fused together, elongate and positioned at the tip of the anal segment which itself tapers and is more elongate ventrally than dorsally (Fig. 23A). These changes facilitate breathing, by tilting the anal segment up through the semi-fluids in which these larvae live.

A new feeding mode, phytophagy, appears at node **169** (*Cheilosia morio* to *Portevina*). However, not all *Cheilosia* are phytophagous, and some retain the plesiomorphic feeding mode of mycophagy (*Cheilosia pagana* and *Cheilosia* fungivores, Table 3). Phytophages and *Cheilosia* mycophages feed in a similar way to *Eumerus* except that phytophages scrape plant tissues, and their mandibular lobes are fused to the mandibular apodeme. The head skeleton including the mandibles and mandibular lobes are usually heavily sclerotized (Fig. 9). These changes result in a rasping organ which varies in size, shape and number of hooks according to species. In general, the harder the food, the fewer and larger the hooks, and the more heavily sclerotized is the head skeleton (Rotheray, 1990). In addition the shape and size of the thorax varies. For example, *Cheilosia*-miners tend to have small, narrow thoraces in relation to *Cheilosia*-borers/tunnellers (Rotheray, 1990). Other apomorphies of the *Cheilosia*-borers include a lightly sclerotized region on the dorsum of the prothorax for protection during boring. *Cheilosia*-borers also tend to be coated in sclerotized spicules to protect the body, and these facilitate gripping the tunnel during movement.

The posterior respiratory process of mycophagous and phytophagous taxa is unusually elaborate and diverse in size and shape, bearing a variety of projections and surface sculptures. The posterior end is sometimes contracted to form a flattened plate (Fig. 23C), comprising (dorsally) the 7th abdominal segment and (ventrally) the anal segment. The margins of this plate are coated in spicules, setae and lappets, with the posterior respiratory process sited towards its centre. Observations of actively feeding larvae suggest that the function of these changes is to protect the spiracular openings from being blocked by debris.

In one group the posterior end is extended, the *Cheilosia morio* group (Fig. 23B). These larvae feed on tree cambium, access to which is either through bark-beetle exit holes, or wounds to the bark. The extended posterior end which projects to the outside through the beetle hole or wound enables the larva to breathe when immersed in tree sap and resin (Burke, 1905).

At the top of this basal sequence, nodes **166** to **164** (Fig. 6), new features appear in relation to the mouthparts, thorax and anal segment. The larvae of these taxa (*Cheilosia*-fungivores, *Ferdinandea*, *Rhingia*) feed in the same way as *Eumerus* and on similar food, semi-liquid fungal/bacterial decay (Table 5). However, the anterior fold of the prothorax is partially coated in sclerotized spicules not larger than surrounding setae (Fig. 10 character c). These spicules probably protect the front of the prothorax during movement. The mandibles are reduced and small in relation

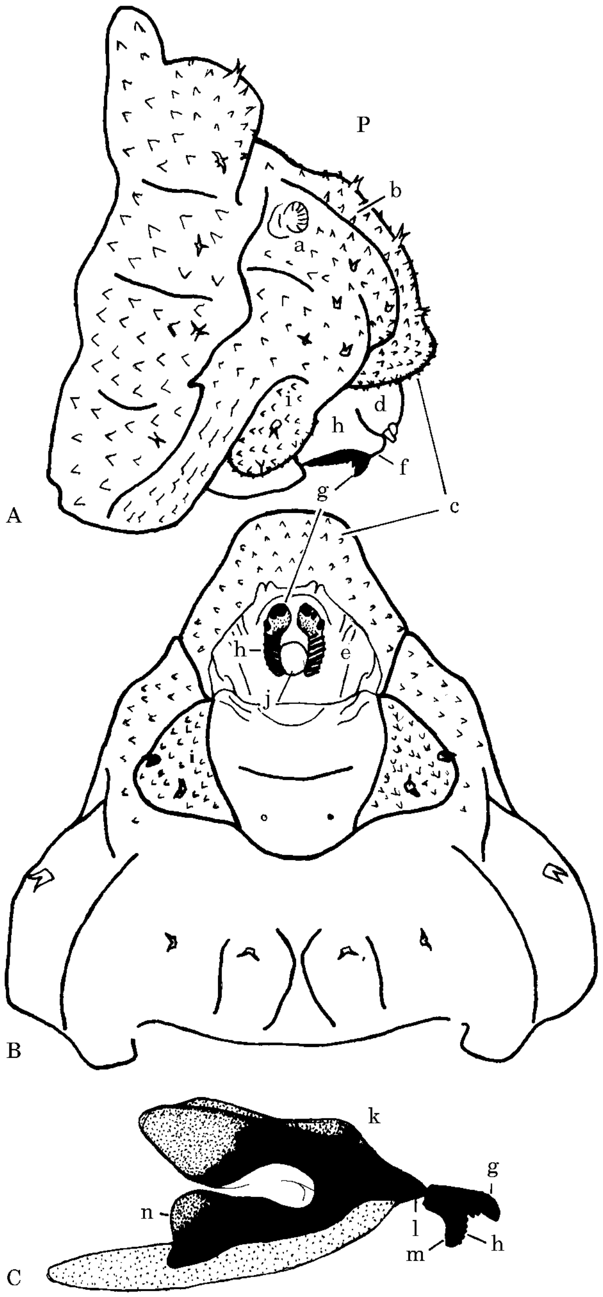

Figure 9. *Cheilosia grossa*, third stage larva (a larva that bores in plant stems). A, prothorax and mesothorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. P = prothorax; M = mesothorax; a = anterior spiracle; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; e = flexible collar; f = dorsal lip; g = mandibular hook; h = sclerotized mandibular lobe; i = lateral lip; j = ventral lip; k = labrum; l = tentorial bar; m = mandibular apodeme and sclerotized mandibular lobe; n = tentorial arm.

TABLE 5. Comparison of Volucella saprophages and entomophages with their sister group, *Ferdinandea*

Character	*Ferdinandea*	*Volucella*	
	Fig. 10	saprophages Fig. 11	entomophages Fig. 13
mandibles	barely projecting from mouth	elongate and thin, not projecting from the mouth	reduced
position of mandibular lobes	partially outside mouth	entirely inside mouth	entirely inside mouth
sclerotization of mandibular lobes	none	little	ridges sclerotized
tip of mandibular lobes	without hooks	without hooks	with hooks
size of mandibular lobes in relation to *Ferdinandea*		large	small
size of lateral lips in relation to *Ferdinandea*	large and well developed	small and inconspicous	
setae on lateral lips	little developed	broad at base, long and fine at tip	little developed
dorsal lips	little developed, setulose dorsally	large and well developed, setulose dorsally	large with ventro-medial groove and coated in spicules
ventral lips	about as broad as mouth	about as broad as mouth	broader than mouth and coated in spicules
size of thorax in relation to abdomen	about as large	broader	narrower
retractability of thorax	not retractable	not retractable	retractable
vestiture of anterior fold	some small spicules	rows of spicules	a few large spicules
papillae supporting antennomaxillary organs	one stage	two stages	two stages
feeding channel	absent	well developed	absent
mesothoracic prolegs	absent	well developed	little developed
abdominal prolegs	absent	little developed	well developed

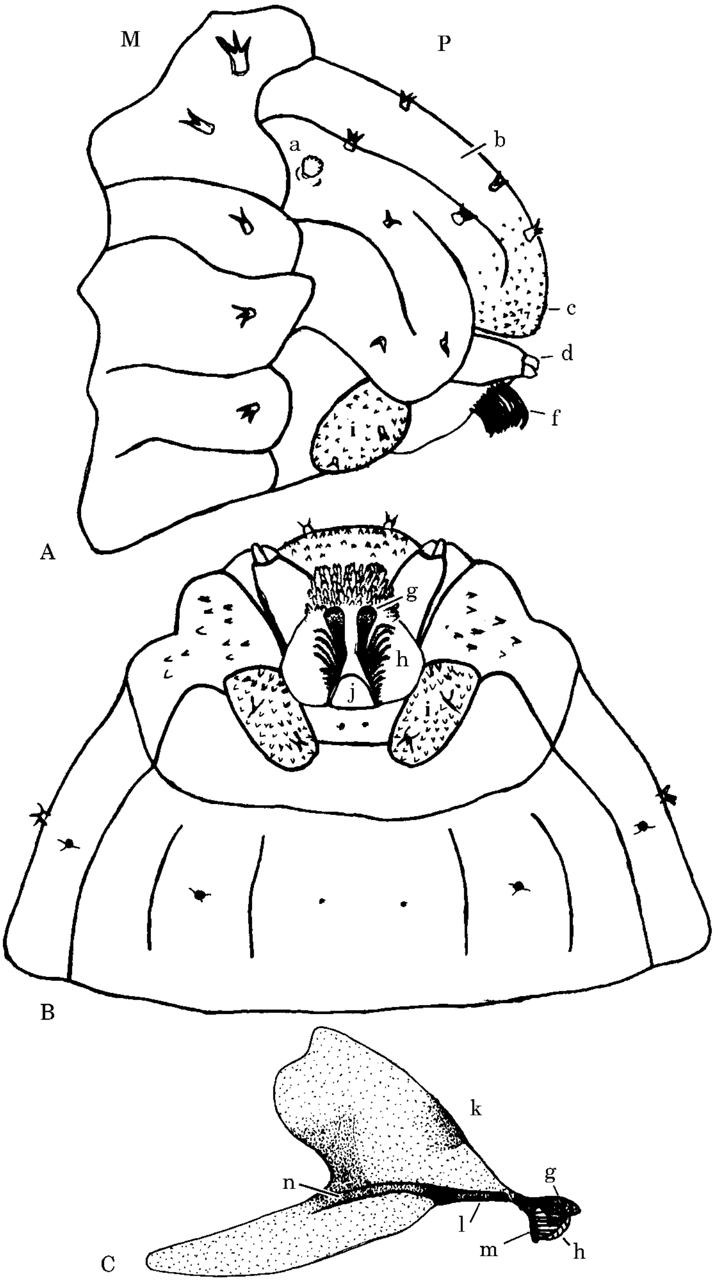

Figure 10. *Ferdinandea cuprea*, third stage larva. A, prothorax and mesothorax, lateral view. B, prothorax and mesothorax, ventral view. C, head skeleton. P = prothorax; M = mesothorax; a = anterior spiracle; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; f = dorsal lip; g = mandible; h = mandibular lobe; i = lateral lip; j = ventral lip; k = labrum; l = tentorial bar; m = mandibular apodeme; n = tentorial arm.

to *Eumerus*, as are the mandibular lobes which only partially coat the margins of the mouth (Fig. 10, character h). These changes appear to be associated with a shift towards scooping food that occurs in thin layers. Additionally, in *Ferdinandea and Rhingia*, the posterior end (of the body) is contracted, as is shown by the position of the sensilla and pattern of folds and grooves (Fig. 23D,E). This change is also associated with life in thin layers of liquid where the anal segment does not need to be tilted up for air exchange.

When immersed in fluids, mycophagous larvae probably grip the substrate using meniscus forces. Frictional forces are additionally created in tunnelling larvae from sclerotized setae on their lateral margins, and short, backwardly-directed setae on the ventral surface (Rotheray, 1988a). The mouth-hooks also grip the substrate when moving.

A further modification for holding on is seen in the leaf-mining larva of *Cheilosia semifasciata*. The larva of this species changes leaf mines several times during its development. It starts a new mine by curling round the edge of a leaf and tunnelling in from the underside, for which a firm grasp is required. This is achieved by a U-shaped grasping organ consisting of two raised folds, one each side of the anus. During locomotion, the eversible, sac-like rectal gills emerge from the anus and are pressed against the substrate. The gills are coated in watery fluids from the anus, so creating meniscus forces to hold the larva in place (Rotheray, 1988b).

Filter-feeding saprophages in Syrphidae

The basal saprophages originate at node **163**, within *Volucella* (Fig. 6; Table 3). They are similar to the entomophages but have modified states in relation to characters of the mouthparts, thorax and posterior end (Table 5). The mandibular hooks are further reduced and eventually lost (Figs 10–12). The mandibular sclerite and apodeme is long and thin, and supports the enlarged mandibular lobes (Figs 10–12). Together the mandibles and lobes form a strain on which large non-food items are caught and some excess moisture removed while micro-organism, the food, passes through (Hartley, 1963; Roberts, 1971). Saprophagous head skeletons change little across the clade, with the main direction of change being an increase in relative size (Figs 11,12). However there are changes to the prothorax, including the development of a feeding channel, mesothoracic prolegs and lateral lips coated with various types of setae (Figs 11–12, characters i, o and p respectively).

To feed in thick, oily fluids such as exuded tree sap, the prothorax contracts along the longitudinal grooves of the dorsum. This converts it into a tapered wedge which is lunged into the fluid. The thorax and mouthparts expand and the dorsal and ventral lips scoop up fluids, which are then strained on the mandibular lobes and micro-organisms pass through. In watery fluids a different mechanism is used. The contracted thorax lunges into the fluid and expands. The mouthparts extend into the fluid. The dorsal and ventral lips expand and contract in a series of repetitive scoop-like movements which open and close the mouth. These movements draw streams of fluid down channels formed either side of the elongated papillae that bear the antenno-maxillary organs and the lateral lips. The width of these channels prevents large particles from going further. Setae on the lateral lips catch other large particles and prevent them from entering and blocking the mouth. The grossly filtered fluids enter the mouth, and further filtering occurs through the mandibular

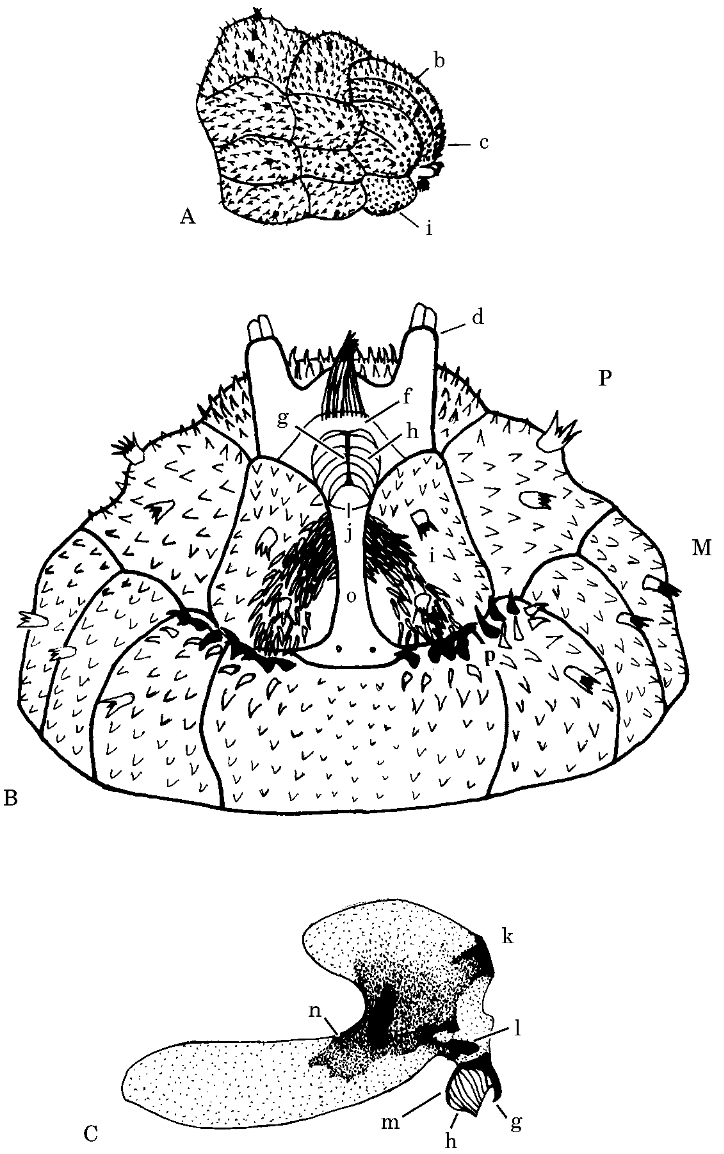

Figure 11. *Volucella inflata*, third stage larva. A, thorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. P = prothorax; M = mesothorax; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; f = dorsal lip; g = mandible h = mandibular lobe; i = lateral lip; j = ventral lip; k = labrum; l = tentorial bar; m = mandibular apodeme; n = tentorial arm; o = feeding channel; p = mesothoracic proleg.

lobes. Excess fluid is expelled down the feeding channel behind the mouth and between the mesothoracic prolegs. Often larvae extend the feeding channel by contracting muscles along a mid-ventral line, and then fluid is expelled between the prolegs. Further filtration and concentration of food occurs within the head skeleton, as described by Hartley (1963) and Roberts (1970).

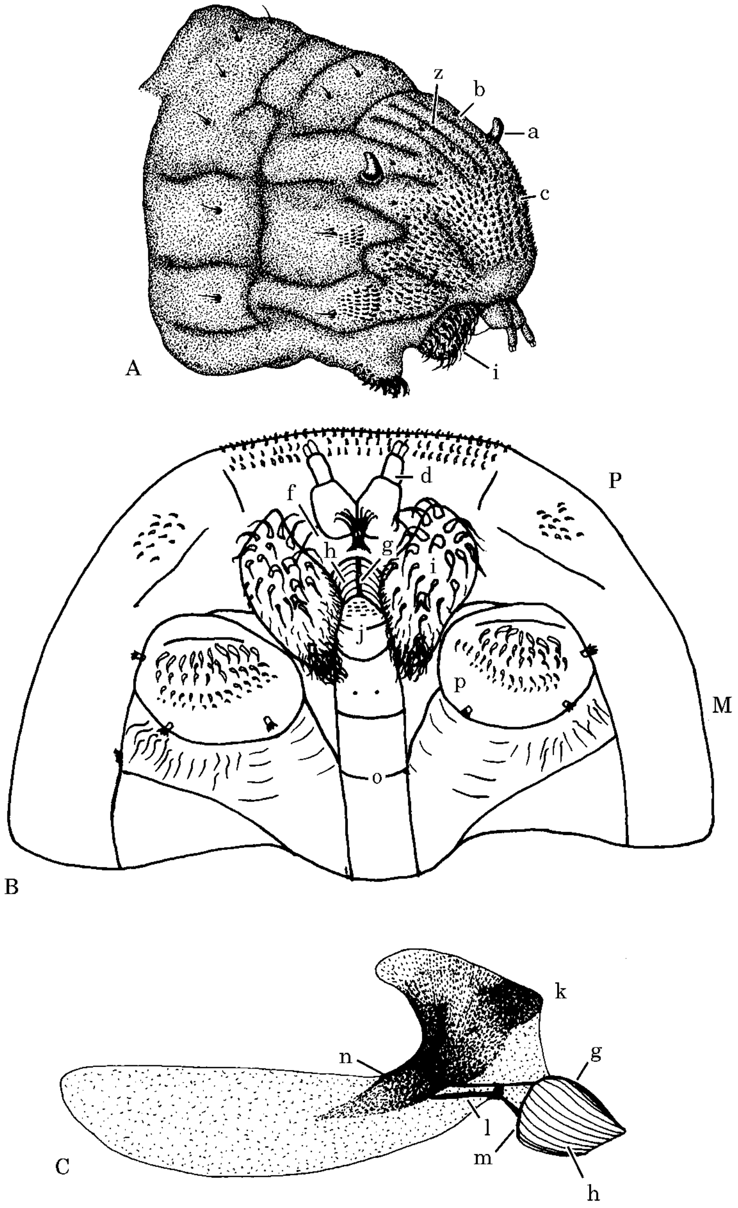

Figure 12. *Myathropa florea*, third stage larva. A, thorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. P = prothorax; M = mesothorax; a = retractable anterior spiracle; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; f = dorsal lip; g = mandible; h = mandibular lobe; i = lateral lip bearing broad setae at base and fine setae at apex; j = ventral lip; k = labrum; l = tentorial bar; m = mandibular apodeme; n = tentorial arm; o = feeding channel; p = mesothoracic proleg; z = mid-dorsal fold between folds bearing sensilla 1–3.

In the saprophages, prolegs with crochets are always present even if reduced, as in the plesiomorphic *V. inflata* (Fig. 17C–E). In basal syrphid taxa, from *Eumerus* to node **164** (*Ferdinandea*), prolegs are absent and locomotory prominences simply appear as segmentally arranged pairs of slight bulges on abdominal segments 1–6, each bearing sensilla groups 9–11 (Fig. 17A, B). Prolegs are distinguished from locomotory prominences by the absence of muscles. Externally, the evidence of muscles is the slight indentation on the surface of the proleg, the planta, showing where the muscles are attached to the integument (Fig. 17C–E, character p). Locomotory prominences lack musculature, and contract and expand in response to haemolymph pressure as waves of muscular contraction pass down the body during locomotion.

In the saprophages, prolegs are on the mesothorax and the first six abdominal segments. The mesothoracic prolegs are always larger than the abdominal prolegs. In *V. inflata* they are transverse in cross-section, with a linear row of crochets at the distal end (Fig. 17C, character c). Crochets probably originate from setae associated with locomotory prominences. From node **161** (*Brachyopa*) to **157** (*Neoascia*) the shape of the abdominal prolegs changes gradually from being transverse to round in cross-section. From node **161** (*Brachyopa*) to node **158** (*Chrysogaster*) the prolegs and crochets are reduced, particularly towards the posterior end. From node **157** (*Neoascia*) to node **153** (*Syritta*), the prolegs project further, and taper with two or more rows of crochets.

From node **152** (*Xylota*) to node **130** (*Parhelophilus*) (Fig 17D, E), prolegs are subcylindrical and about as broad basally as distally, with three or more rows of crochets. The arrangement of crochets varies from abdominal segment 1 to 6, with most crochets facing backwards in segment 1, to most facing sideways out from the body by segment 6. The mesothoracic crochets mostly face backwards, and these prolegs are crescent-shaped. The only exception to this is *Temnostoma*, which appears to have secondarily lost crochets and has reduced prolegs. In *Callicera* the abdominal prolegs are fused medially.

Prolegs function in the following way. As a wave of contraction passes down the body, the prolegs expand and the crochets raise and separate. As the contraction passes, forward momentum presses them into the substrate and the muscles within contract. This pulls the crochets together and anchors them to the substrate.

The change in orientation of crochets from pointing backwards at the front end of the body to pointing laterally at the anal end is not related to locomotion so much as facilitating larvae to grip the bottom substrate when breathing. This is a particular problem for long-tailed larvae because air in the breathing tubes increases buoyancy (Grieg, 1989).

Taxa of clade **143** (*Chalcosyrphus–Callicera*) have varying arrangements of spicules and hooks on the thorax (Figs 21, 22). Observations on a range of species within this sequence show that spicules and hooks have a role in locomotion (Rotheray, 1991). For example, *Criorhina berberina* has a complex arrangement of large and small hooks (Fig. 22B): it occurs in wet, decaying heartwood of trees (Table 3), and also present in decaying heartwood is *Xylota sylvarum*, which has no hooks on the thorax. Decaying heartwood is full of splinters and other fragments. When encountering splinters of wood, *Xylota sylvarum* either pushes against them, ducks past them or retreats. *Criorhina berberina* rarely retreats, and by tilting the thorax, uses its hooks to move splinters out of the way. Thus the larva of *C. berberina* is able to move through dense material, using its hooks to excavate a passage. This latter mechanism probably explains field observations that *X. sylvarum* tends to be most abundant in watery areas of decaying heartwood, with *C. berberina* occurring in firmer places (Rotheray, 1991). Hooks protect the thorax during locomotion through fragment-filled media. Protection may be important in such media, and larvae often have numerous integumental scars on the thorax, indicated by small, black, irregular-shaped blotches (see the photograph of the thorax of *C. berberina* on the front cover of Rotheray, 1993).

The ability to tilt the thorax facilitates locomotion through fragment-filled media. The pattern of grooves on the thorax changes across clade **143** (*Chalcosyrphus–Callicera*), suggesting that the muscles are modified for this role. In the relatively plesiomorphic taxa of the hook-bearing larvae (clade **144**: *Chalcosyrphus–Brachypalpoides*, Fig. 21), the pattern of grooves is little different to taxa at previous nodes. In brief, the lateral grooves appear as approximately parallel lines enclosing three parallel bands of muscle. Above this point, the lateral grooves are considerably modified (Fig. 22). In particular, the middle band of muscle, bearing sensilla groups 4 of the metathorax and mesothorax, has become larger in relation to the other two. Also, a series of smaller grooves exists behind and in front of the larger group of hooks towards which the middle band is directed. This suggests that the middle band of muscle is particularly important for tilting the thorax and moving the hooks. Correlated with these changes are developments in the size, shape and distribution of hooks. In plesiomorphic groups the hooks are generally small and are either single or occur in pairs (Fig. 21). In clade **147** (*Spilomyia–Callicera*), hooks become more numerous and apomorphic in shape, size and distribution (Fig. 22).

This trend reaches its most derived state in *Temnostoma*. These larvae possess a pair of multi-toothed rasps used to excavate a tunnel through moist but firm decaying heartwood (Fig. 22C). The folding pattern of the thorax is highly derived in this taxon, and large bands of muscle are present behind the rasps in a modified arrangement of thoracic segments (Fig. 22C). When these muscles contract, the rasps turn inward in front of the larva and scrape the face of the tunnel. Correlated with these features are changes in overall body shape, secondary loss of crochets and reduced prolegs.

Saprophages are generally immersed in fluids, and have the plesiomorphic mechanism of lifting the anal segment out of the fluid for air exchange. The main changes here are a trend towards an extended breathing tube, and an anal segment reaching its most derived states in clade **139** (the long-tailed larvae, *Blera–Parhelophilus*: Figs 25–27). The plesiomorphic saprophage, *V. inflata*, is however, similar to *Ferdinandea*, and lacks an extended anal segment (Figs 23D and 25A). At the next node, (**161**—*Hammerschmidtia and Brachyopa*), the breathing tube and anal segment are extended (Fig. 25B). The spiracular openings are sited at the tip of an elongate, narrow sclerotized breathing tube with four pairs of branched interspiracular setae (Fig. 25E). The extended anal segment consists of three rings, distinguishable from one another by dorsal transverse grooves, and each bearing a pair of lappets (Fig. 25B, character 1). From this node, the general trend is for the anal segment to extended gradually in length on the basis of these three rings. For example, from node **161** (i.e. *Brachyopa*) to node **139** (Figs 25B–26D), the anal segment extends about equally in each ring and the lappets are equidistant. Between nodes **139** and **137** (*Caliprobola, Blera* and *Lejota*), the anal segment is about 75% of body length due to an extended third ring, i.e. the first two pairs of lappets are close together at the base of the segment, but the third pair is at the end of the segment (Fig. 27A). From node **137** (*Myolepta* and *Sericomyia* onwards), the long anal segment is a result of an extension in the first ring, i.e. the second and third pairs of lappets are together at the end of the anal segment, with the first pair about halfway along its length (Fig. 27C–E).

The extended anal segment can be tilted up so that the posterior respiratory process protrudes through the fluid, held at the surface by water-repellent, inter-spiracular setae (Hartley, 1961). The larva is prevented from floating when breathing by burrowing, and by holding on with its prolegs. At node **131** (*Helophilus–Parhelophilus*), additional support for gripping the substrate during air exchange occurs. The orientation of the crochets on the posterior pair of prolegs is changed from pointing out to the side of the body, to one pointing forwards, and there may be additional crochet-like spicules between the prolegs.

An exception to the trend towards extensions of the anal segment is *Temnostoma*. These larvae are modified for boring in soft decayed wood, and have a contracted anal segment (Fig. 26C).

Anterior spiracles are absent in the plesiomorphic saprophage, *V. inflata*. They are also absent or reduced in clade **159** (chrysogasterines). In other saprophages they are present but small, and possibly only play a minor role in air-exchange. In clade **135** (*Mallota*, etc.), however, they are well developed and can be protected by withdrawing them into invaginated integumental pockets on the prothorax (Fig. 12, character a). A unique development also occurs in some *Chrysogaster*. The posterior respiratory process is sharply tapered for piercing the air spaces of aquatic plants (Fig. 25C, Varley, 1937; Hartley, 1958).

Entomophagy in Syrphidae

The plesiomorphic entomophages are within the current genus *Volucella* (Fig. 6; Table 3). Some species, such as *V. inanis*, are obligatory entomophages, while others like *V. bombylans* and *V. pellucens* are facultative, eating dead and live larvae in the nests of social aculeates (Rupp, 1989).

In relation to the saprophagous *V. inflata*, the thorax and mouthparts vary between the three entomophagous groups, *Volucella*, *Microdon* and clade **120** (pipizines & syrphines), and clearly defined transitions are evident (Table 6). Briefly, in comparison with the saprophagous *V. inflata*, entomophagous *Volucella* have a narrow elongate thorax with reduced lateral lips, mesothoracic prolegs and no feeding channel. However, the dorsal and ventral lips are developed, and the dorsal lip bears a central groove (Fig. 13, character g): both are coated in spicules. The mandibular lobes are reduced, and between the three entomophagous *Volucella* studied they become even more reduced (Figs 13A and 16A, character h). Each ridge comprising the mandibular lobe terminates in a sclerotized hook (Figs 13 and 16, characters h and q).

In terms of gathering food, one of the differences between saprophages and entomophages is that syrphid entomophages have to grip and pierce the integument of prey that are smaller than themselves. Entomophagous *Volucella* grip and tear the prey with the ventral lip and the dorsal lip, which can fold along the central groove. The spicules and hooks which coat these lips assist in holding and tearing the prey (Fig. 13). The elongate and narrow shape of the thorax enables the mouthparts to probe into small spaces for prey, such as into larval combs in nests of aculates.

Microdon larvae feed on the early stages of ants (Formicidae) (Duffield, 1981; Garnett *et al.*, 1985; Barr, 1995), and taxa of clade **120** have diversified to attack soft-bodied Homoptera (Dixon, 1960; Rotheray & Gilbert, 1989). In terms of gripping and piercing prey, the three groups have related but different mechanisms.

TABLE 6. Comparison of entomophagous taxa, *Volucella*, *Microdon* and *Pipizella*

character	*Volucella* Fig. 13	*Microdon* Fig. 14	*Pipizella* Fig. 15
antennomaxillary organs	mounted on broadly separated papillae	elongate with tapered tips	elongate with rounded tips
mandibles	supporting the mandibular lobes, both mandibles work together	fused to the mandibular lobes, mandibles work independently	reduced, with pointed or flattened tips, mandibles work independently
mandibular lobes	entirely inside mouth and appearing as sclerotized strips with apical hooks	fused with the mandibles ventral margin serrated	lost
labial sclerites	not developed on *V. pellucens*, developed in *V. inflata*, Fig. 16, character w	developed forward, but not as much as mandibles	developed forward of the mandibles and sharply tapered at apex
dorsal lip	large and bluntly tapered with ventro-medial groove and coated in spicules	large and sharply tapered with ventral groove and without spicules	large and sharply tapered with ventral groove and without spicules
ventral lip	broader than mouth and coated in spicules	reduced and lacking spicules	broader than mouth and coated in spicules
lateral lips	small and sparsely coated in setae	very developed apically into fleshy but firm tapered projections which close over the antennomaxillary organs when the thorax is retracting	apex formed into sclerotized hooks
notches on mesothorax and metathorax	absent	mesothorax and metathorax with fleshy dorso-lateral notches; mesothoracic notches close over the prothorax and the metathoracic notches close over the front of the larva when the thorax retracts	absent
shape of thorax	narrower than abdomen	very narrow prothorax and mesothorax which are protected under the metathorax; prothorax elongate posteriorly	narrower than abdomen; prothorax elongate posteriorly
retractability of thorax	prothorax retracts into mesothorax	prothorax and mesothorax retract into metathorax	prothorax and mesothorax retract into metathorax
ventral pads on thorax	absent	absent	prothorax and mesothorax with raised pads bearing a different surface sculpture to surrounding integument

continued

Table 6. *continued*

character	*Volucella* Fig. 13	*Microdon* Fig. 14	*Pipizella* Fig. 15
anterior fold	with spicules	spicules absent	spicules absent
anterior spiracles	present	absent	present
locomotory organs	prolegs with crochets, gripping with frictional forces, Fig. 18A, B	locomotory prominences with independent movement along each side of the body, gripping with frictional and meniscus forces	locomotory prominences projecting (Fig. 18C, D, E), without independent movement, gripping with meniscus forces
mesothoracic prolegs	present	absent	absent
locomotory organs at posterior end	proleg with crochets on 6th abdominal segment	locomotory prominences on 6th abdominal segment	grasping bar on anal segment

Unstudied physiological factors are obviously involved too, such as changes to the sensory system enabling potential prey to be recognized, and to the gut to enable prey to be digested.

In clade **125** (*Microdon*, pipizines & syrphines), the thorax is even narrower, more elongate and retractile than in *Volucella*. In *Microdon* the dorsal lip appears as a fleshy tapering projection (Fig. 14, character f). The tapered end lies between the basal papillae bearing the antennomaxillary organs, and ventrally it has a groove along which the mandibles project. The mandibular sclerites have undergone a change in shape and have fused with the mandibular lobes. The result is a pair of elongate, thin, tong-like sclerotized structures bearing a serrated ventral margin (Fig. 14C, character g). Each mandible can move independently of the other. In addition the labial sclerites which lie between the mandibular apodemes are developed forward, as is the labial plate, and together they form an articulated, sclerotized lower lip to the head skeleton (Fig. 14C, characters v and w).

In clade **120**, the dorsal lip has a similar shape (Fig. 15, character f). The mandibles are also capable of independent movement, but instead of a serrated margin, they are narrow with blunt broad tips bearing a sharp edge (Figs 15 and 16B & C, character g). The labial sclerites and labial plate between them project even further forward than *Microdon*, right to the tip of the head skeleton. Furthermore, dorsally the labrum has also developed forward between the mandibles, which now lie at the lateral margins of the head skeleton. The tips of the labrum and the labial sclerites are sharply pointed and heavily sclerotized. The result is an elongate, sharply pointed, sclerotized upper and lower margin to the head skeleton (Figs 15C and 16B, C).

In entomophagous taxa (clade **128**), when searching for prey the thorax expands forwards and sideways in characteristic scanning movements termed casts (Chandler, 1969; Rotheray, 1983). During casting the antennomaxillary organs project forward, and if they touch an item of prey, capture is initiated. In *Microdon* this involves extending the mandibles along the groove of the dorsal lip and grasping the prey using the serrated margins. The prey is then pulled back under the marginal band,

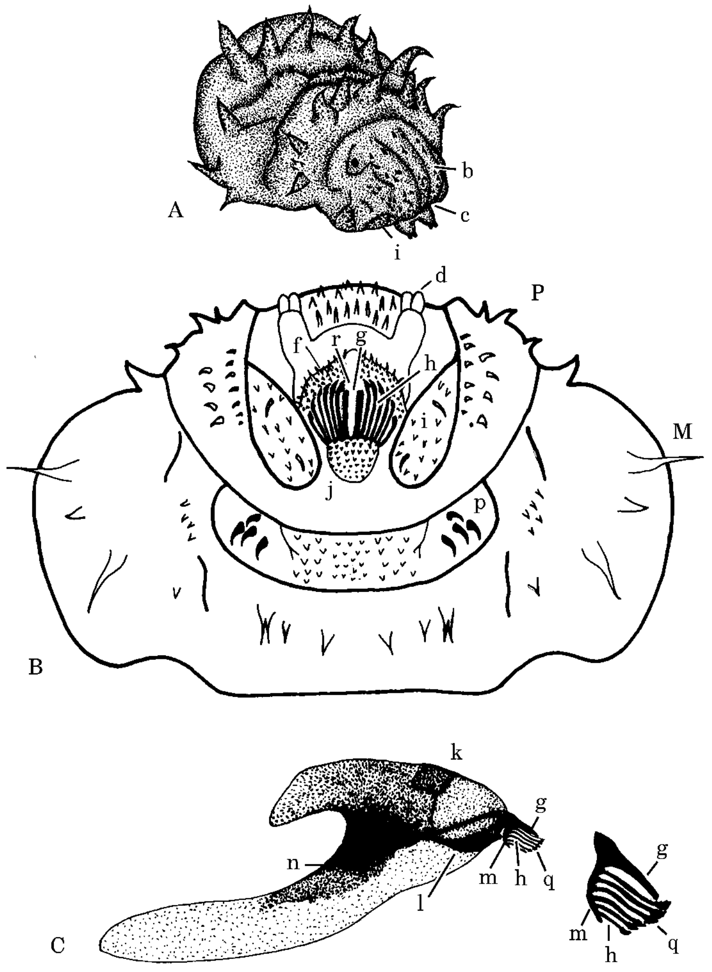

Figure 13. *Volucella pellucens*, third stage larva. A, thorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. P = prothorax; M = mesothorax; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; f = dorsal lip; g = mandible; h = mandibular lobe; i = lateral lip; j = ventral lip; k = labrum; l = tentorial bar; m = mandibular apodeme; n = tentorial arm; p = mesothoracic proleg; q = apical hooks; r = groove in dorsal lip.

where it is impaled on hooks at the base of the labial plate, broken up with the mandibles, and the contents imbibed (Barr, 1994). In aphidophages (clade **120**), sticky saliva is emitted on contact with an item of prey, and the prothorax inverts, exposing the hook-like, sclerotized apex of each lateral lip which snag the prey (Fig. 15, character x). Held firm by saliva and hooks in the inverted prothorax, the pointed end of the head skeleton protrudes along the groove of the dorsal lip and pierces the prey, the mandibles break it up, and the contents are imbibed.

The prothorax and mesothorax of *Microdon* are under the metathorax, which is fixed in a folded-down position such that the anterior point of the larva is the fold bearing sensilla 1 and 2 of the metathorax (Fig. 14A). This places obvious restrictions on the manoeuvrability of the mesothorax and prothorax. This is overcome, to

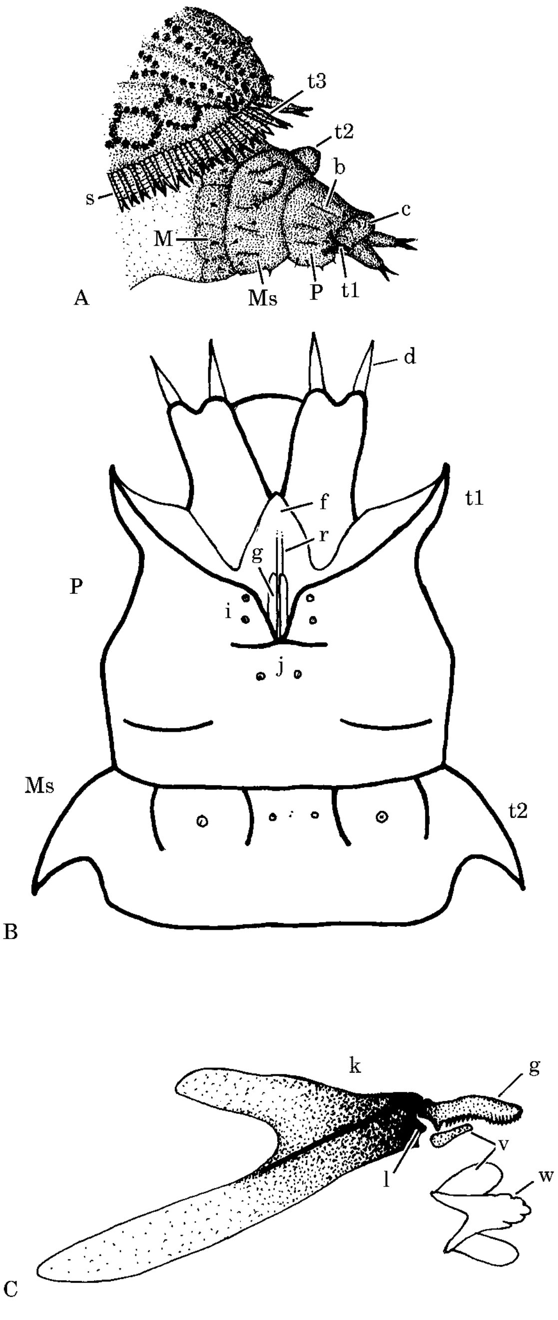

Figure 14. *Microdon mutabilis*, third stage larva. A, thorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. P = prothorax; Ms = mesothorax; M = metathorax; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; f = dorsal lip; g = mandible and mandibular lobes; i = lateral lip; j = ventral lip; k = labrum; l = tentorial bar; r = groove in dorsal lip; s = marginal band of setae; t1–3 = notches in prothorax, mesothorax and metathorax; v = labial plate; w = labial plate and sclerites, ventral view.

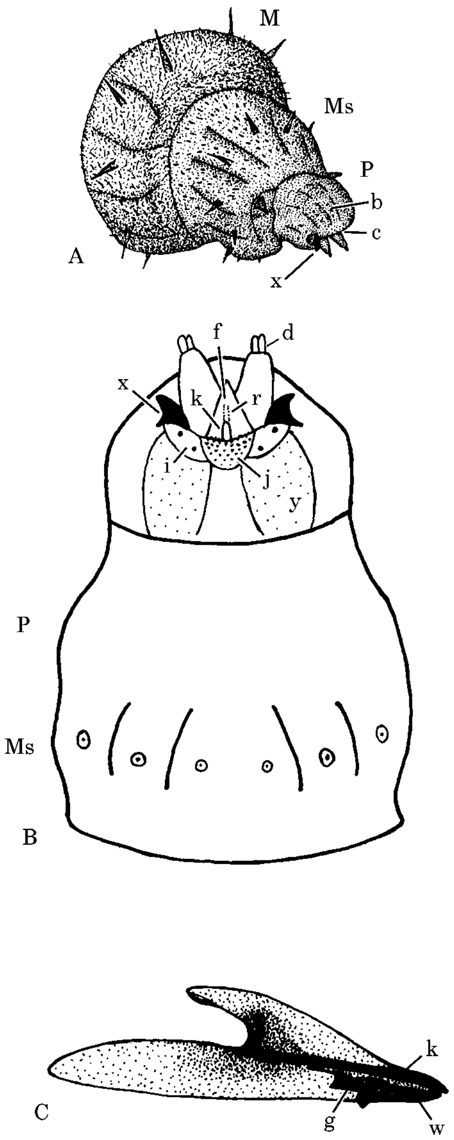

Figure 15. *Pipizella varipes*, third stage larva. A, thorax, lateral view. B, prothorax and mesothorax, ventral view; C, head skeleton. P = prothorax; Ms = mesothorax; M = metathorax; b = longitudinal fold; c = anterior fold; d = antennomaxillary complex; f = dorsal lip; g = mandible; i = lateral lip; j = ventral lip; k = labrum; r = groove in dorsal lip; w = labial sclerite; x = sclerotized hook at apex of lateral lip; y = ventral pads.

some extent, by dorso-medial notches in the metathorax and mesothorax through which the rest of the thorax can extend. Notches bear fleshy projections, one on each side, which together with the tapered apices of the lateral lips, make three pairs of notches, one pair on each segment (Fig. 14A, B). When the thorax retracts, the prothoracic projections close inwards over the antennomaxillary organs, and

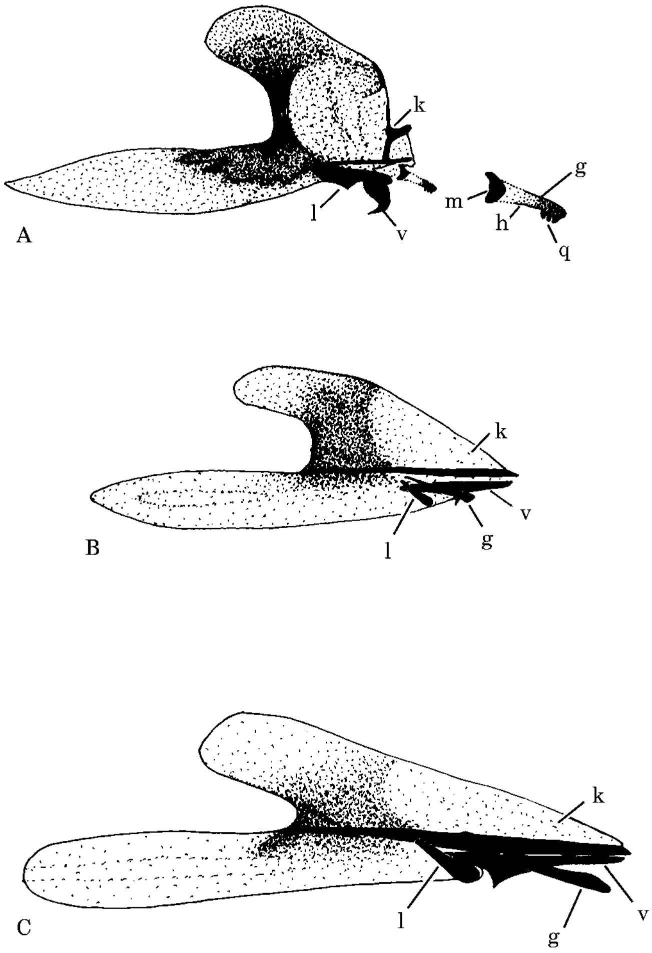

Figure 16. Variation in head skeletons of some entomophagous Syrphidae. A, *Volucella inanis*. B, *Platycheirus scutatus*; C, *Eupeodes luniger*. g = mandible; h = mandibular lobe; k = labrum; l = tentorial bar; m = mandibular apodeme; q = apical hooks; w = labial sclerite.

the mesothoracic ones cover the prothorax. The metathoracic notch can also close if the segment contracts, thereby completely sealing off the mouthparts. Such protection is important when catching prey because worker ants attempt to bite the *Microdon* larva and will attempt to snatch back their larvae and pupae (Barr, 1994)

In aphidophages (clade **120**), the prothorax and mesothorax are capable of retraction under the metathorax so that, as in *Microdon*, the anterior point of the larva is the fold bearing sensilla 1 and 2 of the metathorax. However, the metathorax is not fixed in this position, and can be expanded and contracted like the rest of the thorax (Fig. 15A). In addition, the ventral surface of the prothorax and mesothorax is protected from wear during casting by raised pads bearing a distinctive surface vestiture (Fig. 15, character y).

Locomotory mechanisms are equally varied among the three groups. Entomophagous taxa move on drier substrates than mycophages and saprophages:

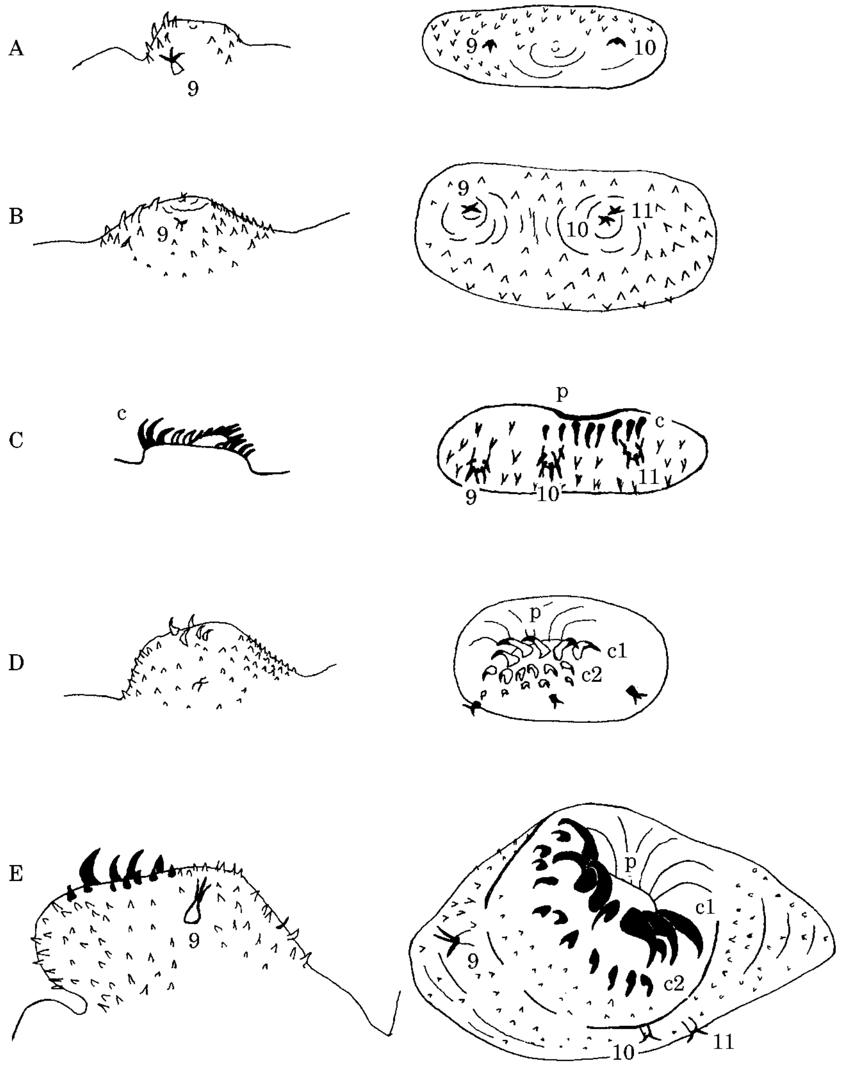

Figure 17. Locomotory organs in Syrphidae on the 6th abdominal segment. A, *Eumerus tuberculatus*. B, *Ferdinandea cuprea*; C, *Volucella inflata*; D, *Xylota segnis*; E, *Myathropa florea*. Left hand column = lateral view; right hand column = apical view; 9,10,11 = sensilla numbers; c = crochets, cl = primary row, c2 = secondary row; p = planta.

aculeate nests in *Volucella*; ant nests in *Microdon*; and plant surfaces in aphidophages. The general mechanism of forward movement in syrphids is a wave of contraction that starts at the posterior end and passes along the body. A critical element is the degree of adherence obtained by the posterior end at the time of initial contraction: a high level of adherence is necessary to prevent slippage and loss of forward momentum (Roberts, 1971).

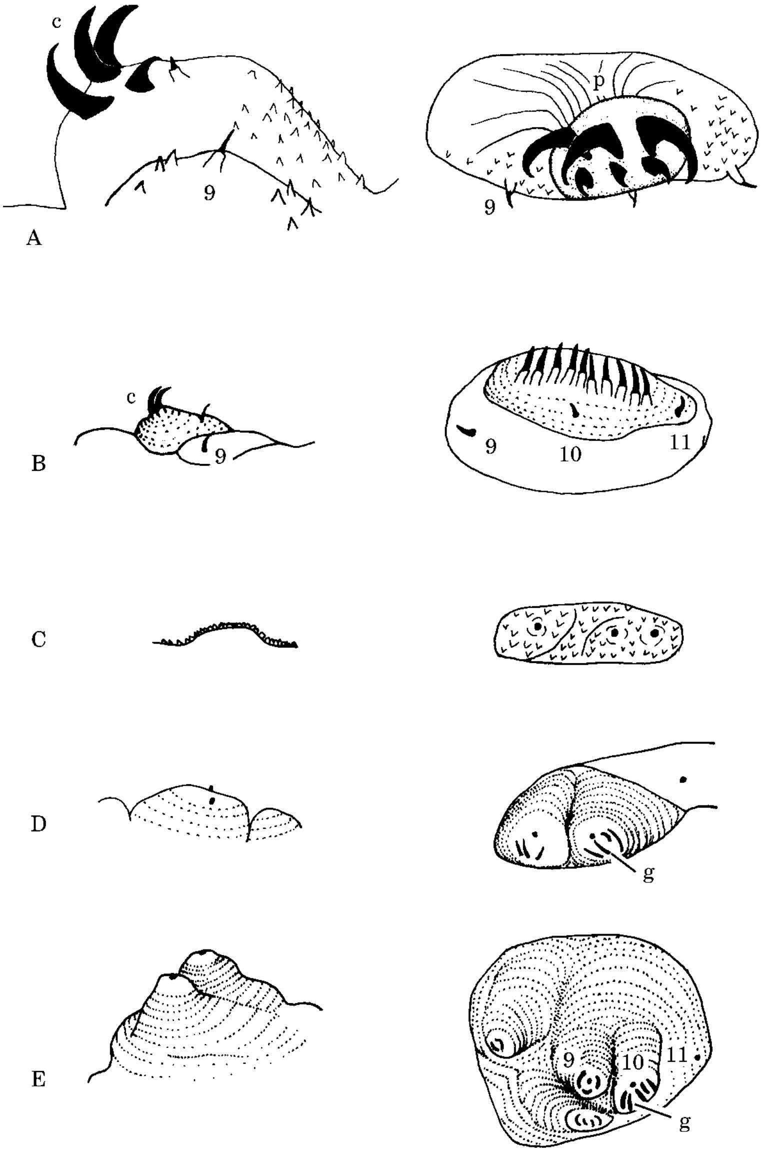

Figure 18. Locomotory organs in Syrphidae on the 6th abdominal segment. A, *Volucella pellucens*. B, *Volucella inanis*; C, *Pipizella varipes*; D, *Syrphus ribesii*; E, *Eupeodes luniger*. Left hand column = lateral view; right hand column = apical view; 9,10,11 = sensilla numbers; c = crochets; p = planta; g = grooves.

In entomophagous *Volucella*, prolegs with crochets are present (Fig. 18A, B). The posterior prolegs on the sixth abdominal segment prevent slippage at the start of movement. The posterior ends are not extended in relation to the most plesiomorphic members of the sister group (e.g. *V. inflata*) (Fig. 24A, B). The mesothoracic prolegs are also used for gripping the substrate, but the anal segment and the mouthparts are not. *V. pellucens* (L.) and *V. zonaria* (Poda) live in *Vespula* nests (Vespidae, Hymenoptera), and both have longer crochets than other *Volucella* species. The open ends of wasp combs face down, and these larvae search for food by moving upside-down, using the long crochets to grip the comb and probing into wasp cells with the narrow thorax. The larva of *V. inanis* (L.) is an ectoparasitoid of vespid larvae, and inserts itself into an individual wasp cell to feed on the occupying larva, using its crochets to hold on to the side of the cell (Rupp, 1989). Unlike other entomophagous *Volucella* it has a smooth integument, lacking projections (Fig. 24A, B).

In *Microdon* the ventral surface is flat without prolegs or projecting locomotory prominences. It is fringed by a marginal band of variously shaped setae within which, on the anal segment, are three pairs of short lappets (Fig. 14, character s; Fig. 24C). In *Microdon*, the ventral surface is barely lifted during movement and larvae appear to 'glide' over the substrate. *Microdon* larvae can also turn on the spot. This mode of progression is a result of their ability to expand and contract each side of each abdominal segment independently. Thus by contracting one side of the body and expanding the other, they can turn in the direction of the contracted side. Minimally lifting the ventral surface from the substrate reduces the chances of ants biting and turning them over. *Microdon* larvae are readily killed if the ventral surface is exposed to ant bites (Donisthorpe, 1927).

Aphidophagous larvae (clade **120**) hunt prey on plants. Plant substrates present considerable barriers to insect locomotion (Southwood, 1973; Strong *et al.*, 1984). The locomotory mechanism overcoming this barrier involves the following characters: a grasping bar at the tip of the anal segment to prevent slippage, a partially smooth ventral surface which helps create meniscus forces from saliva and fluids from the anus, and extra transverse folds across the ventral surface which increase manoeuvrability.

In the most plesiomorphic taxon, *Pipizella*, the ventral surface is coated with dome-shaped vestiture similar to but smaller than that on the dorsal surface (Fig. 24D). In taxa above this node (i.e. clade **119**), the ventral surface is smooth, and in addition to the smooth ventral surface, a network of shallow grooves exists overlying the deeper, segmental pattern of grooves. Most distinctive, however, are modifications to the anal segment present in all members of clade **120** (Fig. 19). In the subclade 121 (*Pipizella–Heringia*), the tip of the anal segment forms a raised transverse bar comprising the reduced third pair of lappets, below which is a transverse fold bearing sensilla 7 (Fig. 19C). In the rest (i.e. clade **119**), this transverse bar is larger and incorporates a pair of lateral lobes defined by grooves and an apparent lateral migration of sensilla 7 (Fig. 19D). From node **111** (e.g. *Platycheirus*) the grasping bar is further modified. At its centre the third pair of lappets are enlarged into a pair of fleshy lobes bearing sensilla 5 and 6. The tips of these lobes have shallow grooves. The lateral lobes bearing sensilla 7 are now larger, better defined, and their tips also have grooves (Fig. 19E). This arrangement of two large and two small lobes changes little throughout the rest of the clade. However, more apomorphic individual taxa have diversified further to develop modes of locomotion that suit particular plant structures. For example, the flattened ventral surface of *Epistrophe* larvae is suited to searching flat leaves; the U-shaped grasping organ of clade **91** (*Eupeodes, Scaeva and Ischiodon*) comprises further modifications to the grasping bar and to the locomotory prominences of abdominal segments 5 and 6, and is used by these larvae for moving about on stems (Fig. 18E; Rotheray, 1987).

The larvae of this entire clade (**120**) grip the substrate using meniscus and frictional forces (Roberts, 1971; Rotheray, 1987). Meniscus forces occur when saliva and/or

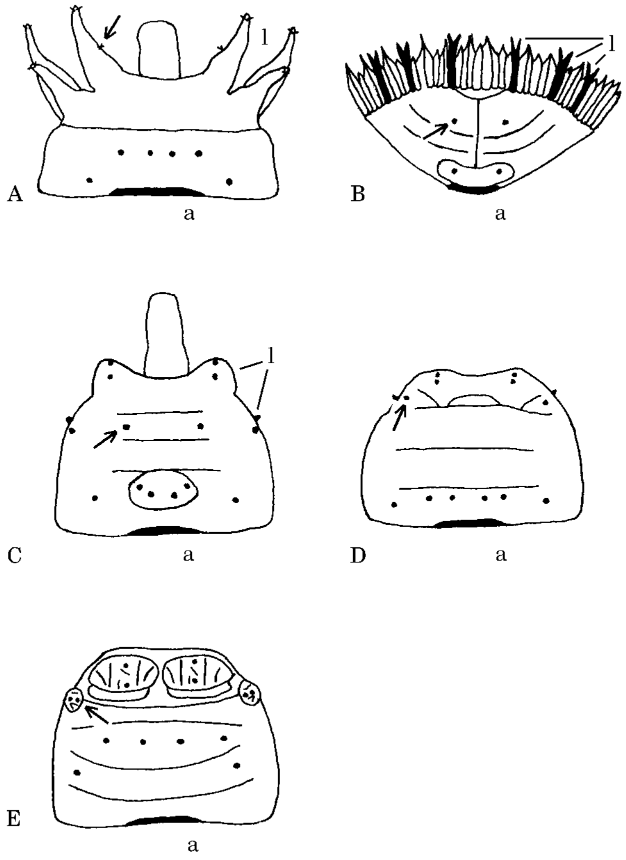

Figure 19. Development of a grasping bar at the tip of the anal segment in aphidophagous Syrphidae. A, outgroup taxon, *Ferdinandea cuprea*. B, outgroup taxon, *Microdon mutabilis*; C, ingroup taxon, *Pipizella varipes*; D, ingroup taxon, *Melanostoma scalare*; E, ingroup taxon, *Platycheirus scutatus*. See text for details. Arrow = position of sensilla 7; l = lappets; a = anus.

fluids from the anus are spread across the ventral surface by the network of shallow grooves and capillary action (Rotheray, 1987). The mouthparts are also used for gripping the substrate (Rotheray, 1987). Locomotion is similar to other syrphid larvae: forward movement is initiated by a wave of contraction starting at the anal segment (Roberts, 1971). Observations on glass sheets confirms that the tip of the anal segment is pressed against the substrate at the start of movement, as illustrated by Roberts (1971). This suggests that the critical problem of avoiding slippage at the start of movement is solved by the modified tip of the anal segment.

Being exposed on plants, these larvae have developed cryptic colour patterns to avoid visually hunting predators such as birds (Rotheray, 1986). The mechanisms underlying crypsis become more complex and substrate-specific during the evolution of the clade. For example, in plesiomorphic taxa the colour patterns are due mostly to pigments in the haemolymph. In more apomorphic taxa, fat bodies aggregated into patterns of stripes, bars and dispersed particles, also play a role. Finally, in the

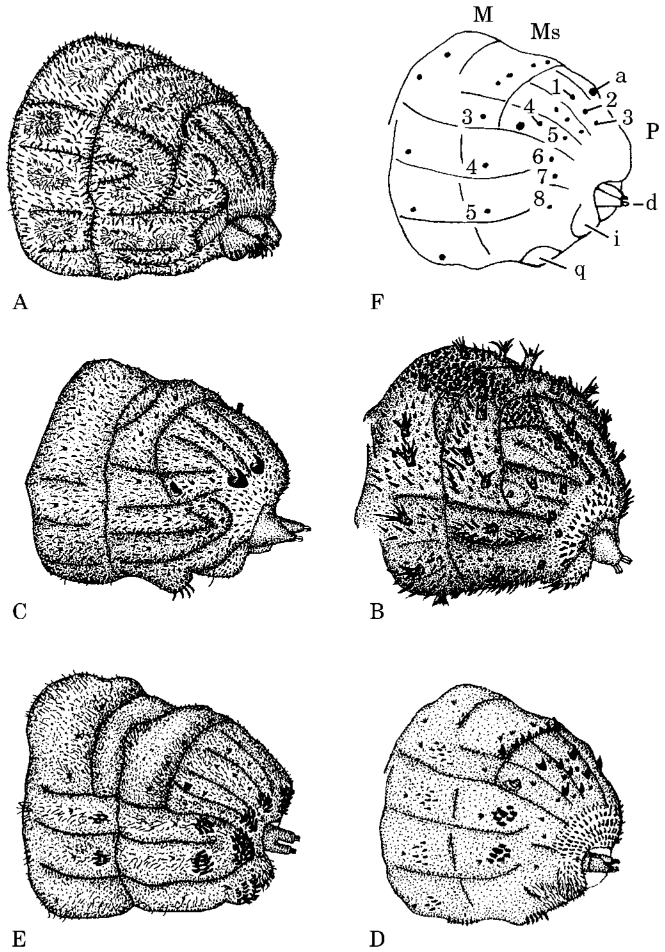

Figure 20. Variation in the thoraces of Syrphidae. A, *Cheilosia longula*. B, *Brachyopa insensilis*; C, *Neoascia podagrica*; D, *Tropidia scita*; E, *Ceriana abbreviata*; F, overview figure showing main features. P = prothorax; Ms = mesothorax; M = metathorax; 1–8 = sensilla numbers; a = anterior spiracle; d = antennomaxillary organs; i = lateral lip; q = mesothoracic proleg.

most derived taxa (clade **93**), aggregations of spicules, fleshy projections and markings on the integument are additionally involved.

Microdon and entomophagous *Volucella* are also vulnerable to attack within nests of social Hymenoptera. The characteristic curved shape of *Microdon* larvae is such that ants are unable to grip and bite the larva. The marginal band of setae helps prevent ants biting the ventral surface. In many individual *Microdon* larvae examined, setae from the marginal band and the dorsal surface appear to have been bitten off. Some *Microdon* species use semiochemicals for additional protection (Akre *et al.*, 1985). Whether *Volucella* larvae are similarly modified to avoid attack is unknown: like *Microdon*, many larvae examined had some of their fleshy projections bitten off.

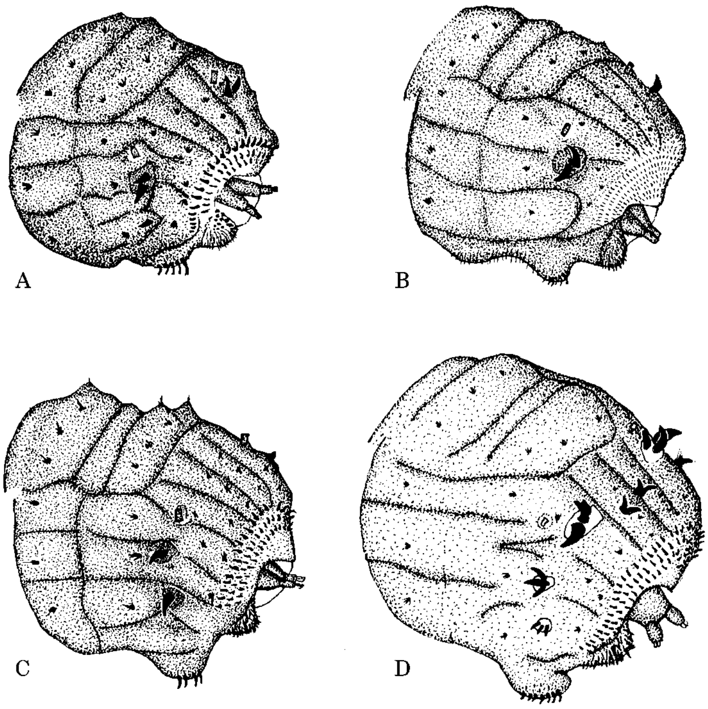

Figure 21. Variation in arrangements of hooks and folds in saprophagous Syrphidae. A, *Chalcosyrphus nemorum*. B, *Brachypalpus laphriformis*; C, *Brachypalpoides lenta*; D, *Spilomyia longicornis*.

GENERIC DIAGNOSES

Diagnoses for aphidophagous taxa (clade **120**) are given by Rotheray & Gilbert (1989). Genera are presented in alphabetical order.

Anasimyia Schiner, 1864

Species examined: lineata Fabricius 1787; *lunulata* Meigen, 1822; *transfuga* Linnaeus, 1758

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; anterior spiracles retractile into inverted integumental pockets on the prothorax; dorsum of prothorax with 8 longitudinal grooves; lateral margins of abdominal segments with a line of setae; last pair of prolegs with most of the large primary crochets facing towards the front of the body; prolegs with primary row of about 6 crochets; some crochet-like spicules between, not in front of, the last pair of prolegs.

Biology. Larva living in pools and ponds where decaying vegetation, particularly *Typha*, accumulates (Hartley, 1961).

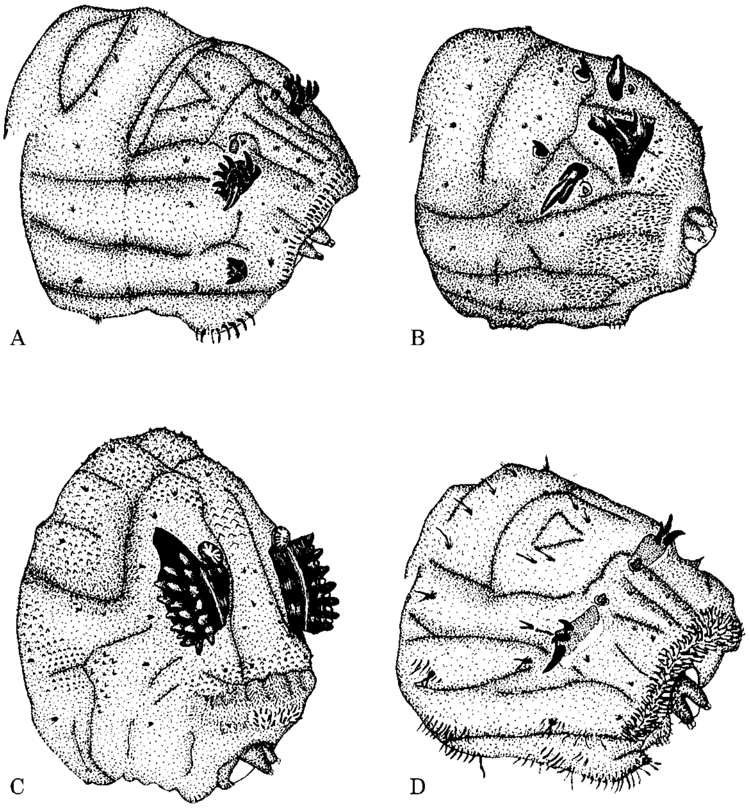

Figure 22. Variation in arrangements of hooks and folds in saprophagous Syrphidae. A, *Milesia virginiensis*. B, *Criorhina berberina*; C, *Temnostoma vespiforme*; D, *Callicera rufa*.

Blera Billberg, 1820

Species examined: fallax Linnaeus, 1758; *humeralis* Williston, 1882 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold with 5–6 rows of sclerotized spicules; larva subcylindrical, with a relatively long anal segment about 75% of body length; first two pairs of lappets at base of extended anal segment, third pair at tip; body coated in fine setae including segment 7 and anal segment; prolegs small with 8–10 primary crochets. Very similar to *Calliprobola* and *Lejota*, but differing from these taxa in having no spicules extending on the lateral margin of the prothorax, between the anterior fold and the mesothorax, and having spiracular openings of the anterior spiracles clustered around a barely inclined apical margin.

Biology. *B. fallax* larvae found in decaying heartwood of *Pinus* trees, particularly old stumps where they may be deep in the roots, or in rot-holes at the cut surface.

Brachyopa Meigen, 1822

Species examined: bicolor Fallén, 1817; *insensilis* Collin, 1939; *pilosa* Collin, 1939; *scutellaris* Robineau-Desvoidy, 1844; *vacua* Osten Sacken, 1875 (Nearctic)

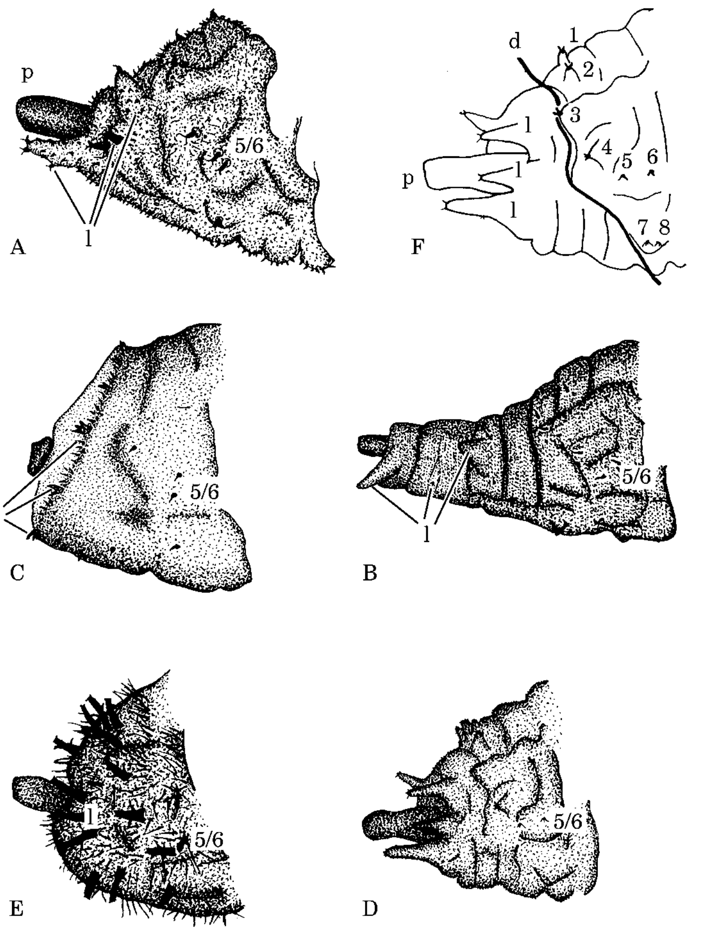

Figure 23. Variation in abdominal segments 7 and 8 (the anal segment). A, *Eumerus tuberculatus*. B, *Cheilosia morio*; C, *Portevinia maculata*; D, *Ferdinandea cuprea*; E, *Rhingia campestris*; F, overview figure showing main features. Lateral views, dorsal side uppermost; l = lappets on segment 8; p = posterior respiratory process on segment 8; 1–8 = sensilla numbers on segment 7; d = line approximating to division between abdominal segments 7 and 8; 5/6 = position of sensilla 5 and 6 on segment 7.

Diagnosis. Larva somewhat dorso-ventrally flattened with mandibles supporting the expanded mandibular lobes; lateral lips large and coated in spicules; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated in transverse spicules; sides of body with gradually elongating projections; anal segment and abdominal segment 7 inclined dorsally, except for two tapering rings at the tip of the anal segment, two pairs of lappets on the basal ring and one pair on the distal ring; posterior respiratory process long and narrow, and base coated in nodules; abdominal segments 2–7 with up to four transverse rows of setae (reduced in *B. insensilis*); prolegs not well developed, and a few crochets may or may not be discernible.

Biology. Larvae either occur in sap runs or in accumulations of decaying sap under bark, where they feed probably on bacteria and other micro-organisms.

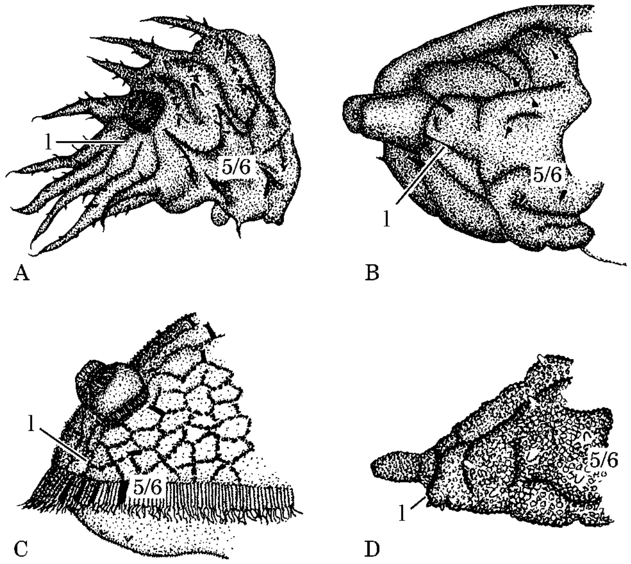

Figure 24. Variation in abdominal segments 7 and 8 (the anal segment). A, *Volucella pellucens*. B, *Volucella inanis*; C, *Microdon mutabilis*; D, *Pipizella varipes*. Lateral views, dorsal side uppermost; 1 = lappets on segment 8; 5/6 = sensilla numbers on segment 7.

Brachypalpoides Hippa, 1978

Species examined: lenta Meigen, 1822

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated in a narrow band of 4–5 rows of spicules, those in the second row the largest; thorax with two groups of 2 large, evenly sized hooks, each group lateral to the anterior spiracle; hooks red-brown in colour; sclerotized plate at base of hooks with several spicules, and on inner margin a large hook-like spicule; prolegs with 6–8 crochets well developed; anal segment with 3 pairs of lappets, middle pair smallest.

Biology. Larva found in decaying heartwood of deciduous trees, particularly in live trees with exposed decay at ground level.

Brachypalpus Macquart, 1834

Species examined: cyanogaster Loew, 1872 (Nearctic); *laphriformis* Fallén, 1816; *oarus* Walker, 1849 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated with a narrow band of 3–4 rows of spicules, those in the first row the largest; lateral margins of mesothorax with two pairs of large backwardly directed hooks, one separated and below the other; larva subcylindrical in cross-section; prolegs with 7 or 8 primary crochets; anal segment with three pairs of lappets, first two about the same size, third pair longest.

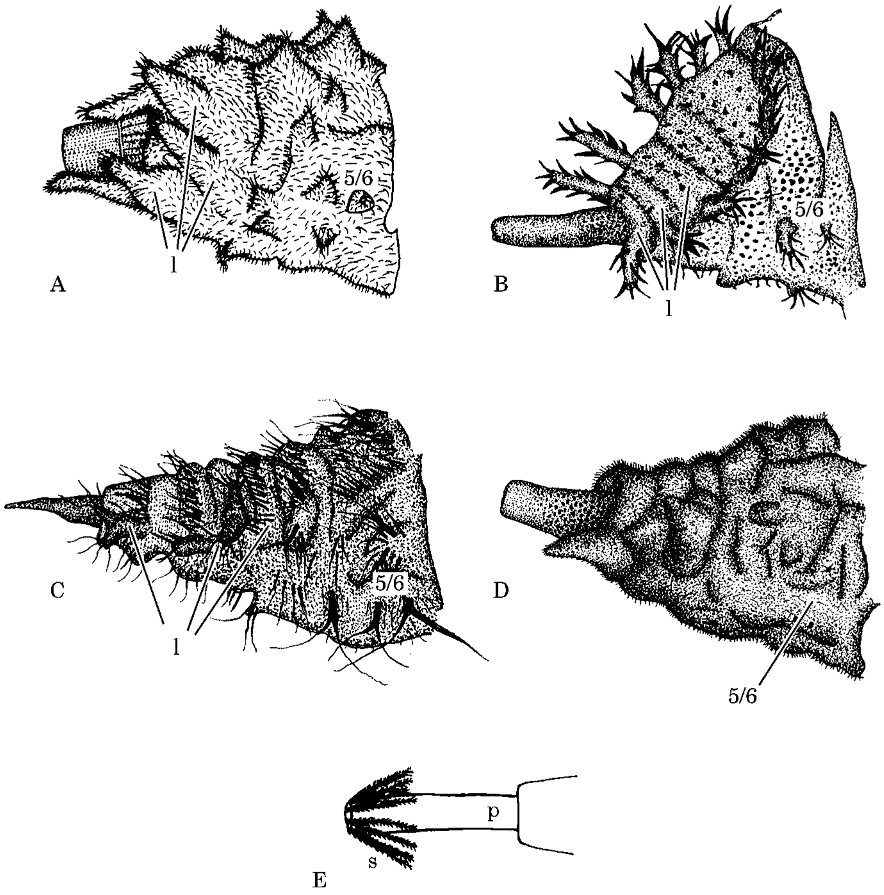

Figure 25. Variation in abdominal segments 7 and 8 (the anal segment). A, *Volucella inflata*; B, *Brachyopa insensilis*; C, *Chrysogaster hirtella*; D, *Tropidia scita*; E, *Sphegina clunipes* (posterior respiratory process). Lateral views, dorsal side uppermost; l = lappets on segment 8; p = breathing tube; s = interspiracular setae; 5/6 = sensilla numbers on segment 7.

Biology. Larvae are found in rot-holes of deciduous trees.

Caliprobola Rondani, 1844

Species examined: speciosa Rossi, 1790

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold with 5–7 rows of sclerotized spicules; larva subcylindrical, with a relatively long anal segment about 75% of body length; first two pairs of lappets at base of extended anal segment, third pair at tip; body coated in fine setae including segment 7 and anal segment; prolegs small with 7 or 8 primary crochets. Very similar to *Blera* and *Lejota*, but differing from these taxa in having spicules on the lateral margin of the prothorax, between the anterior fold and the mesothorax.

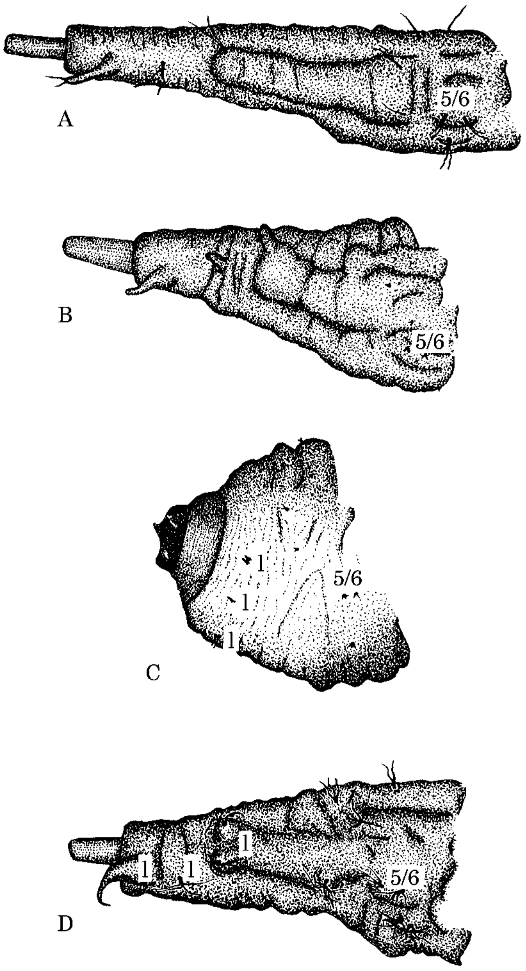

Figure 26. Variation in abdominal segments 7 and 8 (the anal segment). A, *Pocota personata*. B, *Criorhina berberina*; C, *Temnostoma vespiforme*; D, *Callicera rufa*. Lateral views, dorsal side uppermost; 1 = lappets on segment 8; 5/6 = sensilla numbers on segment 7.

Biology. Larva found in decaying heartwood of *Fagus* trees, particularly old stumps where they may be deep in the roots.

Callicera Panzer, 1809

Species examined: aurata (Rossi, 1790); *rufa* Schummel, 1841; *spinolae* Rondani, 1844

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold with a narrow band of densely aggregated thin spicules that become shorter from front to back; thorax with two groups of 3–4 hooks lateral to the anterior spiracles; anal segment bearing a pair of fleshy projections; prolegs partially fused forming a single oval structure on abdominal segments 1–6; posterior respiratory process with transverse spiracular openings.

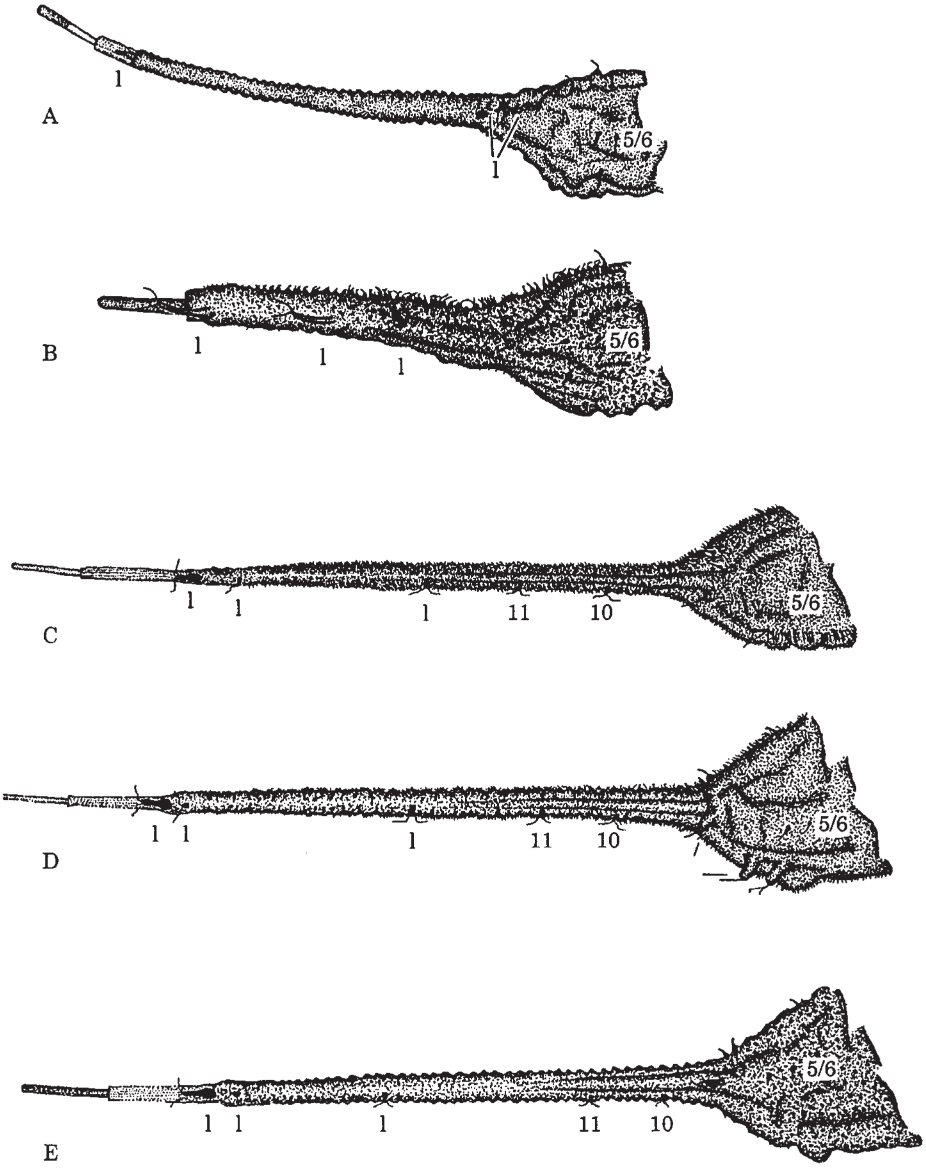

Figure 27. Variation in abdominal segments 7 and 8 (the anal segment). A, *Caliprobola speciosa*. B, *Myolepta luteola*; C, *Myathropa florea*; D, *Helophilus pendulus*; E, *Anasimyia transfuga*. Lateral views, dorsal side uppermost; 1 = lappets on segment 8; 10, 11 = sensilla numbers on segment 8; 5/6 = sensilla numbers on segment 7.

Biology. Larvae in rot-holes. *Callicera rufa* is found in rot-holes on *Pinus* (Coe, 1938; Rotheray & MacGowan, 1990) and in *Larix* (MacGowan, 1994). *Callicera aurata* (= *aenea*) and *C. spinolae* both breed in rot-holes on *Fagus* (Rotheray, 1991; Rotheray & Perry, 1994). However a broader range of trees is likely to be used by all these species.

Ceriana Rafinesque, 1815

Species examined: abbreviata Loew, 1864 (Nearctic); *conopsoides* Linnaeus, 1758; *snowi* Adams, 1904 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated with aggregated groups of spicules; larva somewhat dorso-ventrally flattened with an anal segment extended to varying degrees, and having three pairs of lappets; body coated in setae of variable sizes and densities; prolegs cylindrical with 5–8 primary crochets.

Biology. Larvae found in sap runs.

Chalcosyrphus Curran, 1925

Species examined: nemorum Fabricius, 1805; *metallicus* Wiedemann, 1830 (Nearctic); *metallifera* Bigot, 1884 (Nearctic); *violescens* Megerle, 1803 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated with a narrow band of 3–4 rows of spicules, second row with the largest spicules; larva somewhat dorso-ventrally flattened; thorax with two groups of 1–2 black hooks, each group lateral to the anterior spiracle; below these hooks and separate from them there may be a smaller single black hook; prolegs cylindrical with 6–8 primary crochets; anal segment slightly extended, with three pairs of evenly sized lappets.

Biology. Larvae are found in sap runs and under bark in accumulations of decaying sap.

Cheilosia Meigen, 1822

From the larval point of view this large genus is polyphyletic (Fig. 6). Until more larvae are known phylogenetic relationships cannot be investigated fully. Nonetheless, larvae can be divided into groups based on shared morphologies and feeding mode. All taxa possess mouth-hooks, but sometimes they are reduced and inconspicuous; prolegs are absent and the anterior fold is without spicules.

Mycophagy (*Cheilosia* fungivores)

Species examined: longula Zetterstedt, 1838; *scutellata* Fallén, 1817

Diagnosis. One pair of small and inconspicuous mouth-hooks; mandibular lobes soft and fleshy; dorsal lip with a setal fringe; dorsal surface of abdomen with rows of long and short setae; tip of anal segment with an extended ‘ring’.

Biology. Larvae found in the fruiting bodies of fungi. Infested fungi often lose their shape and appear as brown smudges on the ground. Searching these fungal remnants is the best way to find larvae, and 50 + individuals may be present (Rotheray, 1990).

Wet fungal decay in plants (*Cheilosia pagana*)

Species examined: pagana Meigen, 1822

Diagnosis. Mouth-hooks small and inconspicuous; mandibular lobes soft and fleshy; dorsal lip with a setal fringe; dorsally, body coated in evenly-sized setae; tip of anal segment without an extended 'ring'.

Biology. The only rearing record for *C. pagana* is from decaying roots of *Anthriscus sylvestris* (Umbelliferae). Larvae were collected in late autumn (Stubbs, 1980), and described by Rotheray (1990).

Boring in roots and stems of herbacaeous plants (*Cheilosia* borers)

Species examined: albitarsis Meigen, 1822; *albipila* Meigen, 1838; *antiqua* Meigen, 1822 *canicularis* Panzer, 1801; *fraterna* Meigen, 1830; *grossa* Fallén, 1817; *illustrata* Harris, 1780; *variabilis* Panzer, 1789

Diagnosis. Up to four pairs of mouth-hooks, usually one main pair and smaller ones behind; usually with sclerotized mandibular lobes; dorsal lip smooth, lacking setae; anal segment may be contracted, flattened and obliquely angled forming an anal plate; posterior respiratory process often with ridges, bars and projections; larva often with spicules (Sclerotized setae) on the lateral margins of the thorax and sometimes with a dorsal plate (a sclerotized region on the surface of the prothorax).

Biology. The species of this feeding mode are restricted to particular plants (Rotheray, 1993). For life histories of some of these species see Rotheray (1988a, 1991)

Leaf-mining (*Cheilosia* miners)

Species examined: fasciata Schiner & Egger, 1853; *semifasciata* Becker, 1894

Diagnosis. Six pairs of mouth-hooks; black, sclerotized mandibular lobes; dorsal lip with setal fringe; integument with a dense covering of upright pubescence; anal segment with a projecting transverse bar; posterior respiratory process with three pairs of oval-shaped spiracular openings.

Biology. Foodplants for *C. fasciata* and *C. semifasciata* are given in Rotheray (1993). The life history of *C. fasciata* is considered by Hövemeyer (1987, 1995) and the larva described by Rotheray (1990). The larva of *C. semifasciata* is described by Rotheray (1988b).

Cambium feeding in pines (*Cheilosia morio*)

Species examined: alaskensis Hunter, 1897 (Nearctic); *morio* Zetterstedt, 1838

Diagnosis. One huge pair of mouth-hooks; black, sclerotized mandibular lobes; dorsal lip with setal fringe; prothorax with a dorsal plate; anterior part of body with a pair of dorso-lateral ridges; first abdominal segment with a pair of fleshy, dorsal projections; anal segment extended from about a third to twice body length.

Biology. The larvae of this group excavate cavities in the sapwood of pines. They gain entry to the cambium through wounds and bark beetles holes. Immersed in pine resin, the extended anal segment projects to the outside for respiration. In Europe this feeding mode is represented by *C. morio* (Trägårdh, 1923; Hellrigl, 1992). A number of species are known from the U.S.A., where this feeding mode was first described (Burke, 1905).

Chrysogaster Meigen, 1803; *Orthonevra* Macquart, 1829 & *Lejogaster* Rondani, 1857

Species examined: brevicornis Loew, 1843; *hirtella* Loew, 1843; *metallina* Fabricius, 1777; *solstitialis* Fallén, 1817; *splendens* Meigen, 1822; *splendida* Meigen, 1822.

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior spiracles reduced or absent; anterior fold with pale lightly sclerotized setae; mesothoracic prolegs and lateral lips enlarged, projecting well below the thorax; larva subcylindrical in cross-section; dorsal surface of abdomen with rows of setae; lower lateral margin of abdomen with a prominent ridge fringed with long setae; prolegs small with transverse rows of crochets weakly developed and usually absent on posterior prolegs; anal segment elongated to various degees; tip of posterior respiratory process tapered.

Biology. Larvae of this group are aquatic, in accumulations of decaying vegetation and mud in pools, ponds and slow-moving streams. Some species, like *C. hirtella*, have a remarkably thin and pointed posterior respiratory process which pierces the air spaces of aquatic plants for respiration (Varley, 1937; Hartley, 1958).

Criorhina Meigen, 1822

Species examined: asilica Fallén, 1816; *berberina* Fabricius, 1805; *floccosa* Meigen, 1822; *ranunculi* Panzer, 1804

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; dorsally prothorax with one or two large pairs of hooks on a Y- or triangular-shaped hook base; behind each of the anterior spiracles is a large laterally directed hook, like a pair of cow horns; Y- or triangular-shaped hook base coming between sensilla groups 1 and 2/3 on prothorax so that they are not linear; anterior fold coated in small spicules; other pairs of smaller hooks may also be present on the thorax; a slightly extended anal segment bearing three pairs of lappets, middle pair smallest; prolegs reduced with small pale crochets.

Biology. Larvae found in decaying heartwood of various deciduous trees, including old stumps where they may be deep underground in decaying roots. They also occur in rot-holes.

Eristalinus Rondani, 1845

Species examined: aeneus Scopoli, 1763; *sepulchralis* Linnaeus, 1758

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; anterior spiracles retractile into inverted integumental pockets on the prothorax; dorsum of prothorax with 8 longitudinal grooves; anterior spiracles pale brown; prolegs with crochets in 2 main rows; transverse row of spicules just in front of, not between, the last pair of prolegs; last pair of prolegs with most of the large primary crochets facing the lateral margins of the body.

Biology. *Eristalinus sepulchralis* occurs in accumulations of decaying vegetation in ponds, pools and marshes and also in wet manure. *Eristalinus aeneus* occurs along shorelines in rock pools containing large amounts of decaying seaweed.

Eristalis Latreille, 1804, *Eoseristalis* Kanervo, 1938

Species examined: abusivus Collin, 1931; *arbustorum* Linnaeus, 1758; *intricarius* Linnaeus, 1758; *pertinax* Scopli, 1763; *tenax* Linnaeus 1758

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; anterior spiracles retractile into inverted integumental pockets on the prothorax; dorsum of prothorax with 8 longitudinal grooves; anterior spiracles brown; prolegs with crochets in 2 main rows; last pair of prolegs with most of the large primary crochets facing towards the lateral margins of the body.

Biology. Associated with wet decaying organic material, particularly accumulations of decaying vegetation in ponds and mud and farmyard manure or silage.

Eumerus Meigen, 1822

Species examined: strigatus Fallén, 1817; *tuberculatus* Rondani 1857

Diagnosis. Larva with mouth-hooks and fleshy mandibular lobes outside the mouth; dorsal lip with a setal fringe; antenno-maxillary organs on flattened, oval-shaped lobes; middle pair of lappets divided into two small projections; locomotory organs barely projecting from ventral surface; posterior respiratory process at tip of slightly extended anal segment.

Biology. Larvae living in pockets of fungal decay in the underground parts of plants, particularly bulbs. They survive best when fungal decay is present (Creager & Spruijt, 1935). Many larvae are usually present in each infested bulb.

Ferdinandea Rondani, 1844

Species examined: cuprea Scopoli, 1763; *nigripes* Osten Sacken, 1877 (Nearctic)

Diagnosis. One pair of small, inconspicuous mouth-hooks which do not protrude from the mouth when the larva is inactive; mandibular lobes mostly internal, on either side of the mouth; dorsal lip with a setal fringe; ventral surface of the anal segment with one transverse fold between the anus and the tip of the segment; abdominal segment 7 with sensilla 1–6 on fleshy, rounded papillae; anal segment with three pairs of equal-sized lappets; prolegs absent and the anterior fold is without spicules; posterior respiratory process with a mid-point constriction.

Biology. Larvae found in sap-runs on deciduous trees. Also found in sap-runs associated with caterpillar of the Goat Moth, *Cossus cossus* (Cossidae, Lepidoptera). Larvae often numerous when present. Also found in decaying plants (Brunel & Cadou, 1994).

Hammerschmidtia Schummel, 1834

Species examined: ferruginea Fallén, 1817

Diagnosis. Larva somewhat dorso-ventrally flattened with mandibles supporting the expanded mandibular lobes; lateral lips large and coated in spicules; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated in transverse spicules; sides of body with gradually elongating projections; anal segment and abdominal segment 7 inclined dorsally, except for two tapering rings at the tip of the anal segment, two pairs of lappets on the basal ring and one pair on the distal ring.; posterior respiratory process long and narrow, and base coated in nodules; abdominal segments 2–7 coated in setae; sensilla 1 of abdominal segments 2–7 separated from sensilla 2 by an integumental groove such that sensilla 1 is anterior to 2 (this groove absent in *Brachyopa*); prolegs not well developed and a few crochets may or may not be discernible.

Biology. Larvae either occur in sap runs or, more frequently, in accumulations of decaying sap under bark of fallen *Populus tremula* (Krivosheina & Mamaev, 1967; Rotheray, 1991).

Helophilus Meigen, 1822

Species examined: hybridus Loew, 1846; *fasciatus* Walker, 1849 (Nearctic); *pendulus* Linnaeus, 1758

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; anterior spiracles retractile into inverted integumental pockets on the prothorax; dorsum of prothorax with 8 longitudinal grooves; anterior spiracles pale brown; base of anal segment with three pairs of ventrolateral papillae; prolegs with crochets in 3 or more rows; last pair of prolegs with most of the large primary crochets facing towards the front of the body.

Biology. Associated with wet decaying organic material, particularly accumulations of decaying vegetation in ponds and mud and farmyard manure or silage.

Lejota Rondani, 1857

Species examined: aerea Loew, 1872 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold with 5–6 rows of sclerotized spicules; larva subcylindrical, with a relatively long anal segment about 75% of body length; first two pairs of lappets at base of extended anal segment, third pair at tip; body coated in fine setae including segment 7 and anal segment; prolegs small with 8–10 primary crochets. Very similar to *Calliprobola* and *Blera*, but differing from these taxa in having no spicules on the lateral margin of the prothorax, between the anterior fold and the mesothorax, and in having anterior spiracles with spiracular openings clustered round a fan-shaped inclined apical margin.

Biology. Larva found in decaying heartwood of well-decayed tree stumps.

Mallota Meigen, 1822

Species examined: cimbiciformis Fallén, 1817; *posticata* Fabricius, 1805 (Nearctic); *sackeni* Williston, 1882 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking setae and a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; anterior spiracles retractile into inverted integumental pockets on the prothorax; abdominal segments 2–7 with sensilla 4–6 in a linear row, those on the anal segment mounted on short fleshy papillae; abdomen smooth without a coating of setae; prolegs cylindrical, small and weakly developed with 6 primary crochets; thorax large, conspicuously broader than the abdomen.

Biology. Found in rot-holes of various deciduous trees. Several larvae often found together in rotholes small and large, low and high on trees.

Merodon Meigen, 1803

Species examined: equestris Fabricius, 1794

Diagnosis. Larva with mouth-hooks and black, sclerotised mandibular lobes outside the mouth; dorsal lip smooth, lacking setae; lateral lips and anterior edge of prothorax coated in dome-shaped papillae; middle pair of lappets divided into two small projections; anal segment contracted obliquely.

Biology. Larvae living in the underground parts of plants, particularly bulbs.

Microdon Meigen, 1803

Species examined: eggeri Mik, 1897; *mutabilis* Linnaeus, 1758; *devius* Linnaeus, 1761

Diagnosis. Hemispherical in cross-section with marginal bands of setae; gap in marginal bands of setae at front end of body; prothorax and mesothorax elongate, narrow and retractable into the ventral part of the metathorax under the body; prothorax and metathorax not seen unless the larva is moving, when they project through the gap in the marginal band of setae at the front of the body, this being the dorsum of the metathorax; antenno-maxillary organs sharply tapered; mandibles fused with the mandibular lobes, flattened laterally, and bearing a serrated ventral margin; bridge between the mandibles absent, so that each mandible can move independently of the other; labial sclerites and plate developed forward, but not further than the fused mandibles/mandibular lobes; prothorax and mesothorax with a pair of fleshy appendages on the anterior margin; anterior spiracles absent; anal segment contracted, with lappets reduced, included as part of the marginal band; anal segment with sensilla 7 not on the posterior lappets, but on a separate fold behind the anus; prolegs absent.

Biology. Donisthorpe (1927) suggests that *Microdon* larvae feed on solid pellets ejected from the hypopharygneal pockets of ants. It is now clear, however, that *Microdon* larvae are entomophages of the early stages of ants (Duffield, 1981; Garnett *et al.*, 1985; Barr, 1994).

Milesia Latreille, 1804

Species examined: virginiensis Drury, 1773 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; thorax with two large groups of hooks either side of the anterior spiracles; hooks in the first group in 3 or more rows with a smaller group of two main hooks separated and below; anterior fold coated in a narrow band of 4–5 rows of spicules, those in the middle rows the largest; one pair of lappets at the tip of the anal segment, first two pairs close to each other and reduced to slight bulges; prolegs cylindrical with 7–8 primary crochets.

Biology. Larva found in decaying heartwood of deciduous trees, including rot-holes. The puparium described by Matile & Leclercq (1992) as *Milesia crabroniformis* (F.) is misidentified. It is a *Mallota* species with most of the long-tail missing.

Myathropa Rondani, 1845

Species examined: florea Linnaeus, 1758

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; pale brown anterior spiracles retractile into inverted integumental pockets on the prothorax; dorsum of prothorax with 8 longitudinal grooves; prolegs with crochets in 2 main rows; last pair of prolegs with most of the large primary crochets facing towards the lateral margins of the body.

Biology. Associated with wet decaying vegetation in rot-holes and in decaying heartwood of a wide variety of trees. Occurs in all main microhabitats associated with wet decay in trees, from sap-runs to rot-holes and decaying heartwood in tree roots. Often the most common species encountered in rot-holes and decaying heartwood.

Myolepta Newman, 1838

Species examined: luteola Gmelin, 1788; *nigra* Loew, 1872 (Nearctic); *potens* Harris, 1780; *varipes* Loew, 1869 (Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow extended anal segment about half body length; anterior fold without sclerotized spicules; body coated in fine setae except for segment 7 and anal segment which are coated in papillae, at the tip of which are tufts of setae; prolegs cylindrical with 7 or 8 primary crochets; anal segment with 3 pairs of equidistant lappets.

Biology. Larvae in rot-holes of deciduous trees.

Neoascia Williston, 1886

Species examined: geniculata Meigen, 1822; *meticulosa* Scopoli, 1763; *podagrica* Fabricius, 1775; *tenur* Harris, 1780

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva small, up to 6 mm long, dorso-ventrally flattened with an extended anal segment; anterior fold coated with spicules; dorsally prothorax with a pair of large, backwardly directed hooks; prolegs small with 4 or 5 main crochets; anal segment with 3 pairs of lappets, but the first pair of lappets, at the base of the anal segment, are bifurcated at the tip.

Biology. The few breeding records are from wet manure in farmyards, and from decaying vegetation round the margins of ponds.

Parhelophilus Girschner, 1897

Species examined: frutetorum Fabricius, 1775; *versicolor* Fabricius, 1794

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; anterior spiracles retractile into inverted integumental pockets on the prothorax; dorsum of prothorax with 8 longitudinal grooves; anterior spiracles pale brown; base of anal segment without three pairs of fleshy papillae; prolegs with crochets in 3 or more rows; last pair of prolegs with most of the large primary crochets facing towards the front of the body.

Biology. Associated with accumulations of decaying vegetation, particularly *Typha*, in ponds and slow-moving streams.

Pipizella Rondani, 1856

Species examined: varipes Meigen, 1822

Diagnosis. Mandibles and mandibular lobes fused and entirely inside mouth with a sharp distal margin; labium tapered, and developed forward beyond the mandibles; bridge between mandibles absent so that each mandible can move independently of the other; labial sclerites and plate developed forward to form a tapered lower lip; prothorax and mesothorax retractable into the metathorax, so that when contracted, the metathorax forms the anterior margin of the larva; prothorax elongate, with apex of lateral lips bearing a pair of sclerotized hooks; ventral lip with spicules; dorsal lip with ventral groove; ventral surface of prothorax with modified vestiture, appearing raised and coriaceous; larva flattened in cross-section, with the posterior lappets as rounded projections at the tip of the anal segment; other lappets reduced and part of a posterior transverse grasping bar on the anal segment; body coated in round-tipped pubescence; dorsal sensilla borne on club-tipped papillae; posterior respiratory process lacking dorsal spurs; inter-spiracular setae long and conspicuous (more than half the length of a spiracular opening).

Biology. Associated with ant-tended aphids feeding on roots of umbelliferous plants (Heeger, 1858; Dixon, 1959).

Pocota Lepeletier and Serville, 1828

Species examined: personata Harris, 1780

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; spicule band occupying more than 50% of the anterior fold; larva subcylindrical; extended part of anal segment broad, not much less than half body width, with 3 pairs of equidistant lappets, third pair at tip the longest, first two pairs on short, inconspicuous projections; prolegs cylindrical with 6–8 primary crochets.

Biology. Larvae found in rot-holes of deciduous trees.

Portevinia Goffe, 1944

Species examined: maculata Fallén, 1817

Diagnosis. Larva with mouth-hooks; black, sclerotized mandibular lobes; dorsal lip smooth, lacking setae; end of the body with a flat, inclined anal plate, with a central posterior respiratory process and marginal setae and sensilla; anus parallel to the longitudinal axis of the body; prolegs absent and anterior fold without spicules.

Biology. Living in plant bulbs. The larva of *P. maculata* tunnels the bulbs of *Allium ursinum* (Liliaceae) (Speight, 1986; Rotheray, 1991). Larvae are actively growing and developing during winter.

Psilota Meigen, 1822

Species examined: anthracina Meigen, 1822

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold with more than 5 rows of spicules not reaching sensilla group 1–3 on dorsum of prothorax; anal segment extended to varying degrees and dorso-ventrally flattened; anal segment with three pairs of lappets, first pair with sensilla at tip divided into two groups, middle pair of lappets short and indistinct; prolegs cylindrical with a primary row of 7 crochets; posterior respiratory process with three pairs of oval-shaped spiracular openings.

Biology. Larva found in accumulations of decaying tree sap under bark or in crevices.

Rhingia Scopoli, 1763

Species examined: campestris Meigen, 1822

Diagnosis. One pair of small, inconspicuous mouth-hooks which do not protrude from the mouth when the larva is inactive; mandibular lobes mostly internal, on either side of the mouth; dorsal lip with a setal fringe; body coated conspicuously in stiff, upright pubescence; abdominal segments 6–8 with dorsal sensilla 1–6 on long black stick-like papillae; ventral surface of the anal segment with one fold between the anus and the tip of the segment; three pairs of black, stick-like lappets present; prolegs absent and the anterior fold without spicules.

Biology. Larvae of *R. campestris* were found in cow dung by Coe (1942), who also gives biological details.

Sericomyia Meigen, 1803

Species examined: lappona Linnaeus, 1758; *silentis* Harris, 1776

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking setae and a medial groove; feeding channel present; larva subcylindrical in cross-section with a narrow, extended anal segment, just over body length; anterior fold coated in sclerotized spicules; short, non-retractile, dark brown anterior spiracles; body sparsely coated in pubescence; prolegs cylindrical, small and weakly developed with 6 primary crochets; thorax large, conspicuously broader than the abdomen.

Biology. Larvae associated with peaty pools in moorland habitats (Bloomfield, 1897; Hartley, 1961).

Sphegina Meigen, 1822

Species examined: clunipes Fallén; *elegans* Schummel, 1842; *keeniana* Williston, 1887 (Nearctic); *verecunda* Collin, 1937

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva small, up to 6 mm long, dorso-ventrally flattened with an extended anal segment; anterior fold coated with spicules; prothorax without hooks; prolegs small with 4 or 5 main crochets; anal segment with 3 pairs of lappets, but the first pair of lappets at the base of the anal segment are bifurcated at the tip.

Biology. Larvae found in accumulations of decaying sap under bark, usually in wet situations such as damp, shaded woodland and in partially submerged wood in streams and pools. *Sphegina clunipes* has also been recorded from sap runs.

Spilomyia Meigen, 1803

Species examined: alcimus Walker, 1849; *citima* Vockeroth, 1958; *longicornis* Loew, 1872; *sayi* Goot, 1964 (all Nearctic)

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; thorax with four groups of hooks, one group in an antero-dorsal position on the prothorax, second group in front of the anterior spiracles, third group below and lateral to the anterior spiracles, and fourth group below the third; anterior fold coated in a narrow band of 4–5 rows of spicules, those in the middle rows the largest; one pair of lappets at the tip of the anal segment, first two pairs close to each other and reduced to slight bulges; prolegs cylindrical with 7–8 primary crochets.

Biology. Larva found in decaying heartwood of deciduous trees, including rot-holes.

Syritta Lepeletier and Serville, 1828

Species examined: oceanica Macquart, 1855 (Nearctic); *pipiens* Linnaeus, 1758

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; larva subcylindrical; anterior fold coated with evenly sized spicules about as long as setae on the dorsal surface of the body; prolegs small with 5 or 6 primary crochets arranged as a transverse row across the segment; anal segment with 3 pairs of lappets, first two pairs equal in length, third pair at tip longest.

Biology. Larva found in various kinds of wet, decaying matter including, compost, manure and silage.

Temnostoma Lepeletier and Serville, 1828

Species examined: alternans Loew, 1864; *bombylans* Fabricius, 1805; *vespiforme* Linnaeus, 1758

Diagnosis. Larva sub-cylindrical in cross-section; contracted at both anterior and posterior ends; mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; one very large set of peg-like hooks in three rows anterior and lateral to each of the anterior spiracles and in front of sensilla 3 and 4 of mesothorax; segments, folds and grooves greatly modified: prothorax narrow, elongate and inclined towards the ventral surface, folds bearing sensilla groups 1–3 fused and extended between the hooks; anterio-laterally, the fold bearing sensilla groups 4 and 5 of the prothorax also fused to the longitudinal fold; anterior margin of these fused folds with a triangular-shaped patch of spicules; anterior fold reduced and coated in small spicules; dorsally, integument coated in patches of spicules; metathorax and mesothorax both enlarged; prolegs reduced and crochets absent; anal segment contracted to form an anal plate with a large posterior respiratory process at its centre.

Biology. Larvae burrow in moist decayed wood using their hooks as rasping organs, operated in a forwards-and-backwards motion by huge muscles housed in the mesothorax and metathorax. *Temnostoma* larvae have been found in fallen *Alnus* or *Betula* logs more than 10 cm in diameter, lying in wet, boggy conditions. The larvae tunnel from the lower part of the log, forming circular tunnels running at right-angles to the grain of the wood (C. Kassebeer, *pers. comm.*).

Tropidia Meigen, 1822

Species examined: quadrata Say, 1824 (Nearctic); *scita* Harris, 1780

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated with spicules of various sizes and these extending onto the prothorax and the lateral and dorsal margins of the mesothorax; larva sub-cylindrical with a slightly extended anal segment; prolegs cylindrical with 5–6 crochets; anal segment with 3 pairs of lappets.

Biology. Larva are probably in accumulations of decaying vegetation and mud at the margins of ponds and ditches, but this requires confirmation (DeCleer & Rotheray, 1990).

Volucella Geoffroy, 1762

From the larval point of view, this genus is polyphyletic (Fig. 6). Three groups of species can be recognized on the basis of larval morphology and feeding mode.

Saprophages

Species examined: *inflata* Fabricius, 1794

Diagnosis. Mandibles reduced and supporting the entirely internal and expanded mandibular lobes; dorsal lip with a setal fringe; lateral lips large, and coated with spicules and long setae; thorax as broad as abdomen, and not retractable; anterior fold coated in rows of spicules; anterior spiracles absent; prolegs barely projecting, with 1–2 primary crochets; crochets absent from posterior prolegs; anal segment with three pairs of equal-sized lappets.

Biology Larva found in sap-runs on deciduous trees, including those formed by caterpillars of *Cossus cossus* (Lepidoptera, Cossidae).

Facultative entomophages

Species examined: bombylans Linnaeus, 1758; *pellucens* Linnaeus; *zonaria* Poda, 1761

Diagnosis. Mandibles reduced and supporting reduced mandibular lobes; apex of each ridge of the mandibular lobes with a hook; dorsal lip flat basally, coated in spicules and with a medial groove ventrally; ventral lip large, and coated with spicules; thorax narrower than abdomen; prothorax retractable into mesothorax; prothorax elongate, with a few large sclerotized spicules on the anterior fold; anterior spiracles present; prolegs with 3–5 primary crochets arranged in a transverse row, present on the mesothorax and the first six abdominal segments; dorsum of body with up to four rows of fleshy projections, these longer than the lateral margins.

Biology Larvae found in or around nests of aculeates (Hymenoptera), where they feed on pollen, comb material, and live or dead aculeate larvae and pupae.

Obligatory entomophages

Species examined: inanis Linnaeus, 1758

Diagnosis: Mandibles and mandibular lobes fused and reduced with ridges absent; apex of the mandibular lobes with 3–5 hooks; labial sclerites developed, with an apical hook; dorsal lip flat basally, with a medial groove ventrally; ventral lip large; thorax narrower than the abdomen; prothorax retractable into the mesothorax; prothorax narrow, with a few large sclerotized spicules on the anterior fold; prolegs with up to 10 primary crochets arranged in a transverse row present on the mesothorax and the first six abdominal segments; body dorso-ventrally flattened, smooth, without fleshy projections.

Biology. Larvae found in nests of vespids (Vespidae, Hymenoptera), where they feed as ectoparasites of vespid larvae and pupae. The larva moves into a cell behind its prey, using its crochets to hold on (Rupp, 1989).

Xylota Meigen, 1822

Species examined: abiens Meigen, 1822; *coeruleiventris* Zetterstedt, 1838; *segnis* Linnaeus, 1758; *sylvarum* Linnaeus, 1758; *tarda* Meigen, 1822; *xanthocnema* Collin, 1939

Diagnosis. Mandibles supporting the expanded mandibular lobes; dorsal lip broad, lacking a medial groove; feeding channel present; anterior fold coated with spicules of varying size of which some are longer than setae on the dorsal surface of the body; larva sub-cylindrical with an anal segment extended to varying degrees, and having three pairs of evenly spaced lappets; thorax without hooks; a few aggregated spicules on the lateral margins of the thorax beyond the anterior fold; prolegs cylindrical in shape with 5 or 6 primary crochets usually arranged in a curved row.

Biology. A range of feeding habits are known within this genus, associated mostly with decaying sap and heartwood. *Xylota segnis* feeds in decaying sap under bark and in sap runs, but it has also been found in very different habitats, in silage (Hartley, 1961) and in decomposing potatoes (Blackith & Blackith, 1989). *Xylota coeruleiventris* has been found in sap-filled tunnels of the bark weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *Xylota sylvarum* feeds in decayed heartwood of various trees, including deep underground in tree roots, and above ground in rot-holes. *Xylota tarda* has been found in sap runs on *Populus*, and *X. xanthocnema* in rot-holes.

IDENTIFICATION

Keys to genera follow based on larval characters. Rotheray (1993) provides more details on identification.

Keys to genera using larval characters

1 Anal segment with a single, sclerotized projection bearing spiracular openings, the posterior respiratory process; dorsum of prothorax with longitudinal grooves; anus at the ventral margin of the anal segment (Fig. 2) .... Syrphidae 2

– Not like this .... other families

2 Antenno-maxillary organs mounted on a pair of dome- or cylindrical-shaped basal projections (Fig. 8) 3
PHYTOPHAGES, MYCOPHAGES AND PREDATORS

– Antenno-maxillary organs plus cylindrical-shaped projections both mounted on a second, broader projection; this projection sometimes divided medially almost to base (long-tailed larvae) (Fig. 12) 16
SAPROPHAGES

3 Downwardly projecting, black mouth-hooks present at apex of mouth; in lateral view, mouth-hooks usually protruding from the mouth (Fig. 8) ... 4

– Mouth-hooks reduced and pale, or apparently absent 11

4 Anal segment tapering towards tip with four pairs of lappets; middle pair of lappets divided into two small projections (Fig. 23a) 5

– Anal segment either tapering towards tip with two or three pairs of lappets or, ends in flattened disc 6

5 Dorsal lip (areas between mouth-hooks at base of antenno-maxillary organs) coated in transverse rows of setae (Fig. 8) .... *Eumerus*
IN BULBS AND ROOTS OF LIVE PLANTS
– Dorsal lip lacking rows of setae .... *Merodon*
IN BULBS AND ROOTS OF LIVE PLANTS

6 Anus parallel to longitudinal axis of body; body ends with posterior spiracular process in the centre of a flat, inclined disc fringed with setae (Fig. 23C) .. .. *Portevinia*
IN BULBS AND ROOTS OF LIVE PLANTS
– Anus transverse to longitudinal axis of body 7

7 Mandibular lobes pale and fleshy 8
– Mandibular lobes completely black and sclerotized (Fig. 9) 9

8 Dorsal surface coated densely in alternate, transverse rows of small flattened and tall upright setae; middle pair of lappets reduced in relation to first and third pairs .... *Cheilosia* (in part)
MYCOPHAGOUS, IN FRUITING BODIES OF MACROFUNGI
– Dorsal surface coated in evenly-sized setae; middle pair of lappets about as large as first and third pairs .... *Cheilosia* (in part)
IN DECAYING ROOTS OF HERBACEOUS PLANTS

9 Six-to-eight pairs of mouth-hooks present .... *Cheilosia* (in part)
LEAF-MINERS
– Up to four pairs of mouth-hooks present 10

10 Anal segment extended, distance between lappets is greater than their length; tip of posterior spiracular process with two inclined plates bearing spiracular openings .... *Cheilosia* (in part)
CAMBIUM-FEEDERS THROUGH BARK OF PINE TREES
– Anal segment not extended, distance between lappets less than their length, tip of anal segment sometimes compressed forming a flat disc; tip of posterior spiracular process bearing spiracular openings flat .... *Cheilosia* (in part)
TUNNELLING IN ROOTS AND STEMS OF HERBACEOUS PLANTS

11(3) Larva hemispherical in cross-section with a narrow band of setae round the entire margin of the body except for a notch on the anterior margin through which the prothorax protrudes, this band of setae level with the ventral surface; prothorax and mesothorax very narrow and usually retracted completely into the mesothorax (view from the ventral surface) .... *Microdon*
IN AND AROUND ANT NESTS, PREDATORS OF ANT LARVAE AND PUPAE
– Larva without this combination of characters 12

12 Larva with a colour pattern made up from: pigments in the haemolymph and/or variously coloured fat bodies and markings on the integument; tip of anal segment rounded, bearing sensilla; tip of prothorax with a pair of triangular-shaped sclerotized hooks; prothorax and mesothorax narrow and retractable into the mesothorax; usually free-living on plants .... Key 2
PREDATORS OF SOFT-BODIED HOMOPTERA, SYRPHINAE OF AUTHORS
– Larva without this combination of characters 13

13 Larva without anterior spiracles; dorsal lip with setae (Fig. 11) .... *Volucella inflata*
IN SAP-RUNS
– Larva with anterior spiracles 14
14 larva with prolegs bearing crochets on some of the abdominal segments ... . *Volucella*
IN NESTS OF SOCIAL BEES AND WASPS
– larva without prolegs bearing crochets 15
15 Posterior end of body with sensilla borne on black, stick-like projections; body coated in upright spike-like setae .... *Rhingia*
IN DUNG
– Posterior end of body with sensilla borne on short, conical, fleshy projections; body coated in short, flattened, fleshy setae .... *Ferdinandea*
IN SAP-RUNS
16(2) Broad basal projection bearing antenno-maxillary organs not divided medially 17
– Broad basal projection bearing antenno-maxillary organs divided medially 39
17 Prothorax and mesothorax with hooks which are sclerotized, black and conspicuously larger than any spicules on the anterior margin of the prothorax 18
– Dorsal and lateral margins of the thorax without hooks on the thorax 27
18 Thorax with a single pair of backwardly directed hooks on the antero-dorsal margin of prothorax; anal segment dorso-ventrally flattened with first lappets at base of anal segment, separated into two projections; small larva, up to 12 mm long .... *Neoascia*
PONDS, STREAMS, BOGS ETC IN DECAYING VEGETATION
– Thorax usually with more than a single pair of hooks but if a single pair is present they are lateral to the anterior spiracular processes, not on the antero-dorsal margin of the prothorax; anal segment subcylindrical with sensilla of first lappet not on two separate projections; large larva, more than 12 mm long 19
19 Anterior margin of mesothorax with a row of mostly small hooks, not much larger than spicules on the prothorax; a few similar hooks on the dorsal and lateral margins of the thorax .... *Tropidia*
PONDS, STREAMS, BOGS ETC IN DECAYING VEGETATION
– Hooks elsewhere on the thorax, not forming a row on the anterior margin of the mesothorax 20
20 One hook lateral to each anterior spiracle and below this another separate hook; upper row of spicules on anterior margin of prothorax larger than the rest .... *Brachypalpus*
ROT-HOLES, UNDER BARK
– Hooks arranged differently 21
21 A pair of red-brown hooks lateral to each anterior spiracle .... *Brachypalpoides lenta*
IN WET, DECAYING HEARTWOOD OF DECIDUOUS TREES
– Hooks black, and more than two pairs present 22

22 Larva dorso-ventrally flattened; two hooks lateral to each anterior spiracle and, usually, below these, on a separate base, another small hook .... *Chalcosyrphus*
UNDER BARK
– Larva sub-cylindrical, not flattened; hooks arranged differently 23

23 A group of hooks just behind and lateral to each anterior spiracle, each group comprising 3–4 hooks of which outer hook is the largest; prolegs fused medially .... *Callicera*
ROT-HOLES
– Hooks arranged differently; prolegs separate, forming pairs of oval structures 24

24 Dorsum of prothorax with a 'Y' or triangular-shaped hook base and a pair of "cow horn" shaped, laterally directed hooks behind the anterior spiracles .... *Criorhina*
DECAYING TREE-ROOTS AND ROT-HOLES
– Prothorax without a Y or triangular-shaped hook base and cow-horn hooks 25

25 Larva barrel-shaped, short and compact; a large rasp consisting of 4–5 rows of blunt-tipped hooks lateral to the anterior spiracle; crochets absent .... *Temnostoma*
TUNNELLING FIRM, MOIST WOOD IN LOGS AND FALLEN BRANCHES
– Larva elongate and tapering posteriorly; lacking rasps; crochets present 26

26 Each side of thorax with two groups of hooks: a group of hooks just anterior to each anterior spiracle comprising a primary row of 3–4 large hooks, a second row of intermediate hooks and a third row of small hooks; a separate group of 4–6 hooks is present below .... *Milesia*
ROT-HOLES
– Each side of thorax with four groups of hooks .... *Spilomyia*
ROT-HOLES

27(17) Anterior fold of prothorax with soft, pale setae, not sclerotized 28
– Anterior fold of prothorax with brown, sclerotized spicules 29

28 Prolegs little developed and crochets pale; anterior spiracles reduced or absent; posterior end of body not coated in fleshy papillae .... *Chrysogaster, Lejogaster & Orthonerva*
IN PONDS, STREAMS ETC
– Prolegs well developed with dark brown and black crochets; anterior spiracles present as pale brown sclerotized structures, not reduced; posterior end of body coated in fleshy papillae tipped with setae .... *Myolepta*
ROT-HOLES

29 Anal segment extended, longer than body (head to base of anal segment), a 'long-tailed' larva; thorax broader than abdomen; anterior spiracular processes dark brown and not retractile into pockets on the thorax .... *Sericomyia*
MOORLAND POOLS AND PEAT BOGS

– Anal segment less than body length, if extended to nearly body length, lappets present at base 30

30 Anal segment with three pairs of about equally long, fleshy lappets 31

– Anal segment without three pairs of equally long lappets, one or more pairs of lappets reduced 36

31 Prolegs barely developed with crochets absent or small, little longer than surrounding setae; ventral surface of anal segment between anus and posterior spiracular process with four pairs of sensilla 32

– Prolegs well developed, protruding from ventral surface with pale brown or black crochets longer than surrounding setae; anal segment between anus and posterior spiracular process with two or three pairs of sensilla 33

32 Dorsum of abdomen with either transverse rows of setae or coated in blotches; abdominal segments 2–6 with mid-dorsal sensilla not separated from other dorsal sensilla by an oblique groove .... *Brachyopa*
in sap-runs and under bark

– Dorsum of abdomen evenly coated in setae, not forming transverse rows; abdominal segments 2–6 with mid-dorsal sensilla separated from other dorsal sensilla by an oblique groove .... *Hammerschmidtia*
under bark and in sap-runs

33 First pair of lappets, at base of anal segment, separated at tip into two projections each bearing sensilla; small larva up to 8 mm long ..... *Sphegina*
under bark, sometimes in sap-runs

– First pair of lappets not separated, each lappet consisting of a single fleshy projection 34

34 Dorsal surface with groups of small and large setae; larva somewhat dorso-ventrally flattened .... *Ceriana*
sap-runs, under bark

– Dorsal surface coated in even-sized setae 35

35 Anterior margin of prothorax coated in equal-sized spicules not reaching the longitudinal grooves on the dorsum; large primary crochets arranged as transverse rows with few associated smaller crochets .... *Syritta*
wet compost and manure

– Anterior margin of prothorax coated in variously sized spicules and/or some scattered spicules between the longitudinal grooves on the dorsum; large primary crochets arranged as curved rows with 3–4 rows of smaller crochets behind .... *Xylota*
in sap-runs, under bark and in decaying heartwood, also *X. segnis* in decaying vegetation

36(30) Anal segment about one body length with first two pairs of lappets at base and third pair at tip; one or more pairs of lappets reduced to little more than sensilla and terminal setae 37

– Anal segment about half body length with the three pairs of lappets about equidistant from one another; one or more pairs of lappets reduced 38

37 Larva about 17 mm long including extended anal segment; apices of anterior spiracular processes bearing spiracular openings large, bulging over the sides (view from front of larva); two isolated groups of spicules on the lateral margins of pro- and meso-thorax consisting of about 6 and 8 spicules each .... *Lejota*
PONDS, MARSHES ETC
– Larva about 34 mm long including extended anal segment; apices of anterior spiracular processes small, not enlarged over the sides; two isolated groups of spicules on the lateral margins of pro- and meso-thorax consisting of about 18 and 36 spicules each .... *Caliprobola*
DECAYING HEARTWOOD IN ROOTS OF TREES AND STUMPS
(*Blera* similar to *Caliprobola*)

38 Larva about 10 mm long including anal segment; at tip of anal segment, third pair of lappets not much extended, about as long as basally broad ... . *Psilota*
SAP-RUNS
– Larva about 20 mm long including anal segment; lappets at tip of anal segment as narrow projections, more than twice as long as broad .. *Pocota*
ROT-HOLES

Long-tailed larvae

39(16) Abdominal segments 2–7 with lateral sensilla arranged in a line; abdomen smooth, not coated in setae .... *Mallota*
ROT-HOLES
– Abdominal segments 2–6 with lateral sensillum 4 above 5 and 6 (segment 7 with sensilla 4–6 in a line); abdomen coated in setae 40

40 Last pair of prolegs with the curved tips of most of the large, primary crochets facing forwards to the front of the larva 41
– Last pair of prolegs with the curved tips of most of the primary crochets facing out to the lateral margins of the larva 43

41 Ventral surface with 3 pairs of projections between the anus and the base of the long tail .... *Helophilus*
WET MANURE, PONDS, DITCHES, MARSHES ETC
– Ventral surface without 3 pairs of projections between the anus and the ‘tail’ 42

42 Abdomen with a line of pubescence along the lower lateral margin .... *Anasimyia*
PONDS, MARSHES ETC
– Abdomen with pubescence absent or more evenly distributed, not reduced to a lower lateral line .... *Parhelophilus*
PONDS, MARSHES ETC

43 Transverse row of spicules just in front of last pair of prolegs .... *Eristalinus*
PONDS, MARSHES ETC

– No transverse row of spicules just in front of last pair of prolegs, although a few scattered spicules may be present between the prolegs 44

44 Anterior spiracles pale brown; prolegs with evenly sized spicules below .... *Myathropa florea*
ROT-HOLES, LARGE SAP-RUNS, DECAYING TREE ROOTS, UNDER BARK ETC

– Anterior spiracles dark brown; prolegs with crochets in three rows with spicules gradually becoming smaller below .... *Eristalis*
WET MANURE, PONDS, DITCHES, WET SILAGE, MARSHES, BOGS ETC

Key 2: Larva with colour patterns; thorax narrower than abdomen with a pair of triangular black hooks at the tip of the prothorax; predators; living on plants

1 Posterior respiratory process without dorsal spurs 2

– Posterior respiratory process with dorsal spurs 20

2 Posterior respiratory process dome-shaped in profile; without a central depression at tip 3

– Posterior respiratory process angular in profile, not dome-shaped; with a central depression at tip 4

3 Posterior respiratory process with wavy spiracular openings; interspiracular setae absent or short and inconspicuous .... *Xanthogramma*
IN ANT NESTS

– Posterior respiratory process with straight or slightly curved spiracular openings; interspiracular setae long and conspicuous .... *Doros*
?ANT NESTS IN DECAYING WOOD

4 In dorsal view, posterior respiratory process pale brown with spiracular openings on a white or black plate 5

– in dorsal view, posterior respiratory process pale or dark brown; if pale then spiracular openings not on a white or black plate 8

5 Larva bright shining green with a pair of sometimes inconspicuous, pale dorsal stripes .... *Sphaerophoria*
GROUND LAYER APHIDS

– Larva mostly mottled white and pale brown; if green then with four or five ‘V’–shaped markings on the dorsal surface 6

6 Tip of anal segment with two pairs of short tapering, projections (less than length of posterior respiratory process) .... *Rohdendorfia*
LEAF LITTER ON MOUNTAINS

– Tip of anal segment with one pair of short projections or without such projections 7

7 Front of larva with two stripes, one stripe of fat extending forward of the other .... *Baccha*
GROUND LAYER APHIDS

– Front of larva with two stripes of fat meeting at the same point .... *Platycheirus*
LEAF LITTER AND GROUND LAYER APHIDS

8 Tip of anal segment with a pair of short, fleshy, rounded projections; interspiracular setae long and conspicuous, about half as long as the spiracular openings 9

– Tip of anal segment without a pair of short, fleshy projections; interspiracular setae short and inconspicuous, much less than half as long as the spiracular openings 12

9 Larva coated in round-tipped setae, larva dorso-ventrally flattened in cross-section .... *Pipizella*
ROOT APHIDS IN ANT NESTS

– Larva not coated in round-tipped setae; larva oval or sub-cylindrical in cross-section 10

10 Larva coated in short, upright setae .... *Pipiza*
FLOCCULENT APHIDS, GROUND-LAYER APHIDS AND APHIDS IN GALLS

– Larva not coated in setae 11

11 Larva coated in dome-shaped papillae; larva usually dark brown .... *Heringia* (including *Neocnemodon*)
FLOCCULENT AND GALL-INDUCING APHIDS IN TREES

– Larva smooth, without dome-shaped papillae; larva whitish ...... *Trichopsomyia*
IN PSYLLID GALLS ON RUSHES

12 Posterior respiratory process more than twice as long as broad at base; larva flattened in cross-section, mottled orange and white ... *Meligramma euchroma*
APHIDS ON FRUIT TREES

– Posterior respiratory process less than twice as long as broad at base; if flattened then coloured otherwise 13

13 Posterior respiratory process at tip with a raised bar connecting the two sides; larva sandy coloured .... *Eupeodes nielseni*
APHIDS ON PINE TREES

– Posterior respiratory process at tip without a raised bar connecting the two sides 14

14 Spiracular openings oval-shaped, less than twice as long as broad 15

– Spiracular openings elongate, more than twice as long as broad 16

15 Apex of posterior respiratory process with a pair of posterior projections; large larva, more than 10 mm long .... *Xanthandrus comtus*
GREGARIOUS LEPIDOPTERAN CATERPILLARS ON TREES AND SHRUBS

– Apex of posterior respiratory process without posterior projection; small larva, less than 10 mm long .... *Melanostoma*
LEAF LITTER AND SOME GROUND LAYER APHIDS

16 Larva coated in pointed spicules 17

– Larva coated in dome-shaped papillae 18

17 Posterior respiratory process without inwardly sloping spiracular plates; larva subcylindrical with a mid-dorsal whitish stripe .... *Scaeva*
PINE TREE APHIDS, SOME SPECIES ON A WIDER RANGE OF APHIDS

– Posterior respiratory process with inwardly sloping spiracular plates; larva flattened without mid-dorsal stripe .... *Didea*
ARBOREAL APHIDS

18 Posterior respiratory process with a basal rim; in profile, spiracular plate sloping backwards (*cinctellus*) or not sloping backwards and posterior respiratory process as long as broad (*auricollis*) .... *Meliscaeva*
MOSTLY ARBOREAL APHIDS

– Posterior respiratory process without a basal rim; spiracular plate not sloping backwards and broader than long 19

19 Larva coated in black angular papillae; posterior respiratory process dark brown or black .... *Eriozona*
PINE TREE APHIDS

– Larva coated in translucent dome-shaped papillae; posterior respiratory process pale brown .... *Episyrphus*
WIDE RANGE OF APHIDS

20(1) Interspiracular ornamentation ridge-shaped between posterior pair of spiracular openings 21

– Interspiracular ornamentation cone-shaped between posterior pair of spiracular openings 23

21 Tip of anal segment with a pair of long tapering projections; posterior respiratory process black or dark brown; bark-coloured larva .. *Dasysyrphus*
ARBOREAL APHIDS

– Tip of anal segment without long projections; posterior respiratory process pale brown; green or white and brown larva 22

22 Larva sub-triangular in cross-section; white and brown; more than half length of the spiracular openings extending over the sides of the posterior respiratory process .... *Leucozona*
APHIDS ON GROUND LAYER PLANTS AND SHRUBS

– Larva flattened in cross-section, green; less than half length of the spiracular openings extending over the sides of the posterior respiratory process .... *Epistrophe*
ARBOREAL APHIDS

23 Posterior respiratory process pale-brown about as long as broad and with an orange basal rim; spiracular openings black-lined; dorsal spurs only weakly indicated, not taller than spiracular openings .... *Meliscaeva auricollis*
APHIDS ON SHRUBS AND TREES

– Not entirely as above 24

24 A transverse row of four setae behind posterior respiratory process; dorsal spurs as tall as or taller than basally broad; larva 6–8 mm long ..... *Paragus*
GROUND LAYER APHIDS

– Transversae row of setae behind posterior respiratory process absent; dorsal spurs broader than tall; larva and puparium more than 8 mm long 25

25 Tip of anal segment with a pair of short, rounded projections ..... *Chrysotoxum*
ROOT APHIDS IN ANT NESTS

– Tip of anal segment without rounded projections 26

26 Larva coated in pointed spicules 27

– Larva coated in dome-shaped papillae 28

27 Larva without mid-dorsal whitish stripe; spicules grouped into patches on dorsal surface .... *Eupeodes (Metasyrphus)*
PINE TREE APHIDS, SOME SPECIES ON A WIDER RANGE OF APHIDS

– Larva with mid-dorsal whitish stripe; spicules even in distribution on dorsal surface .... *Scaeva*
PINE TREE APHIDS, SOME SPECIES ON A WIDER RANGE OF APHIDS

28 Sides of the abdomen of larva serrate; tip of anal segment viewed from above transverse, cut straight across .... *Meligramma*
APHIDS ON SHRUBS AND TREES

– Sides of the abdomen of larva not serrate; tip of anal segment rounded when viewed from above 29

29 Posterior respiratory process broader than long or about as long as broad; spiracular openings more than 6 × as long as broad; larva with three pairs of lobes at tip of anal segment and deep grooves dorsally .... *Syrphus*
WIDE RANGE OF APHIDS

– Posterior respiratory process longer than broad; spiracular openings less than 6× as long as broad; larva with one or two pairs of lobes at tip of anal segment and no deep grooves 30

30 In profile posterior respiratory process continuously broadening towards base; abdomen of larva widening towards posterior respiratory process and sub-triangular in cross-section .... *Melangyna*
MOSTLY ARBOREAL APHIDS

– In profile, posterior respiratory process with straight sides towards base; abdomen of larva equally narrow at anterior and posterior ends and oval or sub-cylindrical in cross-section .... *Parasyrphus*
APHIDS ON SHRUBS AND TREES

FINAL DISCUSSION

Previous systematic work on Syrphidae has rarely used larval characters or cladistic methods. However, Rotheray & Gilbert (1989) found larval characters and cladistic methods particularly helpful in resolving generic-level relationships among the Syrphinae (*sensu* Vockeroth & Thompson, 1987), a biologically well-defined group of predators of soft-bodied Homoptera. Larval characters are again the focus in this broader analysis of about 65% of palaearctic syrphid genera.

There are potential pitfalls in analysing some but not all genera (although even all extant genera are but a subset of all the branches of the evolutionary tree). Lack of knowledge and material prevented us from dealing with larvae from biogeographic regions other than the Palaearctic, which may include more basal taxa, and this may make identification of plesiomorphic character states associated with shifts in syrphid nodes unreliable. Furthermore, it is possible that the Syrphidae are paraphyletic. Without including the Schizophora, larval synapomorphies for the Syrphidae may be invalid if they belong to the groundplan of the Schizophora. Without better knowledge of plesiomorphic character states and the monophyly of the Syrphidae, we only point out the more striking morphological changes associated with shifts across the Syrphidae. Despite these restrictions, and based on a limited exploration of syrphid larvae from other regions and Schizophora larvae, we believe that the major features of the tree are unlikely to change.

Differences between the various phylogenetic schemes proposed for the Syrphidae are often because the various ancestral groups that have been selected affect the putative direction of evolution. For example Borisova (1984) suggested the existence of two lines of evolutionary changes, one aquatic and one terrestrial, from her choice of the chrysogasterines as the root taxon; Hartley (1963) decided that the eristalines were primitive, and thought that the rest could be derived from this group, but not the reverse; Roberts (1971) made a detailed analysis of larval mouthparts, and suggested that the eristalines were more derived than *Eumerus* and *Syrphus*. In our cladistic study, an outgroup was used to root the tree, and the results support Roberts' (1971) interpretation and the evolutionary relationships proposed by Krüger (1926). Differences between the phylogeny presented here and a previous version (Gilbert *et al.*, 1994) are mainly due to the discovery of the larva of *Volucella inflata*. With the inclusion of this taxon, entomophagy and saprophagy appear to have single origins, both within the current genus *Volucella*. We are currently investigating further the polyphyly of *Volucella*, which requires analysis of additional character sets from adults and from other taxa such as *Copestylum* and *Graptomyza*, to which they appear to be related (Thompson, 1972; Whittington, 1992).

A feature of the phylogeny is that taxa appear in sequences according to feeding mode. At the base are mycophages and phytophages. All remaining syrphid taxa are in one of two sequences comprising entomophages or saprophages. Possibly these sequences result more from homoplasy due to shared feeding modes than to a process of evolutionary diversification. However, shifts within feeding modes are characterized by well marked trends toward morphological complexity, with succeeding nodes frequently incorporating and/or elaborating on change from previous nodes, with few reversals or losses. Such trends are unlikely if homoplasy accounts for our results. Furthermore, adult stages within feeding modes are often similar, an unlikely situation under homoplasy rather than evolutionary diversification.

An improved classification was not the main aim of our study. However, despite the probability that inclusion of non-palaearctic taxa will alter the tree, some conclusions can be drawn. (Vockeroth & Thompson, 1987) divide Syrphidae into three subfamiles of which one, the Eristalinae, is polyphyletic in our scheme. The other two, the Microdontinae and Syrphinae, are sister-taxa. The position of these two groups has been problematic. Some authors treat them as separate subfamilies (Hull, 1949; Coe, 1953; Vockeroth & Thompson, 1987), and others discuss raising Microdontinae to familial rank (Speight, 1987; Thompson, 1972). Larval characters offer no support at all for these proposals.

One reason *Microdon* is problematic is the apparently highly derived form of both larval and adult stages, making them superfically difficult to relate to other groups. However, as found by Krüger (1926), detailed morphological study reveals similarities. For example in larvae, a contracted anal segment and a role in locomotion involving this segment, reduction of mandibles, and a narrowing of the thorax, all originate at node **164**, as is apparent from *Ferdinandea and Rhingia*. On the basis of anatomical and external characters, Krüger (1926) suggested that *Microdon* originated from a *Rhingia*-like form, and the predatory syrphines were derived from *Microdon*. This mirrors the sequence of our final phylogeny (Fig. 6).

Few authors have considered raising clade **120** (Pipizini + Syrphinae) to family level, yet according to Figure 6, this sequence is the sister group to *Microdon*. Most of the apparently innovative features in clade **120** appear to be simply modified from plesiomorphic conditions in *Microdon*. For example the apomorphic structure of the anal segment with its transverse bar and transverse folds can be derived from the extra fold bearing sensilla 7 first appearing in *Microdon*. The changes in the head skeleton and thorax are most parsimonously viewed as developments from characters originating in *Volucella*, with intermediate states in *Microdon*. Thus larval characters support the idea that *Microdon* belongs to the Syrphidae and that clade **120** is derived from it.

In addition to *Volucella*, our results suggest that *Cheilosia* is not monophyletic. As more larvae are studied, synapomorphies may be found and it is possible that *Cheilosia* will be shown to be monophyletic, like the aphidophage sequence of clade **120**. The generic limits of *Lejogaster* and allied genera are dealt with by Maibach *et al.* (1993), but evolutionary relationships between them have not been investigated.

A particularly plesiomorphic set of species within the basal syrphid taxon, *Eumerus*, may occur in South Africa (Hull, 1964; de Moor, 1973). In particular the fauna includes many small species in the Karooid and semi-arid areas of the southern and western Cape, where the larvae may develop in aloes (Liliaceae) and similar plants (A.E. Whittington and B. Stuckenberg, pers. comm.). By analogy with size relationships within the tree, small size is likely to be plesiomorphic within *Eumerus*, and the morphology of the larvae of these particular species may shed more light on the origin of the family.

In support of this possibility are studies of Afrotropical *Merodon*, a taxon very close to *Eumerus* (Fig. 6). The most plesiomorphic *Merodon* come from South Africa and, northwards towards the Mediterranean, species become more apomorphic (W. Hurkmans. pers. comm.). These plesiomorphic *Merodon* species probably arose in South Africa during the Oligocene or Miocene, and reached Europe after closure of the Tethys Sea, after which species radiated rapidly, accounting for the relative richness of species in the Mediterranean area (W. Hurkmans pers. comm.). *Eumerus* has a similar pattern of species richness within Africa and Europe and a similar history of diversification is probable.

Across the Aschiza, morphological diversification of larval stages is unusually extensive. The trend towards increasing independence of groups of muscles, shown by folds and grooves, appears to underlie these developments. Folds and grooves may be key innovations conferring performance advantages and modifying the selective regime at each stage in their development. If so, their elaboration can explain much of the evolution of the Aschiza. After schizophoran larvae have been included in this scheme, they may well support the hypothesis that the Aschiza is monophyletic. Terminating this trend, the syrphid body form has attained an evolved condition of great manoeuvrability, enabling individual segments, parts of segments and groups of segments to develop independently of one another. These changes, correlated with developments in mouthparts and integumental armature consisting of a wide variety of hooks and spines appear to explain much of the direction and extent of evolution within syrphid larval stages.

ACKNOWLEDGEMENTS

A large number of people have assisted our study of syrphid larvae. We are particularly grateful to Drs Colin Hartley, Christian Kassebeer, Alain Maibach, Chris Maier, Alan Stubbs, Chris Thompson, W. Waitzbauer and Andy Whittington for loaning or giving us larvae to study. We are also grateful to the following individuals for arranging loans of material from their institutional collections: Beverley Holloway (New Zealand Department of Scientific and Industrial Research: Arthopod Collection) for a loan of syrphid larvae; K.C. McGiffen (Center for Biodiversity, Illinois Natural History Survey) for a loan of syrphid larvae; Chris Thompson (Systematic Entomology Laboratory, Smithsonian Institution) for a loan of syrphid larvae; and Nigel Wyatt (Natural History Museum, London) for a loan of pipunculid, phorid, platypezid and syrphid larvae. We thank especially Chris Thompson for helpful discussions at various times. Translations from German were done by FSG with help from Hilary Gilbert, for which we are very grateful; we would like also to thank Valeri Mutin for translating Russian papers. We are particularly pleased to acknowledge the time and interest shown by Colin Hartley, whose pioneering studies of hoverfly larvae were an inspiration to us.

REFERENCES

Akre, RD, Sehlke G, Zack RS. 1985. Chemical mimicry by *Microdon* larvae (Diptera, Syrphidae). *Proceedings of the Washington State Entomological Society* **47:** 754–755.

Albrecht, A. 1990. Revision, phylogeny and classification of the genus *Dorylomorpha* (Diptera, Pipunculidae). *Acta Zoologica Fennica* **188:** 1–240.

Barr, B. 1994. Feeding behaviour and mouthpart structure of larvae of *Microdon eggeri* and *Microdon mutabilis* (Diptera, Syrphidae). *Dipterists Digest* **2:** 31–36.

Blackith, RE, Blackith RM. 1989. Diptera reared from decaying potatoes in Ireland. *Irish Naturalists' Journal* **23:** 71–72.

Bloomfield, EN. 1897. Habits of *Sericomyia borealis* Fln. *Entomologist's Monthly Magazine* **8:** 222–223.

Borisova, VG. 1984. [Two branches in the evolutionary development of syrphid flies]. In 'Studies on the evolution and phylogeny of Diptera'. *Sbornik nauchnykh trudov, M., Ivanovskoe Otdeleniye MOIP* **126:** 18–20 (in Russian).

Boyes, JW, van Brink JM, Boyes BC, Vockeroth JR. 1980. Chromosomes of Eristalinae and Microdontinae (Diptera: Syrphidae). *Miscellaneous Publications of the Genetics Society of Canada* **3:** 1–137.

Brauer, F. 1883. Die Zweiflügler des Kaiserlichen Museums zu Wien. III. [The Diptera of the Kaiser Museum in Vienna. III.] *Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematische-Naturwisschaftiche Klasse* **47:** 1–100 (in German).

Brauer, F. 1891. Die Familien der Diptera. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*. (See Osten-Sacken CR. 1904. *Record of my life work in entomology*. reprinted EW Classey, 1978, page 164).

Brunel, E, Cadou D. 1994. Syrphid larvae (Diptera, Syrphidae) mining the roots of artichoke (*Cynara scolymus* L.) in Brittany. *Dipterists Digest* **1:** 69–71.

Burke, HE. 1905. Black Check in Western Hemlock. *U.S.D.A. Bureau of Entomology. Circular No. 61,* 1–10.

Chandler, AEF. 1969. Locomotory behaviour of first instar larvae of aphidophagous Syrphidae (Dipt.) after contact with aphids. *Animal Behaviour* **17:** 673–678.

Chandler, PJ. 1978. Associations with Plants, Fungi, etc. *The Amateur Entomologist* **15:** 199–211. (*A Dipterist's Handbook*, edited by Stubbs, A. and Chandler, P. The Amateur Entomologist's Society).

Coe RL. 1938. Rediscovery of *Callicera yerburyi* Verrall (Diptera: Syrphidae); its breeding habits, with a description of the larva. *The Entomologist* **71:** 97–102.

Coe, RL. 1942. *Rhingia campestris* Meigen (Dipt., Syrphidae) an account of its life-history and descriptions of the early stages. *Entomologist's Monthly Magazine* **78:** 121–130.

Coe, RL. 1953. *Diptera, Syrphidae. Handbooks for the Identification of British Insects*, Vol. 10(1). Royal Entomological Society, London.

Creager, DB, Spruijt FJ. 1935. The relation of certain fungi to larval development of *Eumerus tuberculatus* Rondani (Syrphidae, Diptera). *Annals of the Entomological Society of America* **28:** 425–437.

Davidson, WM. 1992. Notes on certain species of *Melanostoma* (Diptera; Syrphidae). *Transactions of the Entomological Society of America* **48:** 35–47.

DeCleer, K, Rotheray GE. 1990. The puparium and larval habitat of the hoverfly *Tropidia scita (Diptera: Syrphidae)*. *Entomologist's Gazette* **41:** 157–160.

Disney RHL. 1994. *Scuttle Flies: The Phoridae.* London: Chapman and Hall.

Dittrich W, Gilbert F, Green P, McGregor P, Grewcock, D. 1993. Imperfect mimicry: a pigeon's perspective. *Proceedings of the Royal Society of London* **B251:** 195–200.

Dixon, TJ. 1959. Studies on oviposition behaviour of Syrphidae (Diptera). *Transactions of the Royal Entomological Society of London* **111:** 57–80.

Dixon, TJ. 1960. Key to and descriptions of the third instar larvae of some species of Syrphidae (Diptera) occurring in Britain. *Transactions of the Royal Entomological Society of London* **112:** 345–379.

Donisthorpe, H. 1927. *The guests of British ants.* London: Routledge and Son.

Duffield, RM. 1981. Biology of *Microdon fuscipennis*, with interpretations of the reproductive strategies of *Microdon* species North of Mexico. *Proceedings of the Entomological Society of Washington* **83:** 716–724.

Dušek, J, Láska P. 1967. Versuch zum Aufbau eines natürlichen Systems mitteleuropäischer Arten der Unterfamilie Syrphinae (Diptera). [Search for the structure of a natural system for the central European species of the subfamily Syrphinae (Diptera).] *Acta Scientiarum Naturalium Brno* **1:** 349–390 (in German).

Ferrar P. 1987. A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha. *Entomonograph* **8:** parts 1 & 2.

Garnett WB, Akre RD, Sehlke E. 1985. Cocoon mimicry and predation by myrmecophilous Diptera (Diptera: Syrphidae). *Florida Entomologist* **68:** 615–621.

Gilbert F. 1993. *Hoverflies.* Naturalist's Handbooks, No. 5. London: Richmond Press.

Gilbert F. Rotheray G, Emerson P, Zafar R. 1994. The evolution of feeding strategies. In Eggleton P, Vane-Wright R, eds. *Phylogenetics and Ecology, Linnean Society Symposium Series No. 17.* London: Academic Press 323–333.

Glumac S. 1958. The structure of the male genitalia of certain species of flowerflies (Syrphidae: Diptera) and their significance in phylogenetical classification. *Glasnik Prirod Muzeja Srpske Zemlje, Ser. B Bioloske Nauke* **12:** 99–167.

Glumac S. 1960. Phylogenetic system of the Syrphid-flies (Syrphidae: Diptera) based upon the male genitalia structure and the type of the larvae with characteristics of the family and tribes. *Glasnik prirod Muzeja Srpske Zemlje, Ser. B Bioloske Nauke* **16:** 69–103.

Glumac S. 1980. Effect of larval biology on the process of speciation in the group Syrphoidea (Diptera). *Zbornik radova Prirodno-matematickog fakulteta-Univerzitet u Novom Sadu* **10:** 417–422.

Glumac S, Vujic A. 1990. Some views on the Syrphidae phylogeny. *Abstracts of the 2nd International Congress of Dipterology*, Bratislava.

Goffe ER. 1952. An outline of a revised classification of the Syrphidae (Diptera) on phylogenetic lines. *Transactions Society British Entomology* **11:** 97–124.

Grieg C. 1989. Overwintering behaviour of the larva of *Myathropa florea* L. (Diptera: Syrphidae). *Dipterists Digest* **No. 2:** 11–16.

Hartley JC. 1958. The root-piercing spiracles of the larva of *Chrysogaster hirtella* Loew (Diptera: Syrphidae). *Proceedings Royal Entomological Society of London (A)* **33:** 81–87.

Hartley JC. 1961. A taxonomic account of the larvae of some British Syrphidae. *Proceedings of the Zoological Society of London* **136:** 505–573.

Hartley JC. 1963. The cephalopharyngeal apparatus of syrphid larvae and its relationship to other Diptera. *Proceedings of the Zoological Society of London* **141:** 261–280.

Heeger E. 1858. Neue Metamorphosen einiger Dipteren. [New metamorphoses of some Diptera.] *S. B. Akademie für Wissenschaft Wien* **31:** 295–309 (in German).

Hellrigl K. 1992. Die Fichtenharzfliege *Cheilosia morio* Zett. (Dipt., Syrphidae) als physiologischer Schädling an Fichten in Südtirol. [On the Spruce-resin fly *Cheilosia morio* Zett. (Dipt., Syrphidae), a physiological pest of Spruce in South Tyrol.] *Anzeiger Schädlingskund für Pflanzenschutz und Umweltschutz* **65:** 33–36 (in German).

Hippa H. 1968. A generic revision of the genus *Syrphus* and allied genera (Diptera, Syrphidae) in the Palaearctic region, with descriptions of the male genitalia. *Acta Entomologica Fennica* **25:** 1–94.

Hippa H. 1990. The genus *Milesia* Latreille (Diptera, Syrphidae). *Acta Zoologica Fennica* **187:** 1–226.

Hodson WEH. 1932. A comparison of the larvae of *Eumerus strigatus* Fln., and *Eumerus tuberculatus* Rond. (Syrphidae). *Bulletin of Entomological Research* **23:** 247–249.

Hövemeyer K. 1987. The population dynamics of *Cheilosia fasciata* (Diptera: Syrphidae): significance of environmental factors and behavioural adaptations in a phytophagous insect. *Oecologia* **73:** 537–542.

Hövemeyer K. 1995. Trophic links, nutrient fluxes and natural history in the *Allium ursinum* food web, with particular references to life history traits of two hoverfly herbivores (Diptera: Syrphidae). *Oecologia* **102:** 86–94.

Hull FM. 1949. The morphology and inter-relationships of the genera of Syrphid flies, recent and fossil. *Transactions of the Zoological Society of London* **26:** 257–408.

Hull FM. 1964. Diptera (Brachycera): Syrphidae. *South African Animal Life* **10:** 442–496.

Jervis MA. 1980. Studies on oviposition behaviour and larval development in species of *Chalarus* (Diptera, Pipunculidae), parasites of typhlocybine leafhoppers (Homoptera, Cicadellidae). *Journal of Natural History* **14:** 759–768.

Kessel EL, Buegler ME, Keyes PM. 1973. A survey of the known larvae and puparia of Platypezidae, with a key to ten genera based on immature stages (Diptera). *Wasmann Journal of Biology* **31:** 233–261.

King DG. 1991. The origin of an organ: phylogenetic analysis of evolutionary innovation in the digestive tract of flies (Insecta: Diptera). *Evolution* **45:** 568–588.

Krivosheina NP, Mamaev BM. 1967. [Identification of larvae of dipterous insects inhabiting forests]. 'Nauka', 362pp (in Russian).

Krüger F. 1926. Biologie und Morphologie einiger Syrphidenlarven. [Biology and morphology of some syrphid larvae.] *Zeitschrift für Morphologie und Okologie der Tiere* **6:** 83–149 (in German).

Kuznetsov SYu. 1987. [On some plesiomorphic characters of aphidophagous larvae of hoverflies in the subfamily Syrphinae (Diptera, Syrphidae)]. In Narchyk EP. ed. *Dipterous insects: systematics, morphology and ecology*. Leningrad: Zoological Institute, USSR Academy of Sciences (in Russian) 758–61.

Lioy P. 1864. I Ditteri distribuiti secondo un nuovo metodo di Classificazione naturale (Syrphidi). [The Diptera organised according to a new method of natural classification (Syrphids).] *Atti dell' Instituto Veneto di Scienze, Lettere ed Arti Venezia* **9:** 738–760 (in Italian).

Lundbeck W. 1927. *Diptera Danica 7. (Platypezidae)*. Copenhagen: GEC Gad.

MacGowan I. 1994. Creating breeding sites for *Callicera rufa* Schummel (Diptera, Syrphidae) and a further host tree. *Dipterists' Digest* **1:** 6–8.

Maki T. 1935. Anatomical studies of alimentary canals and their appendages in syrphid flies. *Transactions of Natural History, Formosa* **25:** 379–391.

Maibach A, Goeldlin de Tiefenau P, Speight MCD. 1994. Limites génériques et caractéristiques taxonomiques de plusieurs genres de la tribu de Chrysogasterini (Diptera: Syrphidae). 1. Diagnoses génériques et description de *Riponnensia* **gen. nov.** [Generic limits and taxonomic characterisation of several genera of the tribe Chrysagasterini (Diptera: Syrphidae). 1. Generic diagnosis and description of *Riponnensia* gen.nov.]. *Annales de la Société Entomologique de France* **30:** 217–247 (in French).

Maier CT. 1982. Larval habitats and mate-seeking sites of flower flies (Diptera: Syrphidae, Eristalinae). *Proceedings of the Entomological Society of Washington* **84:** 603–609.

Maier CT. 1987. New distributional and rearing records for Neotropical flower flies (Diptera, Syrphidae). *Proceedings of the Entomological Society of Washington* **89:** 369.

Matile L, Leclercq M. 1992. Répartition en France de *Milesia crabroniformis* (F.) and et *semiluctifera* (Villers), et description de la pupe et des pièces buccales larvaires de *M. crabroniformis* (Dipt. Syrphidae Milesiinae). [Distribution in France of *Milesia crabroniformis* (F.) and *semiluctifera* (Villers), and description of the pupa and larval mouthparts of *M. crabroniformis* (Dipt. Syrphidae Milesiinae).] *Entomologica Gallica* **3:** 101–105 (in French).

McAlpine JF. 1989. Phylogeny and Classification of the Muscomorpha. In: McAlpine JF, Wood DM, eds. *Manual of Nearctic Diptera* Vol. 3: 1397–1502 Monograph No. 32, Research Branch, Agriculture Canada.

Melzer RR, Paulus HF. 1989. Evolutionswege zum Larvalauge der Insekten – Die Stemmata der höheren Dipteren und ihre Abwandlung zum Bolwigs-Organ. [Evolutionary pathways to the larval eyes of insects. Higher Dipteran stemmata and the evolutionary development of Bolwig's organ.] *Zeitschrift für zoologische Systematik und Evolutionsforschung* **27:** 200–245 (in German).

Metcalf CL. 1913. Syrphidae of Ohio. *Ohio State University Bulletin* **31:** 1–123.

Metcalf CL. 1916. Syrphidae of Maine. *Bulletin Maine Agricultural Experimental Station* **No. 253:** 1–264.

Metcalf CL. 1921. The genitalia of male Syrphidae: their morphology, with especial reference to its taxonomic significance. *Annals of the Entomological Society of America* **14:** 169–226.

de Moor FC. 1973. Notes on a syrphid fly, *Eumerus obliquus* (Fabricius) (Diptera: Syrphidae). *Arnoldia* **6(15):** 1–7.

Roberts MJ. 1970. The structure of the mouthparts of syrphid larvae (Dipt.) in relation to feeding habits. *Acta Zoologica* **51:** 43–65.

Roberts MJ. 1971. On the locomotion of cyclorrhaphan maggots (Diptera). *Journal of Natural History* **5:** 583–590.

Rohdendorf, BB. 1974. *The historical development of Diptera.* In: Hocking B, Oldroyd H, Ball GE, eds. Edmonton, Canada: University of Alberta Press.

Rotheray GE. 1983. Feeding behaviour of *Syrphus ribesii* and *Melanostoma scalare* on *Aphis fabae. Entomologica experimentalis et applicata* **36:** 17–21.

Rotheray GE. 1986. Colour, shape and defence in aphidophagous syrphid larvae (Diptera). *Zoological Journal of the Linnean Society* **88:** 201–216.

Rotheray GE. 1987. Larval morphology and searching efficiency in aphidophagous syrphid larvae. *Entomologica experimentalis et applicata* **43:** 49–54.

Rotheray GE. 1988a. Larval morphology and feeding patterns of four *Cheilosia* species (Diptera: Syrphidae) associated with *Cirsium palustre* L. Scopoli (Compositae) in Scotland. *Journal of Natural History* **22:** 17–25.

Rotheray GE. 1988b. Morphology and feeding behaviour of the leaf-mining larva of *Cheilosia semifasciata* (Diptera: Syrphidae). *Journal of Natural History* **22:** 865–873.

Rotheray GE. 1990. The relationships between feeding mode and morphology in *Cheilosia* larvae (Diptera, Syrphidae). *Journal of Natural History* **24:** 7–19.

Rotheray GE. 1991. Larval stages of 17 rare and poorly known British hoverflies (Diptera: Syrphidae). *Journal of Natural History* **25:** 945–969.

Rotheray GE. 1993. Colour Guide to Hoverfly larvae (Diptera, Syrphidae) in Britain and Europe. *Dipterists Digest* **No. 9:** 1–155.

Rotheray GE, Gilbert FS. 1989. The phylogeny and systematics of European predacious Syrphidae (Diptera) based on larval and puparial stages. *Zoological Journal of the Linnean Society* **95:** 29–70.

Rotheray GE, MacGowan I. 1990. Re-evaluation of the status of *Callicera rufa* Schummel (Diptera: Syrphidae) in the British Isles. *The Entomologist* **109:** 35–42.

Rotheray GE, Perry I. 1994. The larva of *Callicera spinolae* with a key to the larvae of British *Callicera* species (Diptera, Syrphidae). *The Entomologist* **113:** 205–210.

Rupp L. 1989. Die mitteleuropäische Arten der Gattung *Volucella* (Diptera, Syrphidae) als Kommensalen und Parasitoide in den Nestern von Hummeln und sozialen Wespen: Untersuchungen zur Wirtsfindung, Larvalbiologie und Mimikry. [The mid-European species of *Volucella* (Diptera, Syrphidae) as commensals and parasitoids in the nests of bees and social wasps: studies on host finding, larval biology and mimicry.] Unpublished PhD Thesis, Albert Ludwigs Universität, Freiburg, Germany.

Schneider F. 1969. Bionomics and physiology of aphidophagous Syrphidae. *Annual Review of Entomology* **14:** 103–124.

Shatalkin AI. 1975a. [Taxonomic analysis of hoverflies (Diptera, Syrphidae). I.]. *Entomologicheskoe Obozreniye* **54:** 164–175 (translated in Entomological Review, Washington).

Shatalkin AI. 1975b. [Taxonomic analysis of hoverflies (Diptera, Syrphidae). II.]. *Entomologicheskoe Obozreniye* **54:** 899–909 (translated in Entomological Review, Washington).

Southwood TRE. 1973. The insect/plant relationship—an evolutionary perspective. *Symposium Royal Entomological Society of London* **6:** 3–30.

Speight MCD. 1986. *Portevinia maculata*: last instar larva and puparium, with notes on the relationship between this hoverfly and its larval hostplant, *Allium ursinum* (Dipt., Syrphidae). *Nouvelles Revue Entomologie* **3:** 37–43.

Speight MCD. 1987. External morphology of adult Syrphidae (Diptera). *Tijdschrift voor Entomologie* **130:** 141–175.

Strong, DR, Lawton, JH, Southwood, TRE. 1984. *Insects on Plants: Community Patterns and Mechanisms.* Oxford: Blackwell Scientific Publications.

Stubbs AE. 1980. The rearing of *Cheilosia paganus* and *Cheilosia fraterna* (Diptera: Syrphidae). *Entomologists' Record and Journal of Variation* **92:** 114–117.

Teskey HJ. 1976. Diptera larvae associated with trees in North America. *Memoirs of the Entomological Society of Canada* **100:** 1–53.

Thompson FC. 1972. A contribution to a generic revision of the neotropical Milesiinae (Diptera, Syrphidae). *Arquivos de Zoologica, Sao Paulo* **23:** 73–215.

Thompson FC. 1990. Biosystematic information: Dipterists ride the third wave. In Kosztarab M, Schaefer CW, eds. *Systematics of the North American Insects and Arachnids: Status and Needs*. Virginia Agricultural Experiment Station Information Series 90–1, 179–201.

Trägårdh I. 1923. Skogsentomologiska Bidrag II. 1. Grankådflugan. *Chilosia morio* Zett. [Forest entomological contributions. II. The Spruce-resin fly. *Chilosia morio Zett.*]. *Meddelanden från Statens Skogsförsöksanstalt* **20:** 401–408 (in Swedish).

Varley GC. 1937. Aquatic insect larvae which obtain oxygen from the roots of plants. *Proceedings Royal Entomological Society of London (A)* **12:** 55–60.

Vockeroth JR, Thompson FC. 1987. Syrphidae. In McAlpine J *et al.*, eds. *Manual of Nearctic Diptera Vol* **2:** Quebec: Agriculture Canada, 713–743.

Vujic A, Glumac S. 1993. Some views on Syrphidae (Diptera) phylogeny. *Zbornik Matitse Srpske za prirodne nauke, Novi Sad* **84:** 13–17.

Whittington AE, 1992. Revision of the Afrotropical species of *Graptomyza* Wiedemann (Diptera: Syrphidae). *Annals of the Natal Museum* **33:** 209–269.

APPENDIX 1

Larval characters for analysing relationships among syrphid genera

Numbers in parentheses after character states show polarity, mostly based on outgroup comparison—(0) = primitive; (1), (2), (3) = derived. Sometimes when outgroups are unscorable for a particular character, the optimization identifies a different state as primitive; nevertheless, the 0 state represents our best estimate of the plesiomorphic state, independent of the character optimization of PAUP. This will be explored in more detail in a future comparison of nematoceran, aschizan, and cyclorrhaphan taxa. To identify transitions we use either taxon names or the node numbers of Figure 6; for example, '**120**' means all the taxa derived from node 120 possess the described character state. The name 'pipizines' is used as a convenient label for refering to taxa derived from node **121**, and the 'syrphines' is used to refer to all taxa derived from node **119**. Saprophagous syrphids are all taxa derived from node **163**; entomophagous syrphids are all those derived from node **128**; phytophagous syrphids are all those derived from node **169** (i.e. most of the *Cheilosia*), plus *Merodon*. Mycophagous syrphids are *Eumerus, Cheilosia pagana, Cheilosia* – fungivores, *Ferdinandea* and *Rhingia.*

Head

1. *Head skeleton with sclerotized strips*. In Lonchopteridae a pair of thin sclerotized strips occur anterodorsally from the pharyngeal sclerite (Ferrar, 1987) (0). In all other taxa these strips are absent (1).
2. *Head skeleton developed anteriorly*. At node **126** (*V. inanis*, *Microdon*, pipizines and syrphines) parts of the labial sclerites project forward beyond the base of the mandibles (character *w*, Figs. 14–16) (1). In *V. inanis* the labial sclerites are hooked at the tip and can be projected forward. They are shown in the presumed resting position in Fig. 16A, character *w*. In other taxa the labial sclerites do not project into the mouth (0).
3. *Apices of the mandibles*. In **121** (pipizines), the mandible is quadrate in shape (Fig. 15C, character *g*) (Rotheray & Gilbert, 1989). In outgroups and all other syrphid taxa the mandibles are differently shaped (0).
4. *The extent to which the mandibles protrude from the mouth*. In outgroups, and phytophagous and mycophagous syrphids, hooked mandibles protrude from the mouth (character *g*, Figs 7, 8) (0). At **164** (*Ferdinandea, Rhingia* and *Volucella* species except *inflata*), the mandibles are reduced and barely protrude from the mouth (Fig. 10B) (1). In saprophagous syrphids (**163**) they are further reduced and do not protrude from the mouth (Fig. 11B) (2). At **125** (*Microdon*, pipizines, syrphines), the mandibles can be extended and retracted from the mouth (Fig. 14B) (3).
5. *Head skeleton with pharyngeal ridges*. A series of ridges run from behind the mandibles to the apex of the head skeleton, as part of a mechanism to separate particles of food from the fluid in which they are suspended (Hartley, 1963; Roberts, 1970). Except for platypezids and pipunculids, these ridges are present in outgroups and phytophagous, mycophagous and saprophagous syrphids as well as in *V. bombylans* and *V. pellucens* (0), but are absent in predacious and parasitic taxa deriving from node **126** (1).
6. *The reduction of the mandibular lobes*. The mandibular lobes are attached to the mandibles and consist

of a series of longitudinal ridges (character *h* in the figures). They are not developed in outgroups (Fig. 7). In most mycophagous and phytophagous syrphids they extend from the mouth and coat the lateral margins of the mouth (Figs 8, 9) (0). In mycophagous *Cheilosia*, *Ferdinandea* and *Rhingia* (**166**) they partially coat the lateral margins outside the mouth (Fig. 10b) (1), and in saprophagous and some entomophagous syrphids (**129**) they do not appear over the lateral margins of the mouth (Fig. 11B) (2). (Unscorable in pipizines and syrphines, i.e. **120**.)

7. *Size of the mandibular lobes inside the mouth*. In all non-entomophagous syrphids the mandibular lobes coat the entire inside of the mouth (Fig. 11B) (0). In *V. bombylans* and *V. pellucens* (**128**) the mandibular lobes are reduced to a short series of ridges (Fig. 13B, C) (1), and from **126** (*V. inanis, Microdon*, pipizines and syrphines) the mandibular lobes are further reduced or are absent (Fig. 16A) (2).
8. *Extent of sclerotization of the mandibular lobes*. In mycophagous, phytophagous and saprophagous syrphids the mandibular lobes are fleshy and little sclerotized (Fig. 8) (0). From **128** (*V. bombylans, V. inanis* and *V. pellucens*) the ridges and tips of the mandibular lobes are sclerotized (Fig. 13) (1). In some *Cheilosia* (**169**) and *Microdon* (**125**) the mandibular lobes are fully sclerotized (Fig. 9) (2); from **120** this character is not scorable.
9. *Fusion of the mandibular lobes with the mandibles*. In some *Cheilosia* (**169**) the mandibular lobes are fused with the mandibular apodeme (Fig. 9) (1). From **125** (*Microdon*, pipizines and syrphines) the mandibular lobes are fused with the mandibular sclerite (Fig. 14C) (2). In other syrphids the mandibular lobes are not fused with the mandibles (Fig. 8) (0).
10. *Mandibular lobes with apical hooks*. From **128** (*Microdon, Volucella* species except *inflata*: [unscorable in pipizines and syrphines]), the longitudinal ridges of the mandibular lobes bear a series of hooks at their apices (Fig. 13) (1). In all other syrphids including *V. inflata* these hooks are absent (Figs 8, 12) (0).
11. *Size of papilla supporting antennomaxillary organs*. The antennomaxillary organs are sited between the mouth and the prothorax and consist of two pairs of light-brown, oval-shaped structures tipped with sensilla. Each pair is borne on a fleshy basal papilla of varying size and shape: papilla broader than tall (Fig. 8A) (0); papilla as tall as broad (1); papilla taller than broad (2). The papilla became relatively longer at **172**, and again at **163** and independently in *Microdon*.
12. *Shape of papilla supporting antennomaxillary organs*. Papilla supporting each pair of antennomaxillary organs consist either of one section (Fig. 8A) (0) (most taxa up to **166**), two sections (Fig. 11) (1) (*Portevinia, Cheilosia morio, Cheilosia-fungivores, Ferdinandea*), or three sections (Fig. 12) (2) (all other taxa above **166**).
13. *Basal section of papilla supporting antennomaxillary organs divided*. In long-tailed larvae from **135** (*Eristalis, Helophilus* etc) and also in *Temnostoma*, the basal section of the papilla supporting each pair of antennomaxillary organs is divided to the base (Fig. 12) (1). In other taxa with two-section papilla, the basal section is not divided, or not divided fully to the base (0).
14. *Setae on dorsal lip*. The dorsal lip is sited between the mouth and the antennomaxillary organs (character *f* in figures). It is not developed in outgroups. in syrphids it may be coated with non-sclerotized setae (Fig. 8) (0); or setae may be absent (Fig. 9) (1); or it may be coated in spicules (sclerotized setae) (Fig. 13) (2). Many changes seem to have occurred in this character during evolution, but one unified grouping occurs among most of the entomophages (from **120**), which have no setae.
15. *Ventral groove in dorsal lip*. In all entomophagous syrphids (from **128**), the dorsal lip has a ventral groove (Figs 13–15) (1); a ventral groove is lacking in other syrphid taxa (Fig. 11) (0).
16. *Size of ventral lip in relation to mouth*. The ventral lip is an oval-shaped organ which lies over the mouth when it is shut (character *j* in figures). The ventral lip is more restricted in its movement than the dorsal lip. Usually, the dorsal lip overhangs the ventral lip. The mouth opens when the dorsal lip moves up. When the dorsal lip moves down, the ventral lip at the base of the mouth closes over the opening. The size of the ventral lip varies in relation to the mouth. In outgroups, mycophagous and phytophagous taxa it is poorly developed or smaller than the mouth (Fig. 8) (0). In saprophages (from **163**) it is as broad as the mouth (Fig. 12) (1), but in entomophagous taxa (from **128**) it is developed and broader than the mouth (Fig. 13) (2).

Thorax

17. *Number of sensilla on the dorsum of the prothorax*. In outgroups, no more than 2 pairs of sensilla are present on the dorsum of the prothorax (0). In all syrphids (i.e. from **173**), more than 2 pairs of sensilla are present (Fig. 2) (1).

18. *Longitudinal grooves on the dorsum of the prothorax*. In all syrphid taxa examined (**173**), longitudinal grooves are present on the dorsum of the prothorax (Fig. 2) (1). In outgroups, the dorsum of the prothorax is usually smooth without longitudinal grooves (0).
19. *Form of tapering of the prothorax*. The dorsum of the prothorax tapers from base to tip in all taxa examined. However in outgroups, the dorsum of the prothorax tapers in a step-like fashion in two stages (0). In all syrphid taxa (**173**) it tapers smoothly in one stage (1).
20. *Contracted thorax*. In *Temnostoma* the thorax is contracted, as shown by the length of the mesothorax and metathorax, each shorter than the length of the first abdominal segment (Fig. 22C) (1). In all other taxa, the metathorax and mesothorax are about as long or longer than the first abdominal segment (0).
21. *Setae on dorso-lateral margin of thorax*. In the *Cheilosia morio* group, the lateral margin of the thorax has a row of long setae (1). In other taxa there is no row of setae on the lateral margin of the thorax (0).
22. *Pairs of projections on the anterior margins of each segment of the thorax*. In *Microdon* the antero-dorsal margins of each segment of the thorax are divided and bear a pair of fleshy projections (Fig. 14A, B) (1). These projections overlap one another when the thorax is contracted, and protect the underlying structures. In other taxa such projections are absent (0).
23. *Length of folds on dorsum of thorax*. In *Sericomyia* the longitudinal folds on the dorsum of the prothorax extend posteriorly across the mesothorax and the metathorax (1). In other syrphid larvae these folds end on the prothorax (0).
24. *Setae accompanying ventral sensilla of metathorax*. From **93** (*Paragus*, *Eupeodes*, *Scaeva* and *Ischiodon*), sensilla pairs 7, 9 and 10 have apical setae (1). These are lacking in all other taxa (0).
25. *Antero-ventral margin of metathorax*. In most taxa, the antero-ventral margin of the metathorax anterior to sensilla pair 6 has no spicules (0). In many saprophagous larvae, it has a band of spicules (also in *V. bombylans*) (1); or a patch of spicules (2).
26. *Absence of a coating of micro-setae on the integument (= vestiture) of the mesothorax anterior of sensilla pair 5*. In syrphid larvae, longitudinal grooves are present along the lateral margins of the mesothorax and metathorax (Fig. 2). On the anterior part of the fold bearing sensilla 5 of the mesothorax, only setae are usually present (Fig. 20A) (0). In many saprophagous taxa (*V. inflata* and most **156**), setae and spicules occur (Fig. 20D) (1); or (*Tropidia*, and most **143**) setae, spicules and one or more hooks (Fig. 21) (2). In a few taxa (**149**: i.e. *Criorhina, Temnostoma, Callicera*) this part of the fold is smooth, without vestiture (Fig. 22D) (3).
27. *Vestiture of mesothorax anterior of sensilla pair 4*. In syrphid larvae, longitudinal grooves are present along the lateral margins of the mesothorax and metathorax. On the anterior part of the fold bearing sensilla 4 of the mesothorax, setae are usually present (0). In many saprophagous taxa (*V. inflata* and most from **156**), setae and spicules may be present (1); finally (*Tropidia*, and **143**) setae, spicules and one or two hooks may be present (2). Hooks are sclerotized brown or black, and are larger than surrounding spicules.
28. *Alignment of mesothorax sensilla pairs 1 and 2*. In most hook-bearing syrphids, these sensilla are not aligned. In *Hammerschmidtia* and at **154** (reversing at **137** & *Syritta*), sensilla pair 2 are posterior but about equidistant to 1 & 3 (1); at **143** (reversing in *Milesia*), sensilla pair 2 become posterior and closer to 1 than 3 (2). In other taxa these sensilla are aligned (0).
29. *The extent the mesothorax overlaps the prothorax*. This character is not developed in outgroups. In phytophages, mycophages, *V. bombylans, V. inflata*, and a few other saprophagous taxa, the mesothorax overlaps the prothorax by about 0.33 length of prothorax (view from the side) (0). In other syrphid taxa (**161** and **127**), the lateral margins of the mesothorax overlap the prothorax by more than 0.33 of the length of the prothorax (view larva from side) (1).
30. *Shape of dorsum of mesothorax*. In saprophagous syrphid taxa (**151**, reversed at **137**), the dorsum of the mesothorax bears crescent-shaped folds (Fig. 22A, D) (1). In other taxa (all plesiomorphic taxa and saprophages from **137**), these folds are transverse (0).
31. *Vertical groove dividing mesothorax and metathorax*. In outgroups and most syrphid taxa, the division between the mesothorax and metathorax is present on the lateral margins as an almost continuous vertical groove (Fig. 20) (0). In some hook-bearing taxa (**143**), this vertical groove is weak or absent (Fig. 22) (1).
32. *Small fold linking anterior end of lateral folds on mesothorax*. In some hook-bearing larvae (**147**), a small fold links the anterior ends of the lateral folds bearing sensilla pairs 4 and 5 (Fig. 22) (1). In other taxa this small fold is absent (0).
33. *Inclined fold bearing sensilla pair 4 on the metathorax and mesothorax*. In *Criorhina* this fold is inclined posteriorly (1). In other taxa this fold is aligned with the longitudinal axis of the thorax (0).

34. *Shape of anterior end of fold bearing sensilla pair 4 on the mesothorax*. In some hook-bearing larvae (**147**), this fold tapers anteriorly just behind the hooks (Fig. 22) (1); in other taxa the fold is round-tipped and does not taper (0).
35. *Colour of hooks on thorax in hook-bearing taxa*. In *Brachypalpoides* the thoracic hooks are red (1). In all other taxa with hooks on the thorax they are black (0).
36. *Number of hooks per sclerotized base*. In *Milesia* and *Temnostoma*, more than 5 hooks are present per hook base (Fig. 22A, C) (1); in other hook-bearing larvae less than 5 hooks are present per hook base (0).
37. *Alignment of the sclerotized base to hooks on the thorax*. In *Temnostoma* the longitudinal axis to the sclerotized base is aligned vertically, to the length of the larva (Fig. 22C) (1); in other hook-bearing taxa the sclerotized base is aligned transversely to the length of the larva (0).
38. *Shape of the sclerotized base to hooks on the thorax*. In *Criorhina* the base of the largest group of hooks is either Y or triangular shaped (Fig. 22B) (1); in other hook-bearing taxa the base has other mostly oval shapes (0).
39. *Size of sclerotized base bearing hooks on the thorax*. Thoracic hooks are usually mounted on a sclerotized base which varies in size. The hook base can be small, not as long as the width of one of the lateral folds bearing sensilla 4/5 of the mesothorax and metathorax (0). Alternatively (**147**), the hook base is large, longer than one of these lateral folds (1).
40. *Hooks present on the anterio-dorsal margin of the mesothorax*. In *Tropidia* hooks are present on the anterio-dorsal margin of mesothorax (Fig. 20D) (1). In other taxa hooks are absent on this margin of the mesothorax (0).
41. *Presence of two groups of small hooks (sclerotized base shorter than width of lateral thoracic folds bearing sensilla 4/5)*. At **145** (*Chalcosyrphus* and *Xylotomima*), the thorax bears two separate groups of small hooks, the more dorsal group consisting of two hooks and the lateral group consisting of one hook (Fig. 21A) (1). In other hook-bearing taxa, hooks are arranged differently (0).
42. *Presence of one pair of hooks posterior to sensilla pairs 6 and 7 of the prothorax*. In *Brachypalpus* a single pair of hooks exists at this site (Fig. 21B) (1). In other hook-bearing taxa hooks are arranged differently (0).
43. *Small mid-dorsal hooks between sensilla pairs 2 and 3 on prothorax*. In *Spilomyia* these hooks are present (Fig. 21D) (1); in other hook-bearing taxa they are absent (0).
44. *Presence of hooks on the dorsum of the prothorax*. In *Criorhina* and *Spilomyia*, hooks are present on the dorsum of the prothorax (1); in other taxa hooks like this are absent (0).
45. *Hooks on the anterior fold*. In *Neoascia* a pair of hooks are present on the anterior fold (Fig. 20C) (1); in other taxa hooks are absent from the anterior fold (0).
46. *Apex of the lateral lips sclerotized*. Either side of the mouth on the anterior margin of the prothorax are a pair of ovoid projecting organs, the lateral lips, bearing sensilla groups 9 and 10. From **120** (pipizines and syrphines), the tips of the lateral lips are hook-like and sclerotized (Fig. 15, character *x*) (1). In all other taxa, lateral lips are not sclerotized (0).
47. *Prolegs on mesothorax*. The prolegs are recognizable by the presence of a planta (an indented region at the apex of the proleg corresponding to the point at which muscles are attached), and crochets are usually present (Fig. 12B, character *p*). Crochets are backwardly directed hooks, larger and more sclerotized than surrounding vestiture. No prolegs are present in outgroups, or in phytophagous, mycophagous or most entomophagous syrphids (all except *Volucella*). Prolegs may be small and not delimited by grooves (*V. inflata*) (0); or they are large and surrounded by grooves (1).
48. *Size of crochets on the mesothoracic prolegs*. In *V. inflata* and *V. bombylans*, the crochets are not much longer than surrounding setae and spicules (0). In other syrphid taxa with mesothoracic prolegs, the crochets are larger and conspicuous with surrounding setae and spicules mostly absent (1). This character is variable in *Brachyopa*: in some species, the crochets are hardly distinguishable, but in others they are clearly different, and we have therefore scored it as 1.
49. *Arrangement of crochets on mesothorax*. Crochets may be arranged in a single row (plesiomorphic, *Syritta*) (0), as a double row (**127** and **157**) (1), as more than two rows (**155**) (2), or crochets may be lost (*Temnostoma*) (3).
50. *Retractile anterior spiracles*. In some long-tailed larvae (**135**), the anterior spiracles can be withdrawn into invaginated integumental pockets (Hartley, 1961) (1); in other taxa, the anterior spiracles are not retractile (0).
51. *Height of anterior spiracles*. The plesiomorphic state is for them to be <2 × tall as broad at base (0); at **135**, they become >2 × tall as broad at base (1).

52. *Anterior spiracles in relation to sensilla 1.* These are aligned transversely with sensilla 1 (0); posterior to sensilla 1 (1); or anterior to sensilla 1 (2). The pattern of evolution in this character is complex, perhaps in part due to the fact that outgroups are unscorable, changing the optimization.
53. *Size of ecdysial scar.* Anterior spiracles with ecdysial scar apparently absent (0); scar large and clearly visible (1). The evolution of this character appears to contain little phylogenetic content.
54. *Number of spiracular openings.* The anterior spiracles have up to 5 spiracular openings (0); or (in two *Cheilosia*, the entomophagous *Volucella*, and **141**) more than 5 openings (1).
55. *Absence of anterior spiracles.* The anterior spiracles are generally sited on the posterior part of the prothorax. In outgroups and most syrphid taxa they are present (0), but are sometimes (*V. inflata*, *Microdon* and **159** [chrysogasterines]) reduced or absent (1).
56. *Position of anterior spiracle in relation to fold bearing sensilla 4 & 5.* In most taxa, the anterior spiracle is sited on the outer lateral margin of fold bearing sensilla 4 & 5 (0); in *Callicera*, the anterior spiracle is on inner lateral margin of fold bearing 4 & 5 (1).
57. *Feeding channel behind the mouth.* The mid-ventral region of the prothorax and mesothorax behind the mouth forms a furrow or feeding channel of varying length (character *o* in figures). In phytophagous, mycophagous and entomophagous syrphid taxa it is short and shallow, forming a smooth-lined furrow which may extend to the posterior margin of the prothorax (0). In other taxa it extends to the posterior margin of the mesothorax (Fig. 12) (1); additionally it may be impressed deeply into the mesothorax (2). The optimization predicts that the change occurred from state 0 to state 2 at **161**, being further modified to state 1 at **162** (*Hammerschmidtia & Brachyopa*) and *Syritta*. Logically it might be better to assume that this character is ordered, and that evolutionary changes went from state 0 to state 1 at **161** and then to state 2 at **158**.
58. *Vestiture of the feeding channel behind the mouth.* Unscorable in outgroups, the vestiture of the furrow may consist of slight transverse folds (*Eumerus*) (0), short setae (**120**, some other taxa) (1), or it is smooth and clear (most taxa) (2).
59. *Size of the lateral lips.* Either side of the mouth on the anterior margin of the prothorax are a pair of ovoid projecting organs, the lateral lips, bearing sensilla groups 9 and 10 (character *i* in figures). They are not developed in outgroups. Lateral lips may be flat and do not project (Fig. 8) (0); at **164** (reversing at **125**) they project slightly, less than they are long (Fig. 10a) (1); at **163**, they project forward more than half their length (Fig. 12a) (2).
60. *Distal end of lateral lips.* This is without long setae (Fig. 8a) (0); or (at **129**, reversing at **161** & **126**, re-evolving at **135**) with long setae (Fig. 12a) (1).
61. *Setae on the inner margin of lateral lips.* These setae may be absent (0); from **129** (lost at **126**), a dense coating of short, fine setae on the inner margin of the lateral lips is present (1).
62. *Projection on the inner margin of the lateral lips facing the mouth.* In many saprophagous larvae (**158**) there is a projection on the inner margin of the lateral lips (1); this projection is absent in other taxa (0).
63. *Base of the lateral lips (view from front of the larva).* This region may be coated in short, basally-flattened setae (Fig. 12b) (gained at **159** & **153**, lost at **142** & *Caliprobola*, regained at **147**) (1); or such setae may be lacking (0).
64. *Developed base of anterior fold.* The anterior fold lies between the antennomaxillary organs and the distal end of the prothorax, i.e. it is the front end of the prothorax curving down to join the head (character *c* in figures). It is not developed in outgroups. In some long-tailed larvae (**136**, lost in *Mallota*) the base of the anterior fold just behind the antennomaxillary organs and before the rows of spicules on the upper part of the anterior fold is elongate (Fig. 12A) (1). In other taxa this region is short and not developed (0).
65. *Sculpture of space between margin of anterior fold and base of antennomaxillary organs.* In some saprophagous taxa (**143, 137** & some other genera; lost in **149**) this space is coated with setae (1); or setae may be lacking, and the surface is smooth and clear (0).
66. *Vestiture of the anterior fold.* The surface may bear vestiture, i.e. a coating of micro-setae of various types: non-sclerotized setae may be present (basal groups, *Myolepta, Microdon*, **159** [chrysogasterines]) (0); or some sclerotized setae with bent tips (spicules) may be present (Fig. 12A) (**166**) (1); occasionally (*Cheilosia morio*) the surface of the anterior fold lacks vestiture and is smooth and clear (2).
67. *Size of vestiture on the anterior fold.* If present, setae or spicules on the anterior fold are not developed, i.e. they are as long or no longer than other vestiture on the thorax (0); at **129** (lost at **159** [chrysogasterines], *Myolepta*, and **125**) the vestiture is longer than the rest of the thorax (1).
68. *Position of rows comprising largest spicules on anterior fold*: middle rows largest (0); anterior rows largest

(1); one anterior row large, the rest small (Fig. 21A) (2). With a complex pattern of changes amongst saprophagous syrphids, this character probably contains little phylogenetic content.

69. *Arrangement of vestiture on the anterior fold.* The vestiture may not be arranged in transverse rows across the anterior fold (0). It may, however, be organized into less than (**163**, reversed in **159** [chrysogasterines] & *Myolepta*) (1) or more than (*V. inflata* & **134**) (2) 5 transverse rows.
70. *Groove separating sensilla 6–8 of prothorax.* At least one groove usually separates these sensilla (0); at **162** (*Hammerschmidtia & Brachyopa*), all three share the same fold (1).
71. *Alignment of sensilla 6 & 7 on prothorax.* These sensilla are sited below and forward of the anterior spiracles. They may be aligned with the horizontal axis of the body (0); or (**168**) sensilla 6 is above sensilla 7 (1).
72. *Division in fold bearing sensilla 4 & 5 of the prothorax.* In some long-tailed larvae (**135**) this fold is partially divided by a posterior groove (1); in other taxa there is no such groove (0).
73. *Prothorax with fold between folds bearing sensilla 1–3.* In some long-tailed taxa (**134**), a fold exists on the dorsum of the thorax between the pair of folds bearing sensilla 1–3 (Fig. 12, character *z*) (1). In other taxa this fold is absent (0).
74. *Alignment of sensilla pairs 1–3 on prothorax.* In *Criorhina* these sensilla are not aligned, and usually the third sensilla is displaced laterally due to the hooks (Fig. 22B) (1). In most other taxa these sensilla are aligned with the longitudinal axis of the body (0).
75. *Tapered prothorax.* In *Temnostoma* the posterior two thirds of the prothorax taper on the mesothorax, which is enlarged and surrounds the prothorax in the same plane, so that the front of the larva is the tapered prothorax and mesothorax (Fig. 22C) (1). In other taxa the posterior part of the prothorax is not tapered (0).
76. *Vestiture on the dorsum of the prothorax.* In outgroups and basal taxa, vestiture is absent or consist of non-sclerotized setae (0); from **129**, a mixture of setae and spines (lightly sclerotized upright setae) (1), or setae, spines and spicules (sclerotized setae with bent tips) (2), occurs, lost in *Myolepta* and most entomophages (**125**).
77. *Isolated grooves on the lateral margins of prothorax.* The sides of prothorax in certain hook-bearing syrphids (**147**, lost in *Milesia*) have at least one isolated groove (1); in other taxa there are no isolated grooves on the sides of the prothorax (0).
78. *Presence of a pair of deep grooves on the dorsum of the prothorax.* In outgroups, phytophagous and mycophagous syrphids, *Ferdinandea* and *Rhingia*, the dorsum of the prothorax has, on either side lateral to the folds bearing sensilla 4 & 5, a pair of short, wide grooves (0). In other taxa (**129**) these grooves, if present, are no deeper than other grooves on the prothorax (1).
79. *Size of prothorax in relation to the first abdominal segment.* In addition to variations in length of the prothorax, there are also variations in the width. In entomophagous syrphid taxa (**128**) the thorax is narrow, often less than half as wide as the first abdominal segment (2). In saprophagous taxa (**163**) the prothorax is usually wider than the first abdominal segment (1). In outgroups and phytophagous and mycophagous taxa, the thorax varies between 0.5–1.0 times the width of the first abdominal segment (0).
80. *Width to length of prothorax.* The width of the prothorax is the distance between the folds bearing the anterior spiracles, and the length is the distance between the first transverse groove behind the longitudinal grooves on the dorsum and the anterior fold. The prothorax is as long as wide (0), longer than wide (**128**) (1), or transverse (**161**), wider than long (2).

Abdomen

81. *Derivation of colour pattern.* The possession of colour patterns is a feature of larvae of taxa derived from **120** (pipizines and syrphines). Colour is absent (0); or (**120**) derived from pigments in the haemolymph (1), the fat body (**111**, reversed to 1 at **117**) (2) or fat body and vestiture (*Meligramma*, and **95** reversed to 2 at **90**) (3).
82. *Presence of fold between ventral sensilla on abdominal segment 7 and the anus.* In entomophagous syrphid taxa (**128**), a fold exists between the ventral sensilla of abdominal segment 7 and the anus so that these sensilla are not on the margin of the segment (1). In other syrphid taxa this fold is absent, and the ventral sensilla are on the margin of the segment (0).
83. *Shape of the anal segment.* In most outgroups and syrphid taxa, the anal segment is either wider or narrower than the preceding segment (0). In some entomophagous taxa (*Baccha & Parasyrphus*) the anal segment is as wide as abdominal segment 7 (1).
84. *Shape of the abdomen in cross-section.* There are three basic shapes: oval to sub-rectangular, as in

most outgroups and syrphid taxa (0); dorso-ventral flattening (1) occurs in *Pipizella* & **106** (reversed to 0 in *Eriozona* & **91**); in *V. inanis* & **99** (lost at **102**) only the lateral margins are flattened, producing a sub-triangular shape (2).

85. *Degree of overlap of abdominal segment 7 over 8*. In outgroups, and phytophagous (most), mycophagous and entomophagous taxa, the anal segment is not developed and the degree of overlap of segment 7 over the anal segment is < 0.33 length of segment 6 (0). In other taxa (*Cheilosia morio* & **158**), the anal segment is extended to varying amounts, and segment 7 overlaps the anal segment by >0.33 length of segment 6 (1).
86. *Projections on abdominal segment 7 and anal segment*. In *Mallota* and *Helophilus* there are three pairs of projections at the base of the long tail. These projections bear sensilla 4 and 7/8 of segment 7, and sensilla 9 of the anal segment, and are longer than papillae supporting other sensilla on these segments (Fig. 27D) (1). In other taxa (unscorable in outgroups, pipizines & syrphines), these sensilla are not on longer papillae than other sensilla (0).
87. *Sensilla 4, 7 and 8 on fleshy papillae longer than those of other sensilla of abdominal segment 7*. In *Helophilus* sensilla 4, 7–8 on abdominal segment 7 are on fleshy papillae longer than those of other sensilla of this segment (1). In other syrphid taxa this arrangement of long and short papillae does not occur (0).
88. *Basal papillae to sensilla 4–6 on abdominal segment 7*. In most syrphid taxa sensilla 4–6 on abdominal segment 7 are borne on basal papillae of varying dimensions. In some taxa these basal papillae are reduced or not longer than papillae supporting sensilla 4–6 on segment 6 (0); or they may be up to 2 × as long as basally broad (1); or papillae are >2 × as long as basally broad (2). In *V. inanis* they are apparently absent (3). Lengthening occurs at **164**, but then most changes are reductions (**155, 128**, etc).
89. *Position of sensilla 4 in relation to sensilla 5 and 6 on abdominal segment 7*. In most syrphid taxa with extended anal segments (appears at **158**, lost **154**, regained **138** and some other taxa), sensilla 4 is aligned horizontally with sensilla 5 and 6 (1). In taxa without extended anal segments, sensilla 4 appears above 5 and 6 (0).
90. *Position of sensilla 2–4 on abdominal segment 7*. In some long-tailed taxa the position of sensilla 2–4 vary in relation to each other. These sensilla may be aligned (0); or (**131**) sensilla 3 and 4 may be posterior to 2 (1); or (**134**) sensilla 3 may be anterior and 4 posterior to 2 (2).
91. *Arrangement of sensilla 1–4 on abdominal segment 7*. In most syrphid taxa and outgroups, the pattern of grooves separating sensilla 1–4 on abdominal segment 7 is the same as on segment 6 (0). However, in some taxa some of these sensilla are separated from one another by grooves on segment 7, but not on segment 6 (1): for example, in *Merodon*, sensilla 1 on segment 7 is separated from sensilla 2 by a fold; this fold is absent on segment 6, and sensilla 1 and 2 are aligned. The optimization suggests a pattern of gains at **172, 159** & *Blera*, with losses at *Cheilosia* (miners), **165, 161** & **125**; however, at least one other possibility seems reasonable, with gains at **172** & *Blera*, and losses at *Cheilosia* (miners), **165, 162, 157** & **125**.
92. *Presence of prolegs on the abdomen*. Unscorable in outgroups, plesiomorphic taxa, and most entomphagous taxa (from **125**). In most saprophagous taxa prolegs are present on the ventral surface of the abdomen. Prolegs differ from other types of locomotory organ by the presence of a planta (an indentation close to the apex where muscles are attached) and crochets (rows of sclerotized hooks longer than surrounding setae or spines round the planta). Prolegs are present on abdominal segments 1–4 or 5 in plesiomorphic saprophages (0), and present on segments 1–6 in all other taxa (1), including entomophagous *Volucella* (this makes the optimization suggest that state 1 is plesiomorphic, with two changes at **163** [1→0] and at **157** [0→1]).
93. *Presence of spicules between prolegs on segment 6*. In some long-tailed syrphid taxa (*Anasimyia & Parhelophilus*) a complete row of spicules occurs between the prolegs on abdominal segment 6 (1). In most taxa, spicules are absent (0). In other long-tailed taxa an incomplete row occurs, with either large medial spicules (*Eristalinus*) (2), or isolated spicules (*Eristalis & Myathropa*) (3). While this pattern of scoring results in an optimization that suggests independent evolution of each state from state 0, it seems more likely that the occurrence of spicules evolved at **134**, and subsequently were modified (and lost in *Helophilus*)
94. *Distance separating paired prolegs on abdominal segments 1–6*. In most proleg-bearing taxa, each proleg is closer to its neighbour on the same segment than their individual diameter (0). In some long-tailed larvae (**136**), however, the paired prolegs are separated by more than their individual diameter (1). In *Callicera* the abdominal prolegs are fused medially, forming a dumbell-shaped locomotory organ on each of the first six abdominal segments (2).
95. *Position of crochets on abdominal segment 6*. Crochet orientation on prolegs of 6th abdominal segment

varies. These crochets may be orientated as on the previous segment (0); at **134**, most crochets may face those of previous segment (1); at **131** most crochets face out towards the sides of the body (2).

96. *Sensilla on prolegs*. Unscorable in outgroups, and phytophagous, mycophagous and most entomophages (except *Volucella*). The plesiomorphic state is when sensilla group 9 is not part of the proleg but sensilla groups 10 and 11 are (Fig. 18b) (0); from **157**, sensilla 9 is part of the proleg along with 10–11 (Fig.17E) (1).
97. *Rows of crochets on abdominal prolegs*. Unscorable in outgroups, and phytophagous, mycophagous and most entomophages (except *Volucella*). The number of rows of crochets on abdominal prolegs varies. The largest, primary crochets are in a row at the apex of the proleg, and beneath them are varying numbers of rows of smaller crochets. Rows of crochets on abdominal prolegs: single (0); double (1); multiple (2); *Temnostoma* has lost its crochets (3). It is difficult to know what the plesiomorphic state is, since *V. inflata* and *V. inanis* have single row, and *V. pellucens* and *V. bombylans* have a double row; the optimization suggests a double row. A single row then evolved at **163**, and a double at **158**.
98. *Number of primary crochets on prolegs of sixth abdominal segment i.e. the first apical row*: 1–3 (0); 4–6(1); 7–9 (2); >9 (3). Unscorable in outgroups, and phytophagous, mycophagous and most entomophages (except *Volucella*). There has been a general increase in the number of crochets in saprophagous taxa, at **155**, (0→1), at **141** (1→2), and then at **147** & **134** (2→3), with several genera where there have been reductions.
99. *Number of primary crochets on prolegs of first abdominal segment*: 1–3 (0); 4–6 (1); 7–9 (2); >9 (3). Unscorable in outgroups, and phytophagous, mycophagous and most entomophages (except *Volucella*). As in character 98, a general increase in number of crochets in saprophagous taxa, at **155** (0→1), **141** (1→2), and **147** & **134** (2→3), with several cases of reductions.
100. *Shape of abdominal prolegs*. Unscorable in outgroups, and phytophagous, mycophagous and most entomophages (except *Volucella*). Prolegs are variously developed. This is best appreciated in ventro-lateral view, where they appear as transverse ridges (0); as ovals (1); as shorter-than-tall cones (2); or cones that are broader at the apex than the base, and taller than broad (3). The pattern is of a general increase in the height of the prolegs in mainly saprophagous taxa, at **157** & *V. pellucens* (0→1), **155** (1→2), and **135** (2→3, reversed in *Anasimyia*).
101. *Position of the planta*. Unscorable in outgroups, and phytophagous, mycophagous and most entomophages (except *Volucella*). The position of the planta varies. The plesiomorphic state is distinctly antero-ventral in position (0); at **157** it becomes antero-dorsal (1); at **155** (most saprophages), it is fully apical in position (2).
102. *Tapered locomotory prominences*. In the *Cheilosia morio* group, the locomotory prominences distinctly taper (1); in outgroups and all other syrphid taxa with locomotory prominences, they are round-tipped (0).
103. *Backwardly directed locomotory prominences*. At **91** (*Eupeodes*, *Scaeva* and *Ischiodon*), on abdominal segments 6 and 7, the tips of the locomotory prominences face backwards (1) (Rotheray, 1987b). Backwardly facing locomotory prominences are lacking in other taxa (0).
104. *Extra lobe on the locomotory prominences of segments 1–7*. In certain aphidophagous taxa (**92**), a posterior lobe appears as part of each locomotory prominence on abdominal segments 1–7 (Fig. 18E) (1). In other aphidophagous taxa this lobe is absent (0).
105. *Larva with ventro-lateral margin*. At **159** (chrysogasterines), the integument projects, forming an almost continuous ventro-lateral margin on abdominal segments 1–7 (1). In other taxa, no continuous margin exists (0).
106. *Vestiture of abdominal segment 7 and the anal segment*. In *Myolepta* the vestiture of abdominal segment 7 and the anal segment consists of nodulate setae (Fig. 27B) (1). In all other taxa, a coating of nodulate setae is absent from these segments (0).
107. *Integument of abdominal segments 1–8*. In *Mallota* and *Temnostoma* the integument is smooth and clear of vestiture or surface sculpture (1). In other taxa vestiture and/or surface sculpture is present (0).
108. *Setal fringe round the lateral margin*. In *Microdon* a setal fringe exists on the dorso-lateral margin at the level of abdominal sensilla pairs 5 & 6, and continuing on to the thorax (Figs 14A, 24C) (1); in all other taxa, a setal fringe is absent at this position (0).
109. *Wart-like blotches on the abdomen*. In *Brachyopa* and *Hammerschmidtia*, the vestiture of the abdomen consists of wart-like blotches (1). In all other taxa, wart-like blotches are absent (0).
110. *Distribution of vestiture on ventral surface of abdomen*. In most taxa the ventral surface of the abdomen

has a more or less complete coating of vestiture (0); at **125** (*Microdon* and pipizines), vestiture is patchily present in (1); from **119** (syrphines) it is completely absent (2).

111. *Dorsal surface of abdomen with vestiture arranged in transverse rows*. At **164** (reversed at **126** & **157**), the vestiture of the dorsal surface of abdominal segments 1–6 is arranged in transverse rows (1). In all other syrphid taxa, transverse rows are absent (0).
112. *Integumental vestiture on abdominal segments 1–7*. Vestiture is absent (0) in outgroups and at **122** (but not **124**, i.e. only *Neocnemodon & Trichopsomyia*); at **172** (the syrphids) it consists of non-sclerotized setae (1); in several taxa (**171**, *Epistrophella*, **95** except *Paragus & Ischiodon*), these include some sclerotized setae (2).
113. *Abdomen with patches of spicules*. In *Eupeodes* spicules form dark patches along the dorso-lateral margins of the abdomen (1). In other genera with spicules, they are more evenly distributed without aggregating into dark patches (0).
114. *Abdomen and thorax with patches of setae*. In *Ceriana*, patches of short and long setae are present on the abdomen (1). In other taxa, including outgroups, long and short setae, if present, are intermingled and do not form patches (0).
115. *Fusion or loss of abdominal sensilla*. In *Pipizella* sensilla 7 and 8 on abdominal segments 1–7 have either fused, or one or other has been lost, because only one sensilla appears at this position (1). In most other taxa there are two sensilla (0).
116. *Position of the mid-ventral sensilla (sensilla 11) on abdominal segments 1–6*. In outgroups and all syrphids except many entomophages, the mid-ventral sensilla, usually sensilla 11, are sited on a locomotory prominence (Fig. 18C) (0). In many aphidophagous taxa (**107**), sensilla 11 is not part of the locomotory prominence and is sited anterior to it (Fig. 18D, E) ((Rotheray & Gilbert, 1989) (1).
117. *Position of sensilla 9–11 on abdominal segments 1–6*. Sensilla 9–11 are equidistant from each other (0); from **167** (reversed in *Cheilosia* [miners]), 10 is nearer to 11 (1); at **129** (except in *V. inflata, V. bombylans & Microdon*, which have state 0), 10 is nearer to 9 (2).
118. *Position of sensilla 7 in relation to 8 on abdominal segments 2–6*. Unscorable in plesiomorphic taxa. Sensilla 7 above 8 (0); 7 above and anterior to 8 (1); 7 aligned and anterior to 8 (2). State 2 appears at **157**, changing to state 0 (*Psilota*) and state 1 (**150**, *Blera*); state 1 also appears in *Pipizella*.
119. *Number of papillae at sensilla group 7/8 on abdominal segments 2–6*. These either consist of one papilla (0); or (from **161** and **125**) of two approximated papillae (1).
120. *Groove separating sensilla 5 and 6 on abdominal segments 2–6*. Unscorable in outgroups. In the plesiomorphic phytophagous and mycophagous syrphids, sensilla 5 and 6 on abdominal segments 2–6 are not separated by a groove (0); from **166** (apart from reversals in *Temnostoma* and *Microdon*), a groove separates these sensilla (1).
121. *Position of sensilla 5 in relation to sensilla 6 on abdominal segments 2–6*. Sensilla 5 directly above 6 (0); 5 slightly above and anterior to 6 (1); 5 nearly or directly anterior to 6 (2). The optimization places state 1 as plesiomorphic, with changes to state 0 in *Eumerus, Cheilosia pagana*, and **171**; the main change is to state 2 at **129**, with several reversals (*V. inflata, Temnostoma, Blera*, **148**)
122. *Positions of sensilla 4 in relation to 5 and 6 on abdominal segments 2–6*. In *Mallota* sensilla 4 is aligned with sensilla 5 and 6 on abdominal segments 2–6 (1). In other syrphid taxa, 4 is above 5 and 6 (0).
123. *Position of sensilla 4 on abdominal segments 2–6 in relation to sensilla 1–3*. In some phytophagous and mycophagous syrphids, sensilla 1–3 are not anterior to 4 (0); in most other taxa these sensilla are anterior to 4 (1). The pattern of change in basal taxa is complex, partly because the optimization places state 1 as plesiomorphic. Most taxa from **129** have state 1.
124. *Position of sensilla 1–2 on abdominal segments 2–6*. In phytophagous and mycophagous syrphids, sensilla 2 is aligned with 1 on the same fold (0). From **129**, sensilla 2 is on a separate fold behind the one bearing sensilla 1 (1).
125. *Distance separating sensilla pair 1 on the first abdominal segment*. In outgroups and most syrphid taxa, each of the sensilla comprising pair 1 on the first abdominal segment is separated by about the same distance as between sensilla pair 1 and sensilla 2 (0). In some aphidophagous taxa (**111**, reversed at **114**), the sensilla comprising pair 1 are closer than this (1).
126. *Papillae on first abdominal segment*. In the *Cheilosia morio* group, the integumental patches through which the pupal respiratory horns project are mounted on papillae (1). In other taxa including outgroups, there are no supporting papillae (0).
127. *The presence of pupal spiracles*. A pair of pupal spiracles usually appear on the dorsum of abdominal segment 1 within a few days of pupariation in all outgroups and most syrphid taxa (0). However, they are absent in certain aphidophagous taxa (**106**) (1).
128. *Presence of cuticular patches on abdominal segment one*. In most syrphid taxa (but not in outgroups), two

patches appear on the dorsum of the first abdominal segment just before pupariation. It is through these patches that pupal respiratory horns protrude in the puparium. These patches are recognizable from their coriaceous appearance in relation to the surrounding integument, and appear at **173** (1). They disappear at **108** (some aphidophages) (0).

129. *Margins of abdominal segments 1–7 flattened with sensilla 3–6 on projections*. Mostly in certain aphidophagous taxa (mainly **95** reversing at **91**, but also **101** and **162**), the lateral margins of the abdomen are flattened and sensilla 3–6 are on tapering projections, which gives the larva a serrate outline (1). In other taxa the lateral margins may be flattened, but lack sensilla 3–6 on projections (0).
130. *Size of basal papilla supporting sensilla 1–4 on abdominal segments 6 and 7*. Abdominal segments 6 and 7 with sensilla 1–4 mounted on papillae, either longer than those supporting sensilla 1–4 on segments 1–5 (1); or as long (0). The main changes here are at **164** (0→1), reversing at *Ferdinandea*, **161** and **126**.
131. *Shape of papillae supporting sensilla 1 on abdominal segments 1–7*. Sensilla pair 1 may be borne on tapering projections on abdominal segments 1–7. In some aphidophagous taxa, these projections are close together and share a common base (1); or they are separated by a distance of their own height or more (2). Tapering projections are absent in outgroups and most other syrphid taxa (0). The main change is at **95** (0→2: also in *Chrysotoxum*), with others at **101** (0→1), **93** (2→1) and *Paragus* (1→2).
132. *Position of ventral sensilla on the ventral surface of abdominal segments 1–7*. The ventral sensilla in most outgroups are sited on the middle fold of each abdominal segment (0). In Pipunculidae and Syrphidae (**174**), the ventral sensilla are on the posterior fold (1).
133. *Width of folds on the ventral surface of abdominal segments 1–6*. In certain aphidophagous taxa (**104**), the fold on the ventral surface of each of the first 6 abdominal segments are not of the same width (1). In all other taxa the folds are about the same width (0).
134. *Number of transverse folds on the ventral surface of abdominal segments 1–6*. In most outgroups the ventral surface of abdominal segments 1–6 have 2 transverse folds (0). In Pipunculidae and Syrphidae (**174**) the ventral surface of abdominal segments 1–6 have 3 transverse folds (1).
135. *Number of transverse folds on the dorsum of abdominal segments 2–6*. In outgroups and most mycophagous and phytophagous taxa, each abdominal segment has up to 3 dorsal folds (0). At **129** (*Volucella, Microdon* and pipizines), there are 3 + 1 divided folds on the dorsum of abdominal segments 2–6 (1). In all other syrphid taxa (**161** & **119**) there are 4 folds (2).
136. *Relative position of dorsal and ventral sensilla on abdominal segments 1–7*. In most outgroups the dorsal and ventral aspects are aligned with the dorsal sensilla above the ventral sensilla (0). In Pipunculidae and Syrphidae (**174**), the dorsal and ventral aspects are mis-aligned, with the ventral sensilla posterior to the dorsal sensilla (Fig. 5) (1).
137. *Degree of non-alignment of dorsal and ventral parts of the body*. In lateral view, dorsal and ventral aspects of abdominal segments 1–7 are aligned in most outgroups (except Phoridae) (0). In Phoridae and Syrphidae (**175**, reversing in Pipunculidae), the dorsal and ventral aspects are not aligned, as shown by the interrupted pattern of grooves on the lateral margins (Fig. 4) (1).
138. *Boundaries of abdominal segments*. In outgroup taxa except Pipunculidae, boundaries between abdominal segments are clearly delimited by grooves in the integument (0). In Pipunculidae and Syrphidae (**174**), segment boundaries are unclear due to secondary grooves and apparent boundary grooves being interrupted (Fig. 4) (1).

Anal segment

139. *Absence of sensilla 7/8 on the anal segment*. In phytophagous, mycophagous and some saprophagous taxa, sensilla 7/8 are present on the anal segment (0). In some *Volucella* species (**128** reversing at **125**) and most saprophagous taxa (**157**), these sensilla are absent (1).
140. *Position of sensilla 7/8 on the anal segment*. Unscorable in most saprophages (clade **157**). In phytophagous and mycophagous syrphid taxa, sensilla 7/8 occur on the inside margin at the base of lappet 3 (Fig. 19A) (0); at **129** reversing at **161** (*V. inflata, Microdon* and the pipizines), sensilla 7/8 occur on a transverse fold on the main part of the segment, immediately below lappet 3 (Fig. 19B, C) (1); in clade **119** (syrphines), they are on the margin of the segment immediately lateral to lappet 3 (Fig. 19D, E) (2).
141. *Position of sensilla 9 on the anal segment*. In some long-tailed taxa (**135**), sensilla 9 occur on the narrow, extended part of segment (1). In most other syrphid taxa with an extended anal segment, they are not sited on the extended part (0).
142. *Position of sensilla pair 3 in relation to sensilla 4–6 on the anal segment*. Scorable only in aphidophagous

taxa. The anal segment is modified in varying ways and the position of the sensilla vary: sensilla pair 3 may be anterior to sensilla groups 4–6 (0); or (**103**) sensilla 3 may be aligned with sensilla 4–6 (1).

143. *Vertical alignment of sensilla 4 and 5 on the anal segment.* Scorable only in aphidophagous taxa. The anal segment is modified and the position of the sensilla vary: sensilla 4 and 5 may be aligned vertically (0); or (*Xanthandrus*, *Toxomerus*, *Syrphus*, **100**, *Leucozona*, **91**) they are not aligned (1).
144. *Alignment of sensilla 1–3 on the anal segment.* Scorable only in aphidophagous taxa. The anal segment is modified and the position of the sensilla vary: sensilla 1–3 may be aligned (0); or not aligned (1). The plesiomorphic state is adjudged to be 1, changing at **119**, reverting at **108**, and state 0 reappearing in *Parasyrphus*.
145. *Sensilla of anal segment on projecting basal papillae.* In most taxa sensilla other than 4–6 occur on basal papillae that project more than those on other abdominal segments (0); in some taxa (*Psilota, Callicera*, **148, 134**), only these sensilla are on basal papillae that project more than on other abdominal segments (1).
146. *Position of sensilla 1–6 on anal segment.* From **127** (*V. pellucens, V. inanis, Microdon*, pipizines & syrphines) and also in *Temnostoma*, sensilla 1–6 are on the posterior margin of the anal segment (1). In all other taxa, some or all these sensilla are sited on the lateral margins of the anal segment (0).
147. *Form of the tip of the anal segment in aphidophagous taxa.* Scorable only in aphidophagous taxa. The tip of the anal segment is modified in varying ways. The tip of anal segment may have 2 pairs of lobes (0); 3 pairs of lobes (1); a transverse ridge (2); or a divided transverse ridge (3). A complex series of changes mainly in individual taxa; the main pattern is a change at **103** (0→2), with modifications at **92** (2→3) and **91** (3→1).
148. *Size and shape of the smaller lateral pair of lobes at the tip of the anal segment.* Scorable only in aphidophagous taxa. The tip of the anal segment is modified and has a pair of lateral lobes of varying shape and size, but smaller than the mid-dorsal lobes. The lateral lobes may be small and oval (< 0.5 length mid-dorsal lobe) (0); at **108**, they become large and oval (> 0.5 length mid-dorsal lobe) (1); and at **98** (reversed at **92**), ridge-shaped (2).
149. *Number of transverse grooves on the ventral surface of the anal segment.* At **125** (*Microdon*, pipizines, *Melanostoma* & *Xanthandrus*), two complete transverse grooves exist between the anus and the tip of the ventral surface of the anal segment (1); at **111** (all other syrphines), the posterior of these transverse folds is divided (2). In all other taxa, 0–1 transverse folds are present (0).
150. *Division of posterior respiratory process.* In *Toxomerus*, the posterior breathing tubes are not fused along their entire length: they appear to be separate except at the extreme base (1). In all other syrphid taxa the breathing tubes are fused along their entire length up to but sometimes excluding the spiracular plates (0).
151. *Longitudinal grooves behind anus.* In syrphid taxa varying numbers and arrangements of grooves are present between the anus and the tip of the anal segment. In most taxa they are transverse or inclined (0). At **159** (chrysogasterines), there is just one longitudinal groove (1); at **158** or **157** (reverting to state 0 at **154**), there are two longitudinal grooves (2).
152. *Colour differentiation of the spiracular plate.* In outgroups and most syrphid taxa, the spiracular plate is unicolorous pale or black, contrasting in colour from the rest of the posterior respiratory process (0). At **118** (reversed at **107**, regained at **105** and *Paragus*), the spiracular plate is similar except that the spiracular openings are black-lined (1); at **113**, the spiracular plate is the same colour as the posterior respiratory process (2).
153. *Projection on the posterior respiratory process.* In *Xanthandrus* there is a rounded projection on the posterior rim of the posterior respiratory process (Rotheray & Gilbert, 1989) (1). In all other taxa this projection is absent (0).
154. *Presence of basal rim to the posterior respiratory process.* In *Meliscaeva*, a basal rim differentiated by its size and colour is present around the posterior respiratory process (1). This is absent in other genera (0).
155. *Posterior respiratory process with a tapered tip.* At **159** (chrysogasterines), the tip of the posterior respiratory process is tapered to varying amounts (1). In outgroups and other syrphid taxa the tip of the posterior respiratory process is truncate (0).
156. *Spiracular plates sloping inward.* In most outgroups and syrphid taxa the spiracular plates are level with each other, or slightly sloping laterally (0). At **96** (*Didea* and *Megasyrphus*), the spiracular plates slope inwards towards each other (1).
157. *Presence of dorsal spurs.* On the posterior respiratory process, a chitinized triangular-shaped projection, the dorsal spur, may be present on the inner margin of each spiracular plate in certain aphidophagous taxa. Dorsal spurs are absent in outgroups and most other syrphid taxa

(0). When present (*Meliscaeva* and from **107**, lost at **100** and **96**, regained by *Meligramma*), they may be short (height less than width) (1); or (**93**, reversed at **91**) tall (height greater than width) (2).

158. *Form of the interspiracular ornamentation*. Carinae at base of interspiracular setae absent (0). Carinae present in aphidophagous taxa (**120**, lost at **102**) and either cone-shaped (1) or (from **98**, reversed at **100** & **93**), elongated and ridge-like (2).
159. *Interspiracular setae*. In outgroups and most phytophagous and entomophagous taxa, interspiracular setae are about as long as the diameter of the spiracular plate (0). In a few genera, setae are shorter than the diameter of the spiracular plate (1), and in others, the setae are long and extend over the sides of the spiracular plate (2). Change has occurred at **161** (reversed in *Temnostoma*), **121** (pipizines) & *Paragus* (0→2), and at **111**, reversed in *Toxomerus* & **94** (0→1).
160. *Form of the spiracular openings*. In outgroups and most syrphid larvae, the spiracular openings are straight, slightly curved at the tips or oval-shaped (0). At **102** (*Xanthogramma* and *Doros*), however, the spiracular openings are distinctly and evenly wavy (Rotheray & Gilbert, 1989) (1).
161. *Length of spiracular openings*. Spiracular openings may be up to 2 × long as broad, as in most outgroups and phytophagous and saprophagous taxa (0). Longer spiracular openings are either between 2 × and 6 × as long as broad (1), or more than 6 × as long as broad (2). A large number of changes occur between the states of this character, and there is probably little phylogenetic content.
162. *Spiracular openings mounted on carinae*. Carinae may be absent, as in outgroups and most non-entomophagous taxa (0). When present they are either short (at **107** [lost at **100**] & *Toxomerus*), so that their height is about the width of a spiracular opening (1), or tall (**121** [reverting to state1 in *Pipizella*] & Paragus), in which case their height is more than the width of the spiracle (2).
163. *Position of spiracular openings*. In outgroups and most non-entomophagous syrphid taxa, the spiracular openings do not appear over the sides of the posterior respiratory process (0). When spiracular openings do occur over the sides of the posterior respiratory process (**108**, lost by *Paragus*), they may have less than 0.5 of their length down the sides (1), or (**97**, reverting to state 1 in *Megasyrphus* & *Dasysyrphus*) more than 0.5 of their length over the sides (2).
164. *Shape of the posterior respiratory process*. In most taxa the posterior respiratory process is parallel-sided (0). At **121** (pipizines), the posterior respiratory process tapers (1). Furthermore, some entomophagous taxa (**107**, reversing to state **0** at **92**, changing to state **1** at **100**) have a posterior respiratory process with an enlarged tip, apparently associated with the development of features such as long spiracular openings, dorsal spur, circular disc and interspiracular ornamentation (2).
165. *Length of sclerotized tube supporting the posterior respiratory organs*. In outgroups and certain phytophagous and entomophagous taxa, the length of the tube is as long as broad or broader (0). Other syrphids have the tube 1–2 times as long as broad (1). A few genera have the tube more than twice as long as broad (2). In some *Cheilosia, Portevinia, Temnostoma, Eupeodes, Scaeva* and *Ischiodon*, there appears to have been a secondary loss of length, although these are scored as 0. The main changes are lengthenings at **161** (0→2), and **121** & **107** (0→1), but there are numerous others.
166. *Fusion of posterior spiracles*. In Lonchopteridae and Platypezidae, the posterior spiracles are separate, i.e. with no basal connection (0). At **175** (Phoridae and Pipunculidae), the posterior spiracles are close, i.e. the base is connected by a sclerotized plate or an area of integument delimited by grooves (1). From **173** (syrphids), the posterior spiracles are fused, forming a single structure (2).
167. *Projections on apical margin on anal segment*. In *Rohdendorfia* there are a pair of tapering projections just above the tip of the anal segment and below the posterior respiratory process (1). Similar projections are absent in all other taxa (0).
168. *Grooves on anal segment*. Lateral to the posterior respiratory process, a series of grooves on the integument of the anal segment is present in *Syrphus* (0), but absent in other taxa (1).
169. *Transverse groove above tip of anal segment*. In certain aphidophagous syrphid taxa (**112**), a deep, transverse groove occurs above the tip of the anal segment (1), but is absent in outgroups and other syrphid taxa (0).
170. *Relative size of the lappets*. At **121, 115** & **103** (reverting at **99, 91** & *Eriozona*), the first two pairs of lappets are reduced, with the third appearing as a pair of round-tipped projections (Fig. 19C) (1). In other taxa, the third pair of lappets are not like this (0).
171. *Tip of the anal segment with locomotory lobes*. At **120** (pipizines and syrphines), the tip of anal segment bears locomotory lobes similar in shape and surface sculpture to locomotory prominences on abdominal segments (1). In other taxa including outgroups, no locomotory organs are present on the tip of the anal segment (0).
172. *Lateral margins of the anal segment*. Most taxa have no rows of setae (0). At **161**, rows of short setae

are present (< length of lappet 1) (1); from **158** (reverting to state 0 at **154**), rows of long setae are present (> length of lappet 1) (2).

173. *Surface sculpture of anal segment.* Unscorable in most entomophages. At **159** (chrysogasterines) & **132** (some long-tailed larvae), the surface sculpture from the base of the anal segment to lappet 2 is of one type with transverse folds, and from lappet 2 to the tip is of another type with longitudinal ridges (1). In other taxa the surface sculpture is unchanged to lappet 3, with longitudinal ridges only beyond this point (0).
174. *Presence of an anal plate.* In *Portevinia* the end segments are contracted, and form an inclined plate with a setal fringe: segment 7 forms the dorsal part, and the anal segment comprises the ventral part (Fig. 23C) (1). In other taxa, although the anal segment may be contracted, anal plates are absent (0).
175. *Orientation of the anus.* In *Portevinia* the anus is parallel to the longitudinal axis of the body (1). In all other taxa the anus is transverse, at right angles to long axis of body (0).
176. *Position of the anus.* In all outgroups, the anus is sited about halfway along the anal segment, well apart from the posterior margin (0). In all syrphid taxa (**173**), the anus is sited right on the anterior margin of the segment (Fig. 2) (1).
177. *Anal segment with first (i.e. anterior) pair of lappets bifurcated.* At **158** (reversed at **154**) and *Spilomyia*, the first lappet on the anal segment is divided so that sensilla 1 and 2 are on separate papillae (Fig. 25C) (1). In other taxa these sensilla are not separated (0).
178. *Length of anal segment in relation to body length.* In outgroups, phytophagous (most) and entomophagous taxa, the length of the anal segment is < half body length (head to tip of abdominal segment 7) (0); in taxa such as *Tropidia* +, the anal segment is 0.5–1 body length (1); in long-tailed taxa, it is > body length (2). Lengthening occured at **157** (0→2; also in *Cheilosia morio*), **139** (1→2) and *Brachyopa* (0→1), with reductions at **155** (2→1), *Psilota* & *Temnostoma* (both 1→0).
179. *Narrowing of the anal segment.* In most long-tailed taxa (**139**, reversed in *Myolepta*), the anal segment narrows to <0.25 body width (1). In other taxa, including outgroups the anal segment tapers, if at all, to >0.25 body width (0).
180. *Retractability of the anal segment.* In outgroups, and most phytophagous, mycophagous and entomophagous taxa, the anal segment is not retractile, with the posterior respiratory process fixed in position (0); in some long-tailed taxa (**158** & *Cheilosia morio*, lost in *Temnostoma*), the anal segment is partially retractile (when retracted, tip of posterior respiratory process always present) (1); or (at **136** & *Blera*) the anal segment is fully retractile (tip of the posterior respiratory process completely withdrawn when fully retracted) (2).
181. *Type of junction between folds of the anal segment.* In long-tailed taxa (**136**), the junctions between folds may either be smooth (1) or succeeding folds may be much narrower so that the tail is indented at each junction, like a series of steps (viewed from above) (0).
182. *Relative size of the 3 rings of the anal segment.* Relative to each other, each of the rings comprising the anal segment vary in the amount they are extended. In outgroups, and phytophagous, mycophagous and entomophagous taxa, the anal segment does not comprise three rings (0). At **161**, the anal segment consists of three equally spaced rings (Fig. 25) (1); at **139** (*Blera, Caliprobola & Lejota*) the first ring is shortest (Fig. 27A) (2); and at **137** (other long-tailed taxa) the first fold is longest (Fig. 27C–E) (3).
183. *Position of sensilla in relation to the posterior spiracles on the anal segment.* In outgroups one pair of sensilla is immediately anterior to the posterior spiracles (0). In Syrphidae (**173**), either no sensilla or more than one pair is anterior to the posterior spiracles (1).
184. *Relative size of dorsal and ventral aspects of the anal segment.* At **173** (phytophagous and mycophagous syrphids), the anal segment is asymmetrical in profile, with an extended ventral aspect (1). At **164** reversing to state 1 at **161** (*Ferdinandea, Rhingia, V. inflata* and entomophagous taxa, but not most saprophages), the dorsal aspect is longest (2). In outgroups, the dorsal and ventral aspects are about equal, and the segment is symmetrical in profile (0).
185. *Middle pair of lappets fused.* In *Eumerus* and *Merodon* there are 4 pairs of lappets (Fig. 3) (0). In all other syrphid taxa (**167**), the middle pairs of lappets are fused together and there are 3 pairs of lappets (Fig. 23D) (1).
186. *Lappets on occurring on the same fold.* The first two pairs of lappets may appear on the same dorsal fold, as in most phytophagous and mycophagous taxa (0); or (*Cheilosia morio* & **129** reversed in *V. inflata*) lappets may each be on one of three folds (1).
187. *Presence of approximated sensilla on the anal segment.* In outgroups the sensilla of the anal segment are separate from each other (0). In all syrphid taxa (**173**), the anal segment has some approximated sensilla, usually appearing together at the tip of the lappets (Fig. 2) (1).

APPENDIX 2

Character states of Syrphidae and outgroup taxa

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Characters	Lonchopteridae	Platypezidae	Phoridae	Pipunculidae	*Eumerus*	*Merodon*	*Cheilosia paganus*	*Cheilosia morio*	*Cheilosia* (miners)	*Cheilosia* (borers)	*Portevinia*	*Cheilosia* (fungivores)	*Ferdinandea*	*Rhingia*	*Volucella inflata*	*Hammerschmidtia*	*Brachyopa*	*Lejogaster*	*Chrysogaster*	*Orthonevra*	*Neoascia*	*Sphegina*	*Psilota*	*Tropidia*	*Syritta*	*Xylota*	*Ceriana*	*Pocota*	*Chalcosyrphus*	*Xylotomima*
1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
5	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	?	?	?	?	0	0	0	0	0	0	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
7	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	?	?	?	?	0	0	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	?	?	?	?	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	1	1	1	0	0	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
12	0	0	0	0	0	0	0	1	0	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
13	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	?	?	?	?	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1
15	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
17	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	0	0
26	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	2	2
27	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	2	2
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	2	2
29	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1
30	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
31	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
32	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0
36	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0
37	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	?	?	0	0
38	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0
39	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
48	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
49	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	1	2	2	0	2	2	2	2	2
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0

Continued

APPENDIX 2. *Continued*

Characters	1 Lonchopteridae	2 Platypezidae	3 Phoridae	4 Pipunculidae	5 *Eumerus*	6 *Merodon*	7 *Cheilosia pagana*	8 *Cheilosia morio*	9 *Cheilosia* (miners)	10 *Cheilosia* (borers)	11 *Portevinia*	12 *Cheilosia* (fungivores)	13 *Ferdinandea*	14 *Rhingia*	15 *Volucella inflata*	16 *Hammerschmidtia*	17 *Brachyopa*	18 *Lejogaster*	19 *Chrysogaster*	20 *Orthonevra*	21 *Neoascia*	22 *Sphegina*	23 *Psilota*	24 *Tropidia*	25 *Syritta*	26 *Xylota*	27 *Ceriana*	28 *Pocota*	29 *Chalcosyrphus*	30 *Xylotomima*
52	?	?	?	?	0	1	1	1	1	1	1	0	0	0	?	1	2	?	?	?	1	0	0	1	1	1	0	1	1	1
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	?	0	0	1	1	0	0	1	1	1	1
54	0	0	0	0	0	0	1	0	0	1	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	1	1	1
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
56	?	?	?	?	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0
57	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	1	2	2	2	2	2
58	?	?	?	?	0	1	2	1	1	2	1	0	1	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2
59	?	?	?	?	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
60	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
62	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
63	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0
64	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1
66	?	?	?	?	0	0	0	2	0	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1
67	?	?	?	?	0	0	0	?	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1
68	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	1	0	1	0	0	0	1	1	1	2	2
69	?	?	?	?	0	0	0	?	0	0	0	0	0	0	2	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1
70	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
71	?	?	?	?	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	1	1	1	1	2	2	1	1	2	2	2	2
77	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
86	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	2	1	1	1	2	2	0	0	0	1	1	1	1	1
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	0	0
90	0	0	0	0	?	?	?	0	?	?	?	?	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
92	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0
96	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
97	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	1	1	1	1	2	2	2	2	2	2	2	2
98	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	1	1	0	0	1	1	1	1	1	2	2	2
99	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2
100	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2
101	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2
102	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Continued

APPENDIX 2. *Continued*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Characters	Lonchopteridae	Platypezidae	Phoridae	Pipunculidae	*Eumerus*	*Merodon*	*Cheilosia pagana*	*Cheilosia morio*	*Cheilosia* (miners)	*Cheilosia* (borers)	*Portevinia*	*Cheilosia* (fungivores)	*Ferdinandea*	*Rhingia*	*Volucella inflata*	*Hammerschmidtia*	*Brachyopa*	*Lejogaster*	*Chrysogaster*	*Orthonevra*	*Neoascia*	*Sphegina*	*Psilota*	*Tropidia*	*Syritta*	*Xylota*	*Ceriana*	*Pocota*	*Chalcosyrphus*	*Xylotomima*
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
110	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	?	?	?	?	0	0	1	1	0	1	1	1	1	1	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
118	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	2	2	0	2	2	2	2	2	2	2
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
120	?	?	?	?	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
121	?	?	?	?	0	1	0	1	1	0	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
122	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	?	?	?	?	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	1	1	1	1	1
124	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	?	?	?	?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
128	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
130	?	?	?	?	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
133	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
134	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
136	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
137	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
138	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
139	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
140	?	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?
141	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
142	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
143	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
144	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
145	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
146	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
147	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
148	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
149	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
150	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
151	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	2	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
154	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
155	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
157	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Continued

APPENDIX 2. *Continued*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Characters	Lonchopteridae	Platypezidae	Phoridae	Pipunculidae	*Eumerus*	*Merodon*	*Cheilosia paganus*	*Cheilosia morio*	*Cheilosia* (miners)	*Cheilosia* (borers)	*Portevinia*	*Cheilosia* (fungivores)	*Ferdinandea*	*Rhingia*	*Volucella inflata*	*Hammerschmidtia*	*Brachyopa*	*Lejogaster*	*Chrysogaster*	*Orthonevra*	*Neoascia*	*Sphegina*	*Psilota*	*Tropidia*	*Syritta*	*Xylota*	*Ceriana*	*Pocota*	*Chalcosyrphus*	*Xylotomima*
158	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
159	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
161	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2
162	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
163	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
165	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
166	0	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
167	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
169	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
171	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	0	0	0	0	0	0	0
173	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
174	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
175	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
176	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
177	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0
178	?	?	?	?	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	2	2	0	1	1	1	1	1	1	1
179	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	0	?	?
180	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
181	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
182	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
183	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
184	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
185	?	?	?	?	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
186	?	?	?	?	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
187	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Continued

APPENDIX 2. *Continued*

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Characters	*Brachypalpus*	*Brachypalpoides*	*Spilomyia*	*Milesia*	*Criorhina*	*Temnostoma*	*Callicera*	*Blera*	*Caliprobola*	*Lejota*	*Myolepta*	*Sericomyia*	*Mallota*	*Eristalinus*	*Eristalis*	*Myathropa*	*Helophilus*	*Anasimya*	*Parhelophilus*	*Volucella bombylans*	*Volucell apellucens*	*Volucella inanis*	*Microdon*	*Pipizella*	*Neocnemodon*	*Trichopsomyia*	*Pipiza*	*Heringia*	*Melanostoma*	*Xanthandrus*
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
4	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	3	3	3	3	3	3	3	3
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
6	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	?	?	?	?	?	?	?
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2	2
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	?	?	?	?	?	?	?
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	?	?	?	?	?	?	?
11	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	2	1	1	1	1	1	1	1
12	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
13	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	?	?	?	?	0	?
14	1	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	2	1	1	1	1	1	1	1	1	1
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	2	2	0	2	2	2	2	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
26	2	2	2	1	3	3	3	1	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
27	2	2	2	2	2	2	2	0	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
28	2	2	2	1	2	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
30	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36	0	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
38	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
47	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?
48	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	?	?	?	?	?	?	?	?
49	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	0	1	1	?	?	?	?	?	?	?	?
50	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	?	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	?	0	0	0	0	0	0	0
52	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	2	1	1	1	0	0	0	?	1	1	1	1	1	1	1
53	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0
54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0

Continued

APPENDIX 2. *Continued*

Characters	31 *Brachypalpus*	32 *Brachypalpoides*	33 *Spilomyia*	34 *Milesia*	35 *Criorhina*	36 *Temnostoma*	37 *Callicera*	38 *Blera*	39 *Caliprobola*	40 *Lejota*	41 *Myolepta*	42 *Sericomyia*	43 *Mallota*	44 *Eristalinus*	45 *Eristalis*	46 *Myathropa*	47 *Helophilus*	48 *Anasimya*	49 *Parhelophilus*	50 *Volucella bombylans*	51 *Volucell apellucens*	52 *Volucella inanis*	53 *Microdon*	54 *Pipizella*	55 *Neocnemodon*	56 *Trichopsomyia*	57 *Pipiza*	58 *Heringia*	59 *Melanostoma*	60 *Xanthandrus*
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
56	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0
57	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0
58	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1
59	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
61	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
62	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
63	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
65	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
66	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
67	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0
68	2	0	1	2	1	1	1	0	0	1	?	1	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?
69	1	1	1	1	1	1	1	1	1	1	0	1	1	2	2	2	2	2	2	0	0	0	?	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	2	2	2	2	2	2	2	2	2	2	0	1	2	1	1	1	1	1	1	1	1	2	0	0	0	0	0	0	0	0
77	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
79	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
80	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0
85	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
88	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0
89	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
92	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?
93	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	2	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?
95	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	1	1	0	0	0	?	?	?	?	?	?	?	?
96	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?
97	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	0	?	?	?	?	?	?	?	?
98	2	2	2	3	0	?	3	2	2	2	2	0	2	3	3	2	3	0	3	1	1	3	?	?	?	?	?	?	?	?
99	2	2	3	3	0	?	0	2	3	2	2	0	2	3	3	3	3	0	3	0	1	3	?	?	?	?	?	?	?	?
100	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	2	3	0	1	0	?	?	?	?	?	?	?	?
101	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	?	?	?	?	?	?	?	?
102	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
103	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
104	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Continued

APPENDIX 2. *Continued*

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Characters	*Brachypalpus*	*Brachypalpoides*	*Spilomyia*	*Milesia*	*Criorhina*	*Temnostoma*	*Callicera*	*Blera*	*Caliprobola*	*Lejota*	*Myolepta*	*Sericomyia*	*Mallota*	*Eristalinus*	*Eristalis*	*Myathropa*	*Helophilus*	*Anasimya*	*Parhelophilus*	*Volucella bombylans*	*Volucell apellucens*	*Volucella inanis*	*Microdon*	*Pipizella*	*Neocnemodon*	*Trichopsomyia*	*Pipiza*	*Heringia*	*Melanostoma*	*Xanthandrus*
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	2
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
112	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	0	2	2	2	2	2	2	2
118	2	2	2	2	2	1	1	1	2	2	2	2	2	2	2	2	2	2	2	?	?	?	0	1	1	1	1	1	1	1
119	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1
120	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
121	2	2	1	1	2	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
122	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
124	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0
128	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
133	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
134	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
135	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	2	2
136	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
137	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
138	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
139	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
140	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	2	2
141	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
142	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
143	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1
144	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	0	0
145	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
146	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
147	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	2	0
148	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0
149	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
151	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
154	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
155	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
157	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
158	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
159	2	2	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	2	2	2	2	2	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
161	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	0	0
162	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	2	0	0

Continued

APPENDIX 2. *Continued*

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Characters	*Brachypalpus*	*Brachypalpoides*	*Spilomyia*	*Milesia*	*Criorhina*	*Temnostoma*	*Callicera*	*Blera*	*Caliprobola*	*Lejota*	*Myolepta*	*Sericomyia*	*Mallota*	*Eristalinus*	*Eristalis*	*Myathropa*	*Helophilus*	*Anasimya*	*Parhelophilus*	*Volucella bombylans*	*Volucell apellucens*	*Volucella inanis*	*Microdon*	*Pipizella*	*Neocnemodon*	*Trichopsomyia*	*Pipiza*	*Heringia*	*Melanostoma*	*Xanthandrus*
163	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
165	2	2	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	1	1	2	1	2	0	0
166	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
167	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
169	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
171	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
173	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?
174	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
175	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
176	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
177	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
178	1	1	1	1	1	0	1	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0
179	?	?	?	?	?	?	?	1	1	1	0	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?
180	1	1	1	1	1	0	1	2	1	1	1	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0
181	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?
182	1	1	1	1	1	1	1	2	2	2	3	3	3	3	3	3	3	3	3	0	0	0	0	0	0	0	0	0	0	0
183	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
184	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
185	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
186	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?
187	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Continued

APPENDIX 2. *Continued*

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Characters	*Toxomerus*	*Platycheirus*	*Pyrophaena*	*Rohdendorfia*	*Baccha*	*Sphaerophoria*	*Allograpta*	*Meliscaeva*	*Episyrphus*	*Betasyrphus*	*Parasyrphus*	*Fagisyrphus*	*Syrphus*	*Melangyna*	*Chrystotoxum*	*Epistrophe*	*Meligramma*	*Epistrophella*	*Xanthogramma*	*Doros*	*Leucozona*	*Didea*	*Megasyrphus*	*Erizona*	*Dasysyrphus*	*Paragus*	*Eupeodes*	*Scaeva*	*Ischiodon*
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
8	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
10	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
13	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
38	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
47	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Continued

APPENDIX 2. *Continued*

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Characters	*Toxomerus*	*Platycheirus*	*Pyrophaena*	*Rohdendorfia*	*Baccha*	*Sphaerophoria*	*Allograpta*	*Meliscaeva*	*Episyrphus*	*Betasyrphus*	*Parasyrphus*	*Fagisyrphus*	*Syrphus*	*Melangyna*	*Chrysotoxum*	*Epistrophe*	*Meligramma*	*Epistrophella*	*Xanthogramma*	*Doros*	*Leucozona*	*Didea*	*Megasyrphus*	*Eriozona*	*Dasysyrphus*	*Paragus*	*Eupeodes*	*Scaeva*	*Ischiodon*
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
79	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
80	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
81	2	2	2	2	2	1	1	2	2	2	2	2	2	2	2	2	3	2	2	2	2	3	3	3	3	3	3	2	2
82	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
83	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	0	0	1	1	1	0	1	1	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
95	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
96	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
97	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Continued

APPENDIX 2. *Continued*

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Characters	*Toxomerus*	*Platycheirus*	*Pyrophaena*	*Rohdendorfia*	*Baccha*	*Sphaerophoria*	*Allograpta*	*Meliscaeva*	*Episyrphus*	*Betasyrphus*	*Parasyrphus*	*Fagisyrphus*	*Syrphus*	*Melangyna*	*Chrystotoxum*	*Epistrophe*	*Meligramma*	*Epistrophella*	*Xanthogramma*	*Doros*	*Leucozona*	*Didea*	*Megasyrphus*	*Erizona*	*Dasysyrphus*	*Paragus*	*Eupeodes*	*Scaeva*	*Ischiodon*
110	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2	2	2	1	2	2	1
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
117	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
118	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
119	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
120	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
121	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
124	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
125	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
126	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
127	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
128	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1	0	0	0	2	2	2	1	2	1	1	1
132	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
133	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
134	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
135	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
136	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
137	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
138	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
141	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
142	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
143	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1
144	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
146	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
147	0	3	0	0	0	0	0	0	0	0	0	0	1	0	2	2	2	2	2	2	2	2	2	2	2	3	1	1	1
148	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	1	1	1	1
149	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
150	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
151	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
152	1	2	2	2	2	2	2	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
154	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
155	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
157	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	0	0	1	2	2	1	1	1
158	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	0	0	2	2	2	2	1	1	1	1	1
159	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	2	0	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
161	0	0	1	1	0	1	1	2	2	2	1	1	2	1	2	1	1	1	2	2	2	2	2	2	2	0	2	2	2
162	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	2	1	1	1
163	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	2	1	0	2	2	2
164	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	1	1	1	1	2	2	2	2	2	0	0	0	0

Continued

APPENDIX 2. *Continued*

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Characters	*Toxomerus*	*Platycheirus*	*Pyrophaena*	*Rohdendorfia*	*Baccha*	*Sphaerophoria*	*Allograpta*	*Meliscaeva*	*Episyrphus*	*Betasyrphus*	*Parasyrphus*	*Fagisyrphus*	*Syrphus*	*Melangyna*	*Chrystotoxum*	*Epistrophe*	*Meligramma*	*Epistrophella*	*Xanthogramma*	*Doros*	*Leucozona*	*Didea*	*Megasyrphus*	*Erizona*	*Dasysyrphus*	*Paragus*	*Eupeodes*	*Scaeva*	*Ischiodon*
165	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	2	0	0	1	1	1	0	1	1	0	0	0
166	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
167	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
169	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
170	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0
171	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
173	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
174	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
175	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
176	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
177	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
178	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
179	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
182	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
183	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
184	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
185	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
186	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
187	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

APPENDIX 3. Character state changes

Node	Ancestor	Character	Ancestral state	Derived state
1 Lonchopteridae	176	1	0	1
2 Platypezidae	176	5	0	1
3 Phoridae	175	none		
4 Pipunculidae	174	5	0	1
		137	1	0
5 *Eumerus*	173	14	1	0
		52	1	0
		58	2	0
		121	1	0
		123	1	0
6 *Merodon*	172	14	0	1
		58	2	1
7 *Cheilosia paganus*	168	54	0	1
		121	1	0
8 *Cheilosia morio*	169	12	0	1
		21	0	1
		66	0	2
		85	0	1
		102	0	1
		126	0	1
		178	0	2
		180	0	1
		186	0	1
9 *Cheilosia* (miners)	170	91	1	0
		117	1	0

Continued

APPENDIX 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
10 *Cheilosia* (borers)	171	54	0	1
		58	1	2
		123	0	1
11 *Portevinia*	171	12	0	1
		165	1	0
		174	0	1
		175	0	1
12 *Cheilosia* (fungivores)	166	12	2	1
		58	2	0
13 *Ferdinandea*	165	12	2	1
		58	2	1
		88	2	1
		130	1	0
14 *Rhingia*	165	none		
15 *Volucella inflata*	163	25	0	1
		26	0	1
		27	0	1
		47	1	0
		48	1	0
		55	0	1
		88	2	1
		117	2	0
		121	2	1
		123	1	0
		186	1	0
16 *Hammerschmidtia*	162	28	0	1
17 *Brachyopa*	162	52	1	2
		68	0	1
		76	1	2
		178	0	1
18 *Lejogaster*	159	65	0	1
19 *Chrysogaster*	160	none		
20 *Orthonevra*	160	none		
21 *Neoascia*	157	45	0	1
		65	0	1
22 *Sphegina*	156	58	2	1
		68	0	1
23 *Psilota*	155	25	0	2
		29	1	0
		118	2	0
		145	0	1
		178	1	0
24 *Tropidia*	154	25	0	1
		26	1	2
		27	1	2
		40	0	1
		65	0	1
		123	1	0
25 *Syritta*	153	28	1	0
		29	1	0
		49	2	0
		57	2	1
26 *Xylota*	152	65	0	1
27 *Ceriana*	151	52	1	0
		89	0	1
		114	0	1
28 *Pocota*	142	none		
29 *Chalcosyrphus*	145	none		

Continued

Appendix 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
30 *Xylotomima*	145	none		
31 *Brachypalpus*	146	42	0	1
32 *Brachypalpoides*	146	35	1	2
		68	2	0
33 *Spilomyia*	148	25	2	0
		43	0	1
		44	0	1
		89	0	1
		98	3	2
		177	0	1
34 *Milesia*	148	26	2	1
		28	2	1
		36	0	1
		68	1	2
		77	1	0
35 *Criorhina*	149	33	0	1
		38	0	1
		44	0	1
		52	1	0
		74	0	1
		98	3	0
36 *Temnostoma*	150	13	0	1
		20	0	1
		36	0	1
		37	0	1
		49	2	3
		75	0	1
		97	2	3
		107	0	1
		120	1	0
		121	2	1
		146	0	1
		159	2	0
		165	2	0
		178	1	0
		180	1	0
37 *Callicera*	150	56	0	1
		94	0	2
		145	0	1
38 *Blera*	140	29	1	0
		52	1	0
		91	0	1
		118	2	1
		121	2	1
		180	1	2
39 *Caliprobola*	140	63	1	0
		99	2	3
40 *Lejota*	138	25	0	2
41 *Myolepta*	137	26	1	0
		27	1	0
		52	1	0
		66	1	0
		67	1	0
		69	1	0
		76	1	0
		106	0	1
		179	1	0
42 *Sericomyia*	136	23	0	1

Continued

Appendix 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
		98	2	0
		99	2	0
43 *Mallota*	135	26	1	0
		64	1	0
		76	1	2
		86	0	1
		88	0	1
		107	0	1
		122	0	1
44 *Eristalinus*	134	93	0	2
45 *Eristalis*	133	none		
46 *Myathropa*	133	52	1	2
		98	3	2
47 *Helophilus*	131	68	0	1
		86	0	1
		87	0	1
48 *Anasimya*	130	14	0	1
		98	3	0
		99	3	0
		100	3	2
49 *Parhelophilus*	130	25	0	1
50 *Volucella bombylans*	128	25	0	1
		48	1	0
		117	2	0
51 *Volucella pellucens*	127	88	0	2
		99	3	1
		100	0	1
52 *Volucella inanis*	126	84	0	2
		88	0	3
53 *Microdon*	125	11	1	2
		22	0	1
		55	0	1
		66	1	0
		108	0	1
		117	2	0
		120	1	0
		123	1	0
54 *Pipizella*	121	84	0	1
		115	0	1
		118	0	1
		147	0	1
		162	2	1
55 *Neocnemodon*	122			
56 *Trichopsomyia*	123			
57 *Pipiza*	124	165	2	1
58 *Heringia*	124			
59 *Melanostoma*	119	147	0	2
60 *Xanthandrus*	118	143	0	1
		153	0	1
61 *Toxomerus*	112	143	0	1
		150	0	1
		159	1	0
		162	0	1
62 *Platycheirus*	114	147	0	3
63 *Pyrophaena*	115			
64 *Rhodendorfia*	115	167	0	1
65 *Baccha*	116	83	0	1
66 *Sphaerophoria*	117			

Continued

Appendix 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
67 *Allograpta*	117			
68 *Meliscaeva*	109	154	0	1
69 *Episyrphus*	110			
70 *Betasyrphus*	110			
71 *Parasyrphus*	107	83	0	1
		144	1	0
72 *Fagisyrphus*	106			
73 *Syrphus*	105	143	0	1
		147	0	1
		165	1	0
		168	0	1
74 *Melangyna*	105	161	2	1
75 *Chrysotoxum*	103	131	0	2
76 *Epistrophe*	99			
77 *Meligramma*	101	81	1	2
		157	0	1
78 *Epistrophella*	101	112	1	2
		165	1	2
79 *Xanthogramma*	102			
80 *Doros*	102			
81 *Leucozona*	97	143	0	1
82 *Didea*	96			
83 *Megasyrphus*	96	163	2	1
84 *Eriozona*	94	84	1	0
		165	1	0
		170	1	0
85 *Dasysyrphus*	93	163	2	1
86 *Paragus*	92	112	2	1
		131	1	2
		152	0	1
		159	0	2
		161	2	0
		162	1	2
		163	2	0
87 *Eupeodes*	91	113	0	1
88 *Scaeva*	90			
89 *Ischiodon*	90	112	2	1
90	91	81	3	2
91	92	84	1	0
		103	0	1
		129	1	0
		143	0	1
		147	3	1
		157	2	1
		165	1	0
		170	1	0
92	93	24	0	1
		104	0	1
		147	2	3
		148	2	1
		164	2	0
93	94	131	2	1
		157	1	2
		158	2	1
94	95	159	1	0
95	97	81	2	3
		112	1	2
		129	0	1

Continued

APPENDIX 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
		131	0	2
96	95	156	0	1
		157	1	0
97	98	163	1	2
98	103	148	1	2
		158	1	2
99	98	84	1	2
		161	2	1
		170	1	0
100	99	143	0	1
		157	1	0
		158	2	1
		164	2	1
101	100	129	0	1
		131	0	1
102	100	84	2	0
		158	1	0
		160	0	1
		161	1	2
		162	1	0
		165	1	0
103	104	142	0	1
		147	0	2
		170	0	1
104	106	133	0	1
		161	1	2
105	104	152	0	1
106	107	84	0	1
		127	0	1
107	108	116	0	1
		152	1	0
		161	2	1
		162	0	1
		164	0	2
		165	0	1
108	111	128	1	0
		144	0	1
		148	0	1
		157	0	1
		161	0	2
		163	0	1
109	108			
110	109	157	1	0
111	118	81	1	2
		125	0	1
		149	1	2
		159	0	1
112	111	169	0	1
113	112	152	1	2
114	113	125	1	0
115	114	161	0	1
		170	0	1
116	113	165	0	1
117	116	81	2	1
		161	0	1
118	119	152	0	1
119	120	110	1	2
		135	1	2

Continued

APPENDIX 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
		140	1	2
		144	1	0
		161	1	0
120	125	46	0	1
		58	2	1
		81	0	1
		147	1	0
		158	0	1
		171	0	1
121	120	3	0	1
		159	0	2
		162	0	2
		164	0	1
		165	0	1
		170	0	1
122	121	112	1	0
123	122	165	1	2
124	123	112	0	1
125	126	4	1	3
		8	1	2
		9	0	2
		52	0	1
		53	1	0
		54	1	0
		59	1	0
		67	1	0
		76	2	0
		91	1	0
		110	0	1
		119	0	1
		139	1	0
		149	0	1
		161	2	1
126	127	2	0	1
		5	0	1
		7	1	2
		14	2	1
		60	1	0
		61	1	0
		76	1	2
		97	1	0
		98	1	3
		111	1	0
		130	1	0
127	128	14	0	2
		29	0	1
		49	0	1
		99	0	3
		146	0	1
128	129	7	0	1
		8	0	1
		10	0	1
		15	0	1
		53	0	1
		54	0	1
		79	0	2
		80	0	1
		82	0	1

Continued

Appendix 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
		88	2	0
		139	0	1
129	164	6	1	2
		16	0	2
		60	0	1
		61	0	1
		67	0	1
		76	0	1
		78	0	1
		117	1	2
		121	1	2
		123	0	1
		124	0	1
		135	0	1
		140	0	1
		161	1	2
		186	0	1
130	131	93	0	1
131	132	90	2	1
		95	2	1
132	134	173	0	1
133	132	93	0	3
134	135	69	1	2
		73	0	1
		90	0	2
		95	0	2
		98	2	3
		99	2	3
		145	0	1
135	136	13	0	1
		14	1	0
		50	0	1
		51	0	1
		60	0	1
		68	1	0
		72	0	1
		100	2	3
		141	0	1
		161	2	1
136	137	64	0	1
		94	0	1
		180	1	2
		181	0	1
137	138	28	1	0
		30	1	0
		65	0	1
		76	2	1
		182	2	3
138	139	89	0	1
139	141	88	1	0
		178	1	2
		179	0	1
		182	1	2
140	139	27	1	0
		68	1	0
141	151	54	0	1
		98	1	2
		99	1	2

Continued

Appendix 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
142	141	25	0	2
		63	1	0
143	142	26	1	2
		27	1	2
		28	1	2
		31	0	1
		65	0	1
144	143	68	1	2
145	144	25	2	0
		41	0	1
146	144			
147	143	14	1	0
		32	0	1
		34	0	1
		39	0	1
		63	0	1
		77	0	1
		88	1	0
		98	2	3
		99	2	3
148	147	121	2	1
		145	0	1
149	147	26	2	3
		65	1	0
		99	3	0
150	149	14	0	1
		89	0	1
		118	2	1
151	152	30	0	1
		53	0	1
		76	1	2
152	153	14	0	1
		68	0	1
		88	0	1
153	154	53	1	0
		63	0	1
		76	2	1
154	155	28	0	1
		52	0	1
		89	1	0
		151	2	0
		172	2	0
		177	1	0
155	156	14	1	0
		49	1	2
		53	0	1
		76	1	2
		88	2	0
		97	1	2
		98	0	1
		99	0	1
		100	1	2
		101	1	2
		178	2	1
156	157	26	0	1
		27	0	1
		52	1	0
157	158	49	0	1

Continued

APPENDIX 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
		92	0	1
		96	0	1
		100	0	1
		101	0	1
		111	1	0
		118	0	2
		139	0	1
		161	0	2
		178	0	2
158	161	62	0	1
		85	0	1
		89	0	1
		97	0	1
		151	0	2
		172	1	2
		177	0	1
		180	0	1
159	158	55	0	1
		63	0	1
		66	1	0
		67	1	0
		68	0	1
		69	1	0
		88	2	1
		91	0	1
		98	0	1
		105	0	1
		123	1	0
		151	2	1
		155	0	1
		173	0	1
160	159	none		
161	163	14	0	1
		29	0	1
		57	0	2
		60	1	0
		69	2	1
		80	0	2
		91	1	0
		119	0	1
		130	1	0
		135	1	2
		140	1	0
		159	0	2
		161	2	0
		165	0	2
		172	0	1
		182	0	1
		184	2	1
162	161	57	2	1
		70	0	1
		109	0	1
		129	0	1
163	129	4	1	2
		11	1	2
		16	2	1
		52	0	1
		59	1	2

Continued

Appendix 3. *Continued*

Node	Ancestor	Character	Ancestral state	Derived state
		69	0	2
		79	0	1
		92	1	0
		97	1	0
		98	1	0
164	166	4	0	1
		59	0	1
		88	0	2
		111	0	1
		130	0	1
		165	1	0
		184	1	2
165	164	91	1	0
166	167	6	0	1
		12	0	2
		52	1	0
		66	0	1
		120	0	1
		123	1	0
		161	0	1
167	172	117	0	1
		165	0	1
		185	0	1
168	167	71	0	1
169	168	8	0	2
		9	0	1
		58	2	1
170	169	11	1	0
		123	1	0
171	170	14	0	1
		112	1	2
		121	1	0
172	173	11	0	1
		91	0	1
173	174	17	0	1
		18	0	1
		19	0	1
		112	0	1
		128	0	1
		166	1	2
		176	0	1
		183	0	1
		184	0	1
		187	0	1
174	175	132	0	1
		134	0	1
		136	0	1
		138	0	1
175	176	137	0	1
		166	0	1