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The phylogeny and systematics of European predacious Syrphidae (Diptera) based on larval and puparial stages

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The external larval morphology of predacious Syrphidae is examined and compared with that of other groups of syrphids. Predacious larvae form a distinctive, monophyletic group. Relationships among 29 of the 34 European genera and subgenera are analysed using cladistic methods based on larval and puparial characters. Interpretation of the cladogram suggests that, within Syrphinae, a system of five tribes can be recognized and that a major trend has been a shift from ground layer to arboreal larval habitats, with an increasing degree of obligate dependence on soft-bodied Homoptera as prey. Generic diagnoses with biological and taxonomic notes are given and a key to genera based on larvae and puparia is provided.

KEY WORDS:—Phylogeny – systematics – predacious – syrphid – larva – puparia – cladistics.

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INTRODUCTION

Following a long period of controversy when various proposals were put forward (Matsumura & Adachi, 1917a, b; Curran, 1925; Sack, 1932; Fluke, 1931, 1933, 1935, 1950; Frey, 1946; Hull, 1949; Goffe, 1943, 1944, 1952; Coe, 1953; Glumac, 1960; Hippa, 1968) the most widely accepted classification of predacious Syrphidae (Syrphinae & Pipizini) is based on Dušek & Láska (1967) and Vockeroth (1969).

These revisions are largely derived from studies of adult characters, although Vockeroth (1969) was aware of the potential value of the larval stage for the taxonomy of the group, and Dušek & Láska (1967) used some larval characters to support their generic designations. In particular, Dušek & Láska (1967) found that within genera larvae were similar in shape, colour and characters on the posterior respiratory process (prp) demonstrating the value of larval characters for defining limits to genera. However, one of the problems facing Dušek & Láska (1967) and Vockeroth (1967) was that few larvae were available for study and published descriptions lacked necessary detail. Furthermore some of these were based on misidentifications (Vockeroth, 1969; Rotheray, 1986a). Recently, the larval stages of many more species have become available for study (Goeldlin de Tiefenau, 1974; Kula, 1983; Rotheray, 1986a, 1987a, 1988 and the collections of T. J. Dixon, J. C. Hartley and G. E. Rotheray now at the Royal Museum of Scotland). This material, plus loaned material acknowledged below, has made it possible to attempt to classify predacious syrphids using only larval characters.

Such a taxonomic analysis of larval stages offers an independent test of the currently accepted classification of this group. This is all the more relevant as numerous problems concerning the validity of some taxa (e.g. *Epistrophella* Dušek & Láska, 1967; *Fagisyrphus* Dušek & Láska, 1967; *Melangyna* (*Meligramma*) Frey, 1946; vide Vockeroth, 1969) and the proper placement of others (e.g. whether Pipizini belong to the Syrphinae (Hartley, 1961) or to the Milesiinae (Vockeroth, 1969)) still exist and might be better understood through thorough analysis of larval characters such as the mouthparts (Vockeroth & Thompson, 1987).

Although predacious larvae are the best known of all the various groups of syrphid larvae, we have found that their very distinctive external morphology has been only superficially described and sometimes misunderstood. Many previous authors (Metcalf, 1916; Vimmer, 1933; Heiss, 1938; Bhatia, 1939; Scott, 1939; Brauns, 1954; Hennig, 1952; Dixon, 1960; Dušek & Láska, 1959a, b, 1960a, b, 1961, 1962; Goeldlin de Tiefenau, 1974) have ignored the mouthparts, the ventral surface, and chaetotaxy in morphological and taxonomic studies. Misinterpretations include, for example, Metcalf (1916) who apparently confused the segmentation of the head and thorax with the result that his "prothorax" is, in reality, the mesothorax, an error which was not corrected by subsequent authors.

In this paper the external morphology of larvae and puparia of predacious syrphids is described and compared with larval stages of other syrphid groups, and relationships between genera examined using cladistic methods. Although the analysis is a partial one because larval stages of five of the 34 currently recognized European genera and subgenera were not obtained (the world total is 51 genera and subgenera, F. C. Thompson, personal communication), our principal conclusion is that a study of larval stages is a major aid in understanding the phylogeny of this group. A phylogeny, once established, will form a vital key in understanding the evolutionary ecology and biology of the predatory larval habit.

MATERIAL AND METHODS

Third stage larvae and/or puparia of 60 species were examined (see Appendix for list of material). As far as possible, living and preserved larval stages were studied; puparia, which retain most of the larval characters, were sometimes all that was available.

We wanted to use as objective a method as possible to produce groupings of taxa, and therefore chose to use a numerical technique. We used cladistic analysis, now so well established as to need no justification, and which is acknowledged to be very helpful in deducing the phylogeny of monophyletic groups (see Sokal, 1985). We used mainly parsimony (program PAUP, written by D. W. Swofford for the IBM-pc), but also used compatibility methods (program CLINCH, written by K. L. Fiala & G. F. Estabrook, implemented on the IBM 3081 of Cambridge University) for preliminary analysis.

Cladistic methods attempt to reconstruct evolutionary history by assuming that the phylogeny will be reflected in a nested pattern of shared derived characters. Parsimony and compatibility methods are different ways of dealing with inconsistencies in the phylogenetic information of different characters

(Felsenstein, 1983): parsimony looks for a phylogenetic tree of minimum length with the minimum number of parallel evolutionary events or reversals; compatibility uses only characters that contain no inconsistencies and looks for the largest set of compatible characters (Meacham & Estabrook, 1985), rejecting incompatible characters.

Our preliminary analysis using compatibility followed a hierarchical approach to secondary clique analysis (Meacham & Estabrook, 1985). We only present phylogenies obtained from parsimony methods since they were similar to but more detailed than those from compatibility; however, the results from compatibility were very influential in the one decision about recoding that we make (see below).

For the analysis using parsimony, the great flexibility of PAUP proved invaluable. For all runs, the relevant parameter settings were: MAXTREE = 100, HOLD = 5, MULPARS, ADDSEQ = CLOSEST, ROOT = ANCESTOR, OPT = DELTRAN. One run on the basal species used ALLTREES; otherwise, SWAP = GLOBAL was used. All characters had equal weighting, and all multistate characters were set to 'unordered', that is, any state derivable from any other. All runs resulted in multiple equally-parsimonious cladograms, which were then used as input to the program CONTREE, to calculate the 'strict' consensus tree (Rohlf, 1982).

Polarity of character states was determined by the outgroup method (Bishop, 1982). Although polarity is not used by PAUP to calculate the minimum length tree we give below our *a priori* assessment of polarity for comparison with the character table and the resulting consensus trees. For all runs, the consistency index of character 33 (colour) was lower, often much lower than other characters (always <0.22), indicating a low phylogenetic utility: for this reason we deleted it from all analyses.

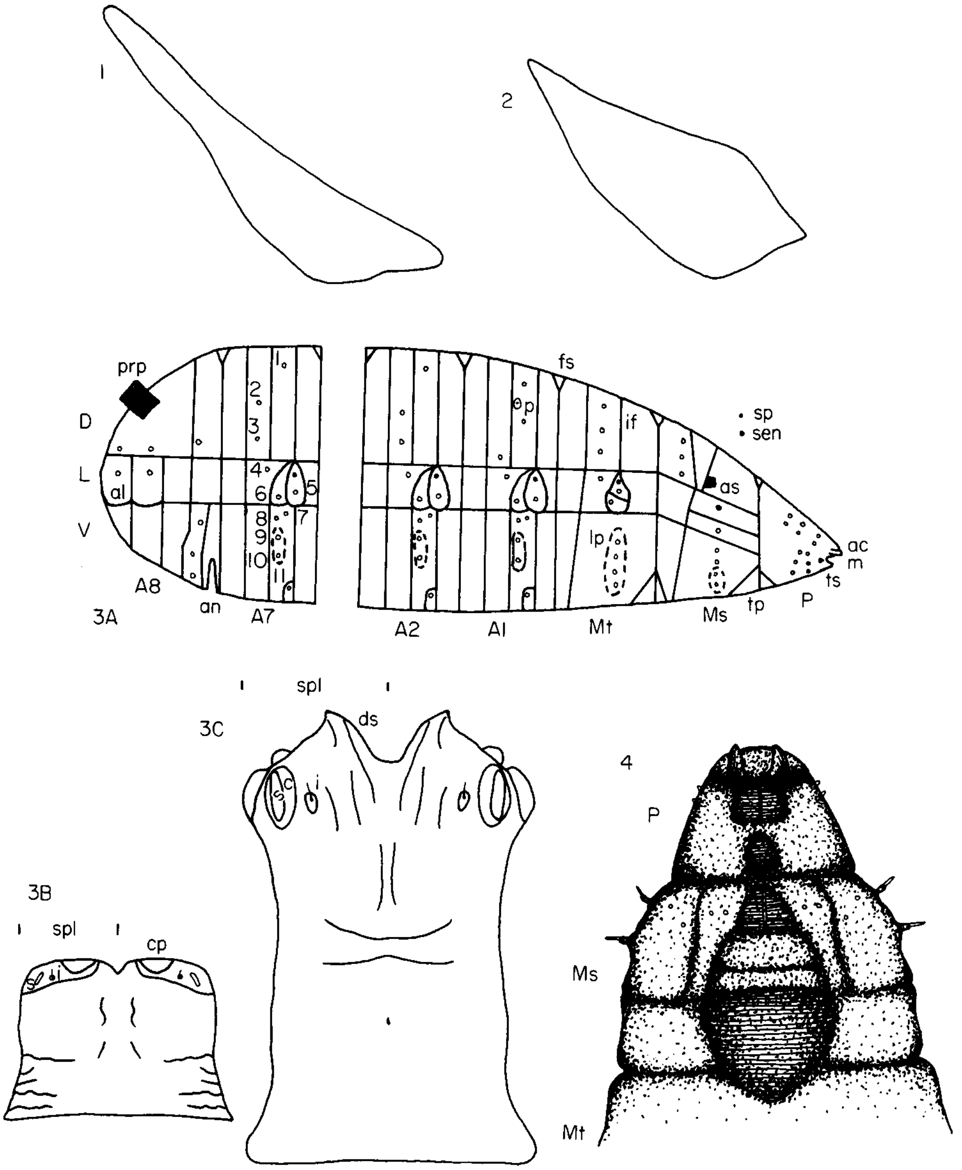
MORPHOLOGY OF THE THIRD STAGE PREDACIOUS LARVA

General features

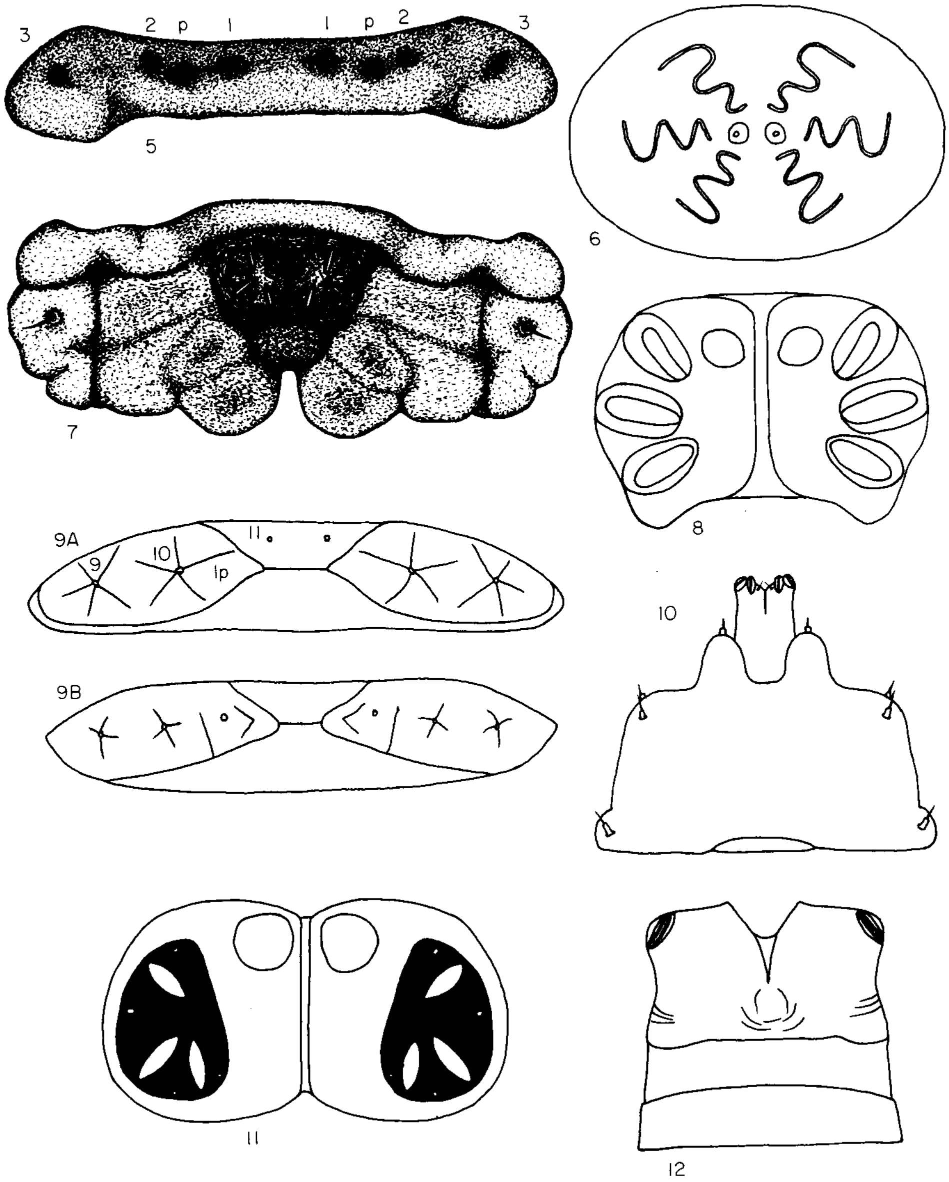
Head. The head is much reduced (Hartley, 1963). Dorsally, above the mouth, are a pair of antennal tubercles. Laterally, on either side of the mouth, is a pair of black pointed or triangular sclerites (Bhatia, 1939). These sclerites grip the prey during feeding, as can be seen by gently pulling prey from the mouthparts of a feeding larva.

Mouthpart structure forms one of the most distinctive features of predacious syrphid larvae. The mouthparts are pointed and adapted for piercing (Hartley, 1963). Mouthparts were studied by picking them out, with forceps, from the anterior end of puparia. Apart from minor differences in degree of sclerotization there is considerable uniformity in the shape and relative positions of the various parts of all species studied (Appendix). The mandibles of *Scaeva* and *Eupeodes* larvae differ from the general pattern in being subrectangular distally (Fig. 1) and the mandibles of larvae of *Pipiza*, *Neocnemodon*, *Heringia* and *Pipizella* in being quadrate (Fig. 2). Apart from these exceptions the head and mouthparts are of little value in separating genera but mouthpart structure provides an important recognition character for the group as a whole.

Thorax. Previous authors (e.g. Metcalf, 1916; Bhatia, 1939; Dušek & Láska, 1959a; Goeldlin de Tiefenau, 1974) confused the mesothorax with the



Figures 1–4. Fig. 1, Mandible of *Scaeva pyrastri*, lateral view. Fig. 2, Mandible of *Pipiza luteitarsis*, lateral view. Fig. 3. A, Map of the external morphology and chaetotaxy of a third stage predacious syrphid larva, al = anal lobes; an = anus; as = anterior spiracle; ac = antennomaxillary complex; fs = fold between segments; if = integumental folds; lp = locomotory prominence; m = mouth; p = patch of differentiated integument indicating position of pupal horns; prp = posterior respiratory process; sp = spiracle; sen = sensilla; tp = thoracic pads; ts = triangular sclerite at the side of the mouth; D = dorsal; L = lateral; V = ventral; P = prothorax; Ms = mesothorax; M = metathorax; A1, 2, 7, 8 = abdominal segments, segments 3–6 not shown as they are the same as 2 and 7; 1–11 = numbered sensilla. B, Posterior respiratory process of *Baccha obscuripennis*, anterior view, cp = circular plate; i = interspiracular ornamentation; s = spiracular slit; spl = spiracular plate. C, Posterior respiratory process of *Melangyna cincta*, anterior view, ds = dorsal spur. Fig. 4, Ventral surface of prothorax (P), mesothorax (Ms) and anterior part of metathorax (Mt) showing thoracic pads in *Syrphus ribesii*.



Figures 5–12. Fig. 5, Dorsal view second integumental fold of first abdominal segment of *Platycheirus scutatus*, 1, 2, 3 = sensilla; p = patch of differentiated cuticle indicating position where pupal horns will project. Fig. 6. Dorsal view, prp in *Xanthogramma pedissequum*. Fig. 7, Dorsal view, anal segment (A8) in *Syrphus ribesii*. Fig. 8, Dorsal view, prp in *Xanthandrus comtus*. Fig. 9, A, Ventral surface of second integumental fold of second abdominal segment in *Syrphus ribesii*, 9, 10, 11 = sensilla; lp = locomotory prominence. B, Ventral surface of second integumental fold of second abdominal segment in *Platycheirus scutatus*. Fig. 10, Ventral view, anal segment in *Pipiza luteitarsis*. Fig. 11, Dorsal view, prp in *Baccha obscuripennis*. Fig. 12, Anterior view, prp in *Meliscaeva auricollis*.

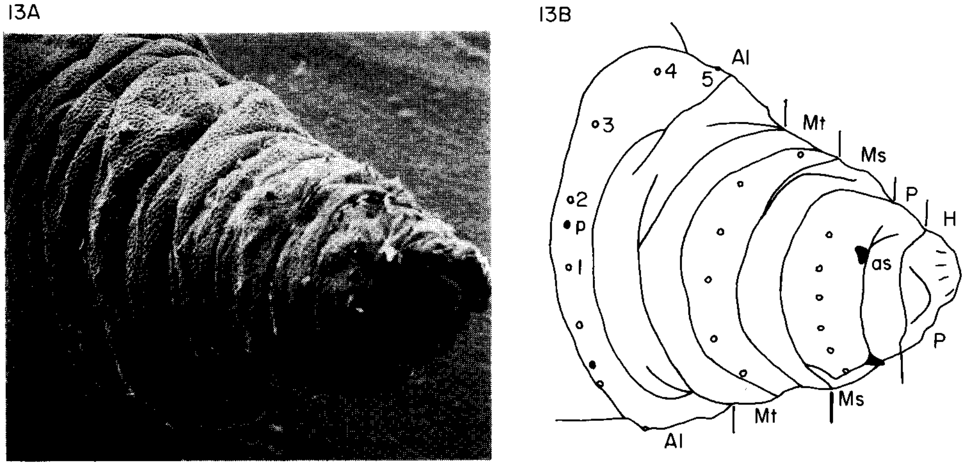


Figure 13. A, B, Dorso-lateral view of the anterior end of the third stage larva of *Platycheirus clypeatus*. A, scanning electron photomicrograph. B, Drawing made from photomicrograph, for explanation of numbers and letters see Fig. 3A, except that H = head, upper row of numbers and letters (Al, Mt, Ms, P, H) is the interpretation of segment boundaries according to Metcalf (1916), the lower row (Al, Mt, Ms, P) is the interpretation suggested in this study, see section the morphology of the third stage predacious larva for further details.

prothorax, perhaps because as with other groups of dipteran larvae, it was assumed that the anterior spiracles must be located on the prothorax. The result was that the next fold behind the one with the anterior spiracles was considered to be the mesothorax because no other was available between it and the metathorax: this "mesothorax" has no dorsal sensilla. Also the fold immediately anterior to the one with the spiracles, which has dorsal sensilla, had to be part of the head (see Fig. 13).

This lack of uniformity in sensilla patterns can be resolved once it is recognized that the anterior spiracles are, in fact, situated on the mesothorax. The "head" of authors is the prothorax, and their "mesothorax" is no more than the anterior fold of the metathorax (Fig. 13). This conclusion leads to uniformity not only in chaetotaxy but also in the pattern of transverse folds and structure of the ventral surface of the thorax. Compared with other groups the thorax of predacious larvae is greatly modified. The segments are easily differentiated from the abdominal segments in that they are narrower (Fig. 3). Dorsally, the prothorax is about half as wide or less than the mesothorax and the mesothorax about half as wide as the metathorax. The metathorax is about 0.6 times as wide as the first abdominal segment. Furthermore, on dorsal and lateral aspects of all three segments, surface pubescence or vestiture (Metcalf, 1916) is sparser and smaller. Often, vestiture is absent from the prothorax. Ventrally, raised pads are present on each segment differentiated by their surface sculpture of faint stippling and grooves (Fig. 4). These pads are possibly protective in limiting wear during the characteristic and very frequent prey-searching movement referred to as casting (Chandler, 1969; Rotheray, 1983) in which the thorax is repeatedly expanded on to the substrate. Unlike other dipteran groups (see Hinton, 1955) there is a locomotory prominence on the ventral surface of the metathorax. The anterior thoracic segments are able to expand fully and to retract into the metathorax. Diapausing or resting larvae characteristically retract the head, pro- and mesothorax into the metathorax.

The long, narrow prothorax, the position of the spiracles on the mesothorax, the absence or reduction of vestiture and the retractability of these segments are all interpreted as adaptations for catching, holding and piercing the small bodies of their prey. Following prey capture, the pro- and mesothorax are retracted and often the prey is lifted from the substrate. The prey is held by a pair of pointed sclerites at the sides of the mouth and sticky saliva in the inverted 'cup' caused by the retraction of the pro- and mesothorax. Possibly, the spiracles are better protected from being coated in saliva and prey secretions within the folds of the retracted mesothorax than if sited on the prothorax.

Abdomen. The abdomen consists of eight segments which, except for the first and eighth (anal) segments, are uniform in shape, size and external morphology. The first abdominal segment differs from the rest in not having sensilla pair 1 anterior to sensilla pair 2 (Fig. 3) and in some genera, for example, *Melanostoma* and *Platycheirus*, there are a pair of round patches or spots of differentiated cuticle between sensilla pairs 1 and 2 (Fig. 5). These spots indicate the place on the puparium through which the pupal horns appear. The anal segment is considerably modified with the posterior respiratory process (prp, Fig. 3) on the dorsal surface and, ventrally, the anus on the anterior margin. The tip of the anal segment is modified into a series of 2, 4, or 6 lobes of varying sizes and positions. These lobes grip the substrate at the start of a movement cycle which is initiated from the anal segment (Roberts, 1971). In some genera there are backwardly pointed projections on the anal segment above the lobes. In *Dasysyrphus* these projections break up the body outline as part of crypsis (Rotheray, 1986b).

Mid-dorsal projections may be present. Dorsally and laterally vestiture consists of pointed spines or flat papillae. The ventral surface of the abdomen is very distinctive. Vestiture is reduced, blunt-tipped or absent giving the integument a clear, shining appearance. Apart from the integumental folds the ventral surface is covered with a network of grooves about 0.45 mm wide. These grooves probably facilitate the spread of saliva and fluids from the anus across the ventral surface enabling larvae to hold on to the substrate (Rotheray, 1987b). Also present on abdominal segments 1–7 are pairs of locomotory prominences. These vary in shape from elongate ovals to cones. They lack crochets or musculature (*cf.* Hartley, 1961). Two or three sensilla and shallow grooves are present on the surface of each locomotory prominence.

Chaetotaxy

In predacious syrphid larvae segmental sensilla (*sensu* Hartley, 1961) may be with or without basal papillae and apical setae. Unlike most milesiine larvae (Hartley, 1961) there is only one apical seta per sensillum. Setae taper to a point in most genera except *Pipizella* in which they are club-tipped (Dixon, 1960). Sensilla were uniform in their numbers and positions on segments in all taxa examined except *Pipizella* (Table 1). This contrasts with milesiine genera, many of which are characterized by their sensilla (Table 1). The only genus with a different pattern of sensilla was *Pipizella* in which there was one less pair of sensilla: either sensilla 7 and 8 have fused or one or other has been lost. Dorsal and dorsolateral sensilla are usually borne on papillae and have setae. Laterally, papillae are always present but setae variably so. On the ventral surface setae are absent, except on the metathorax of larvae of *Eupeodes* and *Scaeva*, and papillae are either short or absent. Overall, the position, number and type of segmental sensilla are of limited value for separating genera but provide good recognition characters for the group as a whole.

Diagnostic characters for the predacious third stage syrphid larva (Syrphinae + Pipizini)

Pointed mouthparts and a pair of triangular or pointed sclerites at the sides of the mouth; anterior spiracles on the mesothorax; thorax narrower than the abdominal segments and with reduced vestiture or vestiture absent; prothorax elongate; protective pads on the ventral surface of the thorax; pro and mesothorax capable of retracting completely into the metathorax; chaetotaxy (pairs of sensilla) prothorax 12, mesothorax 9, metathorax 10, abdominal segments 1–7 11 (10 in *Pipizella*), anal segment 8; sensilla with or without basal papillae and apical setae, never more than one apical seta per sensillum; ventral surface of the abdomen usually without apical setae and vestiture or vestiture reduced; usually ventral surface appears as a clear shining strip with a network of shallow grooves between the integumental folds; locomotory prominences on the metathorax and first seven abdominal segments; tip of the anal segment with up to 3 pairs of lobes; posterior spiracles borne on a short sclerotized process on the anal segment; spiracular slits radial, and straight except *Xanthogramma* in which they are wavy; with cryptic colour patterns and shapes.

Characters used in the analysis

Characters were chosen from the entire body of the larval and puparial stages. Character state distributions are given in Table 2. The numbers below correspond to those used in Table 2. Numbers in parentheses after character states show polarity and unless otherwise stated—(0) = primitive; (1) = derived; (2) = further derived.

TABLE 1. Numbers of pairs of sensilla on various segments of third stage syrphid larvae

	Prothorax	Mesothorax	Metathorax	Abdominal segments 1–7	Anal segment
*Volucella**	10	3	9	10	7
*Rhingia**	12	8	8	9	6
*Eristalis**	12	9	9	11	8
*Neoascia**	12	9	9	11	8
*Brachyopa**	12	10	9	11	7
*Syritta**	13	11	10	11	8
*Sphegina**	13	12	11	12	9
*Chrysogaster**	13	12	12	11	9
Cheilosia	11	9	9	10	7
Syrphinae & Pipizini	12	9	10	11†	8

*Data from Hartley (1961).
†10 in *Pipizella*

TABLE 2. Character state distributions in Syrphinae + Pipizini for characters used in cladistic analysis. (See Appendix for species studied.) Numbers in left-hand column and remaining columns represent characters and states discussed in text under 'Characters used in the analysis'.

Character	*Pipiza*	*Pipizella*	*Neocnemodon*	*Heringia*	*Melanostoma*	*Xanthandrus*	*Platycheirus*	*Pyrophaena*	*Baccha*	*Sphaerophoria*	*Episyrphus*	*Meliscaeva*	*Paragus*	*Dasysyrphus*	*Meligramma*	*Epistrophella*	*Didea*	*Megasyrphus*	*Eupeodes*	*Scaeva*	*Syrphus*	*Melangyna*	*Fagisyrphus*	*Epistrophe*	*Leucozona*	*Parasyrphus*	*Chrysotoxum*	*Xanthogramma*	*Eriozona*
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	0
2.	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
3.	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	0	0
4.	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	0	0
5.	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
6.	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
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	0	1	0
8.	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
9.	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	0
10.	0	–	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11.	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
12.	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
13.	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	1	0	0	0
14.	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
15.	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1	2	2	1	1	0	0	0	0	0	0	2	0	2
16.	0	0	0	0	0	0	1	1	1	0	1	1	2	2	2	1	2	2	2	1	1	1	1	1	1	1	1	1	2
17.	0	1	0	0	0	0	0	0	0	0	0	0	2	1	2	2	1	1	0	0	1	1	1	2	1	0	1	0	0
18.	1	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0
19.	2	2	2	2	0	0	1	1	1	1	1	1	2	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0
20.	2	1	2	2	0	0	0	0	0	0	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
21.	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1
22.	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	2	1	2	2	1	1	1	1	2	1	1	1	2
23.	0	0	0	0	0	1	2	2	2	2	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
24.	1	1	1	1	0	0	0	1	0	1	2	2	0	2	1	1	2	2	2	2	2	1	1	1	2	1	2	2	2
25.	1	1	1	2	0	0	0	0	1	1	0	0	1	1	1	2	1	1	0	0	0	1	1	1	1	1	1	0	0
26.	1	1	1	1	0	0	0	0	0	0	0	0	0	2	1	1	2	2	0	0	2	2	2	2	2	2	2	1	2
27.	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
28.	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	2	2	0	0	0	0	0	0	0	0	1	0	1
29.	0	0	0	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
30.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	2	2	1	1	0	2
31.	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	2	2	2	2	0	0	0	0	0	0	2	0	0
32.	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	2	2	2	1	1	0	1	0	1	0	0
33.	0	0	0	0	2	2	0	0	1	2	1	1	0	0	0	0	0	0	0	2	1	2	1	2	1	0	0	0	0
34.	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	0	0
35.	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	1

1. *Pupal horn.* A pair of pupal spiracles or horns are sometimes thrust through the patch of differentiated cuticle on abdominal segment 1 within a few days of pupariation. This character is shared with milesines. The presence of pupal horns is considered the primitive condition and their absence the derived condition (1).

2. *Patches of differentiated cuticle on abdominal segment one in the larval stage.* This character is shared with milesines and their presence is considered the primitive condition (0) (Fig. 5), their absence the derived condition (1).

3. *Ventral surface.* The ventral surface is usually clear of vestiture (1) or has the vestiture reduced in size (0) compared with vestiture on the dorsal surface.

4. *Mandibular shape.* In most species the mandibles are elongate and pointed (1). The Pipizini have quadrate mandibles (0) (Fig. 2).

5. *Apical setae on sensilla of metathorax.* In *Scaeva* and *Eupeodes* sensilla pairs 7, 9 and 10 have apical setae (1). These are lacking (0) in all other genera.

6. *Backwardly directed locomotory prominences.* In *Scaeva* and *Eupeodes* on segments 6 and 7 of the abdomen the tips of the locomotory prominences face backwards (1) (Rotheray, 1987b). Backwardly facing locomotory prominences are lacking in other genera (0).

7. *Spiracular form.* A characteristic feature of predacious syrphid larvae are the straight radial spiracular slits (0) (Hartley, 1961). In *Xanthogramma* however, although the spiracular slits are radial, they are distinctly wavy (1) (Fig. 6).

8. *Prp rim.* *Meliscaeva* larvae possess a basal rim (1), differentiated by its size and colour, around the prp. This is absent (0) in other genera.

9. *Dorso-lateral spicules.* In *Eupeodes* the spicules are almost touching, forming dark patches along the dorso-lateral margin (1). In other genera spicules are more evenly distributed without aggregating into dark patches (0).

10. *Position of sensilla pair 8 in relation to pair 7.* In most genera sensilla pair 8 is anterior to sensilla pair 7 (0), but in *Baccha* and *Episyrphus* this is not so (1).

11. *Grooves on anal segment.* Lateral to the prp there are sometimes a series of grooves on the integument of the anal segment. These are virtually absent (0) in many genera, but numerous in *Syrphus* (1) (Fig. 7).

12. *Number of abdominal sensilla.* In *Pipizella* there are ten pairs of sensilla on abdominal segments 1–7 (1). In other genera there are 11 pairs of sensilla (0).

13. *Shape of abdomen.* From above, the abdomen of the larval stage usually widens towards the anal segment (1). In a few genera (e.g. *Baccha*, *Parasyrphus*) the abdomen does not widen and is narrow and parallel (0).

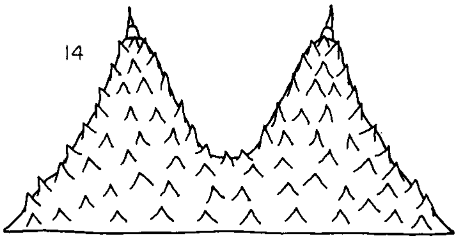
14. *Posterior projection on prp.* In *Xanthandrus comtus* there is an apical projection posterior to the prp (Fig. 8), a unique derived state (1).

15. *Mid-dorsal projections.* Sensilla pair 1 may be borne on tapering projections on abdominal segments 1–7. On each segment these projections may be close together and share a common base (1) (Fig. 14) or be separated by a distance of their own height or more (2). The absence of projections is considered the primitive condition (0).

16. *Derivation of colour pattern.* The possession of colour patterns is a distinctive feature of predacious syrphid larvae: the colour is derived from pigments in the haemolymph (0), the fat body (1) or fat body and vestiture (2).

17. *Shape of larva in cross-section.* There are three basic shapes: oval to sub-rectangular (0); dorso ventrally flattened (2); or only the lateral margins flattened to produce a sub-triangular shape (1).

14



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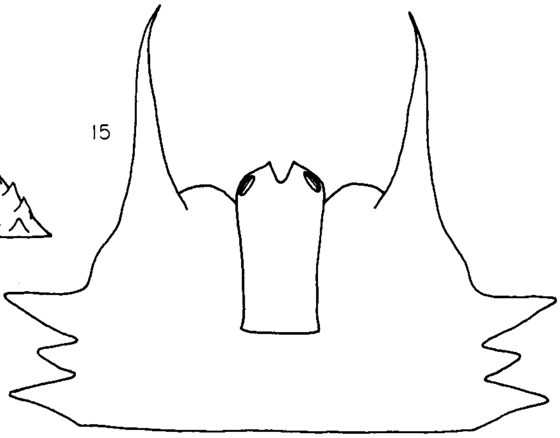

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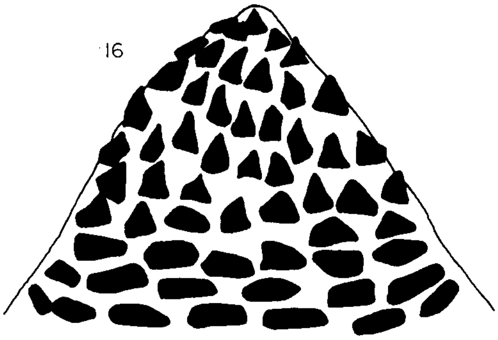

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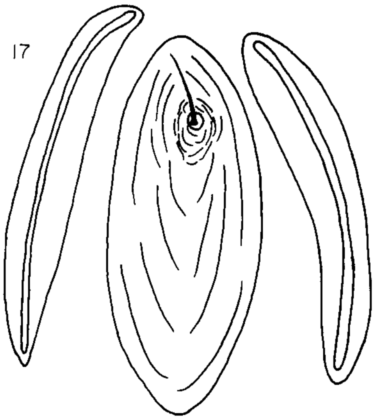

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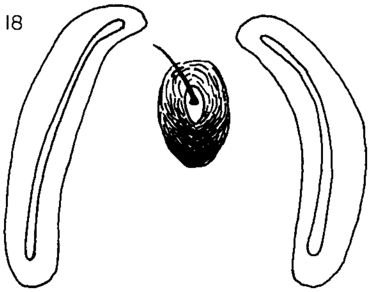

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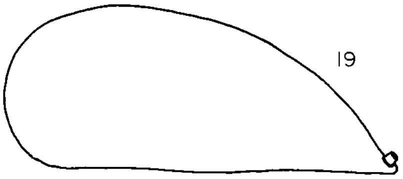

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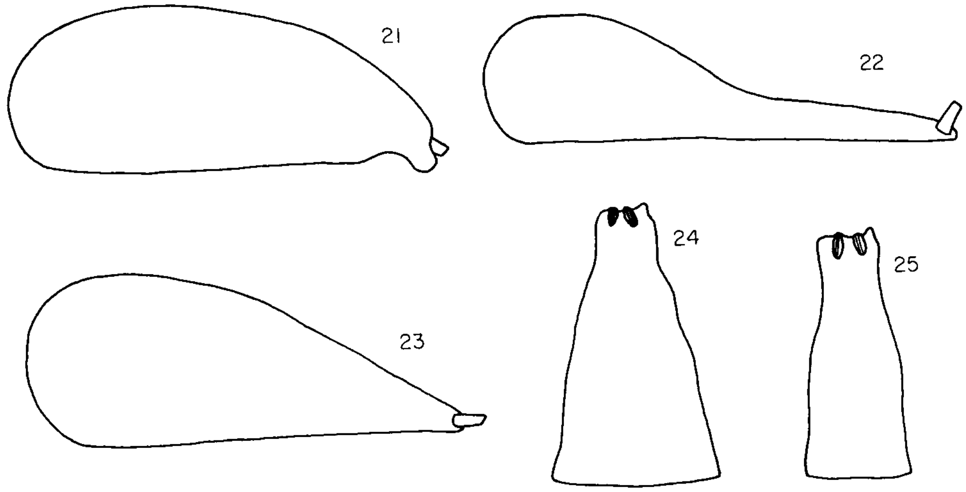
Figures 14–20. Fig. 14, Anterior view, mid-dorsal projections from second abdominal segment of *Dasysyrphus tricinctus*. Fig. 15, Dorsal view, anal segment (A8) in *Dasysyrphus tricinctus*. Fig. 16, Anterior view, lateral lobe bearing sensilla 4 (not shown) in *Eriozona syrphoides*. Fig. 17, Dorsal view, interspiracular ornamentation between spiracular slits 2 and 3 on prp of *Epistrophe grossulariae*. Fig. 18, Dorsal view, interspiracular ornamentation between spiracular slits 2 and 3 on prp of *Syrphus vitripennis*. Fig. 19, Lateral view, puparium of *Platycheirus peltatus*. Fig. 20, Lateral view, puparium of *Baccha obscuripennis*.



Figures 21–25. Fig. 21, Lateral view, puparium of *Scaeva selenitica*. Fig. 22, Lateral view, puparium of *Meligramma triangulifera*. Fig. 23, Lateral view, puparium of *Parasyrphus punctulatus*. Fig. 24, Lateral view, prp of *Meligramma triangulifera*. Fig. 25, Lateral view, prp *Parasyrphus punctulatus*.

18. *Sensilla, at the tip of the anal segment, borne on papillae.* Sensilla on the anal segment are with (1) or without (0) basal papillae.

19. *Interspiracular setae.* In most genera short setae are present between the spiracular slits on the prp (1). In a few genera setae are absent (0) and in others, e.g. Pipizini, the setae are long and conspicuous (2).

20. *Spiracular slits mounted on carinae.* Carinae may be absent (0). When present they are usually short so that their height is about the width of the spiracular slit (1), or tall in which case their height is more than the width of the spiracle (2).

21. *Dorsal spurs.* On the prp dorsal spurs may occur. Their absence is considered the primitive condition (0). When present they may be short, that is, height less than width (1), or tall in which case their height is more than their width (2).

22. *Position of spiracular slits.* In the primitive condition the spiracular slits do not appear over the sides of the prp (0). When spiracular slits do occur over the sides of the prp they may have less than 0.5 of their length down the sides (1), or more than 0.5 of their length over the sides (2).

23. *Spiracular plate.* The spiracular plate may be unicolorous (0) (entirely pale or black and contrasting in colour from the rest of the prp) or the spiracular slits may be pale but black lined (1) or the spiracular plate not differentiated in colour from the rest of the prp (2).

24. *Length of spiracular slits.* Short spiracular slits are up to 2 × long as broad (0). Longer spiracular slits are either between 2 × and 6 × as long as broad (1) or more than 6 × as long as broad (2).

25. *Length of prp.* The primitive condition may be a short prp (as long as broad or broader) (0). Most genera have a prp 1–2 times as long as broad (1). A few genera have a prp more than twice as long as broad (2), and there appears to have been a secondary loss of length in *Scaeva* and *Eupeodes*, although these are scored as 0.

26. *Shape of prp.* One state is considered to be a parallel prp (0) and another is a tapering prp (1). An enlarged tip (2) is associated with the development of various features of the prp such as lengthening of the spiracular slits, appearance of the dorsal spur, circular disc and interspiracular ornamentation (Fig. 3).

27. *Position of sensilla 11 on the abdominal segments.* In the primitive condition sensilla pair 11 are on a ridge-like locomotory prominence (0) (Fig. 9b). In the derived condition the locomotory prominence has become more cone-like and sensilla pair 11 is not part of the locomotory prominence but is usually anterior to sensilla pair 10 (1) (Fig. 9a).

28. *Projections on the anal segment.* Projections may be absent (0) or they may be rounded (1) or pointed (2).

29. *Groove above anal lobes.* Just above the anal lobes a deep, transverse groove occurs in some genera (1) but not in others (0).

30. *Interspiracular ornamentation.* Between the spiracles on the prp most genera have small cone shaped carinae (0) from which setae sometimes appear (Fig. 18). Their absence is considered a derived condition (1). A further derivation (2) is considered to be the occurrence of ridges instead of cones (Fig. 17).

31. *Integumental vestiture.* In the primitive condition vestiture consists of short, blunt-tipped papillae (0). Alternatively papillae may be pointed (1) and, sometimes, sclerotized (2).

32. *Anal lobes.* The tip of the anal segment may have 1 (0), 2 (1) or 3 (2) pairs of lobes.

33. *Colour.* The colour of larvae is green (0), translucent (1) or otherwise patterned (2) (Rotheray, 1986b).

34. *Spiracular plates sloping inward.* In most species the spiracular plates are level or slightly sloping laterally (0). In *Didea* and *Megasyrphus* the spiracular plates slope inwards towards each other (1).

35. *Sensilla 3–6 on projections.* Sensilla 3–6 may be borne on tapering projections which give the larva a serrate outline. The absence of projections is considered the primitive condition (0) and their presence the derived condition (1).

GENERIC RELATIONSHIPS

Generic limits

The pattern of character states provide considerable support for most of the generic boundaries erected since 1960 by Dušek & Láska (1967), Vockeroth (1969) and Hippa (1968) (Fig. 27). Species within genera show consistent character states (see Appendix). Several genera that are very similar as adults have completely different larvae (e.g. *Syrphus* and *Epistrophe*). In view of the earlier confusion in generic limits based on adults, larval morphology can be used to help resolve some of these problem areas.

The Pipizini (see Table 3)

The Pipizini are a well-defined aggregate according to mandible structure (Fig. 2), various characters of the prp, shape of the ventral surface and colour patterning (Table 2). That they properly belong within Syrphinae, and not elsewhere (see Vockeroth, 1969), is supported by their sharing with the

TABLE 3. Tribal level classifications within Syrphinae

Author	Tribal ranking and included genera						
Wirth *et al.* (1965)	Bacchini *Baccha*	Melanostomini *Xanthandrus* *Melanostoma* *Platycheirus* *Pyrophaena*	Paragini *Paragus*	Pipizini *Pipiza* *Heringia* *Parapenium* *Neocnemodon*	Chrysotoxini *Chrysotoxum*	Syrphini remaining genera (see Table 2)	
Dušek & Láska (1967)	Sphaerophorini *Sphaerophoria*	Melanostomini *Platycheirus* *Baccha* *Melanostoma* *Xanthandrus* *Episyrphus* *Megasyrphus* *Eriozona*	Xanthogrammini *Xanthogramma* *Doros*	Chrysotoxini *Chrysotoxum*	Paragini *Paragus*	Dideini *Didea*	Syrphini remaining genera (see Table 2)
Vockeroth (1969)	As Wirth *et al.* (1965) except Pipizini excluded from Syrphinae						
Kloet & Hincks (1976)	Bacchini *Baccha*	Melanostomini *Xanthandrus* *Melanostoma* *Platycheirus* *Pyrophaena*	Chrysotoxini *Chrysotoxum*	Paragini *Paragus*	Syrphini remaining genera (see Table 2)		
Torp (1984)	Paragini *Paragus*	Bacchini *Baccha*	Melanostomini *Xanthandrus* *Melanostoma* *Platycheirus* *Pyrophaena*	Chrysotoxini *Chrysotoxum*	Syrphini remaining genera (see Table 2)		
This study	Pipizini *Pipizi* *Pipizella* *Heringia* *Neocnemodon*	Paragini *Paragus*	Melanostomini *Melanostoma* *Xanthandrus*	Bacchini *Baccha* *Sphaerophoria* *Platycheirus* *Pyrophaena*	Syrphini remaining genera (see Table 2)		

Syrphinae (*sensu* Stubbs & Falk, 1983) the following synapomorphies which corroborate the hypothesis of predacious Syrphidae as a monophyletic group: (a) mouthparts pointed and adapted for piercing; (b) a pair of pointed sclerites at the sides of the mouth; (c) anterior spiracles sited on the mesothorax; (d) prothorax elongate; (e) ventral surface of the thorax with protective pads; (f) ventral abdominal sensilla lacking apical setae and (g) prp with three pairs of radial spiracular slits. Additionally, the genitalia of *Heringia* and *Pipiza* species are apparently most similar to *Melanostoma* species (Glumac, 1960). Thus from an examination of larval characters, as predicted by Vockeroth & Thompson (1987), the pipizines can be placed in their correct subfamily.

Within the Pipizini generic boundaries have altered according to various authors. Our analysis suggests that *Pipizella* Rondani, 1856, is a valid monophyletic taxon on the basis of the following characters: lateral margins flattened (ch 17, derived); carinae supporting spiracular slits short (ch 20, primitive); projections on the anal segment absent (ch 28, primitive) and the autapomorphic character 12, abdominal segments with ten, not 11, pairs of sensilla. *Pipiza* Fallén, 1810 also appears to be a valid taxon from the nature of the vestiture which consists of unsclerotized spicules (ch 31, derived). However, in all cladistic analyses we tried, *Neocnemodon* and *Heringia* were considered virtually identical. F. C. Thompson (personal communication) in his unpublished world list synonymises *Neocnemodon* under *Heringia*, and we concur, although we have not seen the larva of the type species of the former, *Cnemodon latitarsis* Egger, 1865.

Meligramma Frey, 1946

Dušek & Láska (1967) regard *Meligramma* Frey, 1946, as a full genus which includes two species, *guttata* Fallén, 1817, the type species of the genus, and *triangulifera* Zetterstedt, 1843. Vockeroth (1969) reduced *Meligramma* to a subgenus of *Melangyna* Verrall, 1901. In our analysis no sister group relationship between *Meligramma* and *Melangyna* was found (Fig. 27). The more important differences between *Meligramma*, including *guttata* the type species, and *Melangyna* including *quadrimaculatum* Verrall, 1873, its type species, are that *Meligramma* has: mid-dorsal projections (ch 15, derived); colour pattern arising from the fat body and vestiture (ch 16, derived); dorso-ventral flattening (ch 17, derived); spiracular plate unicolorous (ch 23, primitive); prp tapering (ch 26, derived); one pair of anal lobes (ch 32, primitive); sensilla 3–6 borne on projections (ch 35, derived). Thus evidence from the larval stages supports Dušek & Láska (1967) in giving *Meligramma* full generic status.

Fagisyrphus Dušek & Láska, 1967

The type species of this genus, *cincta* Fallén, 1817, is sometimes included in *Meligramma* (Kloet & Hincks, 1976; Stubbs & Falk, 1983). Other authors, for example, Torp (1984), accept Dušek & Láska (1967) in placing it in a separate genus, *Fagisyrphus* Dušek & Láska, 1967. However our analysis suggests a close relationship to *Melangyna* (Fig. 27). The larva of *cincta* shares most derived characters with *Melangyna*, including *quadrimaculatum* Verrall, 1873, its type species: chs 16, 17, 19–22, 24–27, 30, 32 (Table 2) except that it has unicolorous spiracular plates (ch 23, primitive) and a translucent colour pattern (ch 33, derived). Colour patterns are unreliable characters at our level of analysis (see above). Thus we propose to synonymize *Fagisyrphus* under *Melangyna* on the strength of the shared characters referred to above.

Epistrophella Dušek & Láska, 1967

Epistrophella was erected for the species *euchroma* Kowarz, 1885. Dušek & Láska (1967) consider it to be closely related to *Epistrophe* Walker, 1852, on the grounds that male genitalia are similar. Vockeroth (1969) reduces it to a sub-genus of *Epistrophe*. Our analysis, however, indicates a closer relationship to *Meligramma* (Fig. 27). The larva of *euchroma* shares most derived characters with *Meligramma* including *guttata*, its type species: chs 15, 17, 19, 20, 22, 24, 26, 27, 30, 31 and 35 (Table 2) except that dorsal spurs are weakly indicated in *euchroma* (ch 21) and the prp is more than twice as long as broad (ch 25).

However, the similarity in the majority of characters outweigh these differences and we therefore synonymize *Epistrophella* under *Meligramma*. Furthermore, the adult stages are very similar between *euchroma* and *Meligramma* (Stubbs & Falk, 1983). Also Vockeroth (1969) cautions against over-reliance on genitalia characters within Syrphinae because several highly modified forms exist without corresponding changes in other characters. The genitalia of *euchroma* appear to be just such a case.

Megasyrphus Dušek & Láska, 1967

Dušek & Láska (1967) erected this genus for the single species, *annulipes* Zetterstedt, 1838, primarily on the basis of male genitalia. Vockeroth (1969) and F. C. Thompson (personal communication) consider that *Megasyrphus* is closely related to *Eriozona*. However our analysis suggests a closer relationship to *Didea* (Fig. 27). The larva of *annulipes* shares most of its derived characters with *Didea* including *fasciata* Macquart, 1834, the type species of this genus: chs 15–20, 24–28, 30, 31, 35 (Table 2) and one synapomorphic character, the inwardly sloping spiracular plates (ch 34), except that the spiracular slits extend by less than half their length down the sides of the prp (ch 22, derived). On the basis of these similarities we propose to synonymize *Megasyrphus* under *Didea*.

Compatibility analysis

CLINCH found several maximal-sized cliques, differing mainly in the position of one genus, *Paragus*. This genus fluctuates greatly in its tree position as certain characters appear or disappear from the maximal clique. We take this as evidence of a high degree of convergent evolution in its characters (see also the parsimony analysis below). CLINCH was run on the obvious basal species (*Melanostoma*, *Xanthandrus*, the Pipizini, *Platycheirus*, *Pyrophaena*, *Baccha*, *Sphaerophoria*, *Episyrphus*) plus *Paragus*, to check where *Paragus* should be placed. All three of the maximal cliques (23 characters) placed *Paragus* either on the pipizine line (two cliques) or branching off from *Melanostoma* (one clique). This indicates that *Paragus* is an aberrant primitive group, and should not appear in the advanced *Dasysyrphus* group where convergence places it in some cliques. This also implies that what are considered *a priori* to be important evolutionary changes of state, the loss of pupal horns (character no. 1) and the loss of cuticular patches (no. 2), have occurred independently in *Paragus*; we accept this implication, making the Pipizini the sister-group of *Paragus*. Characters 1

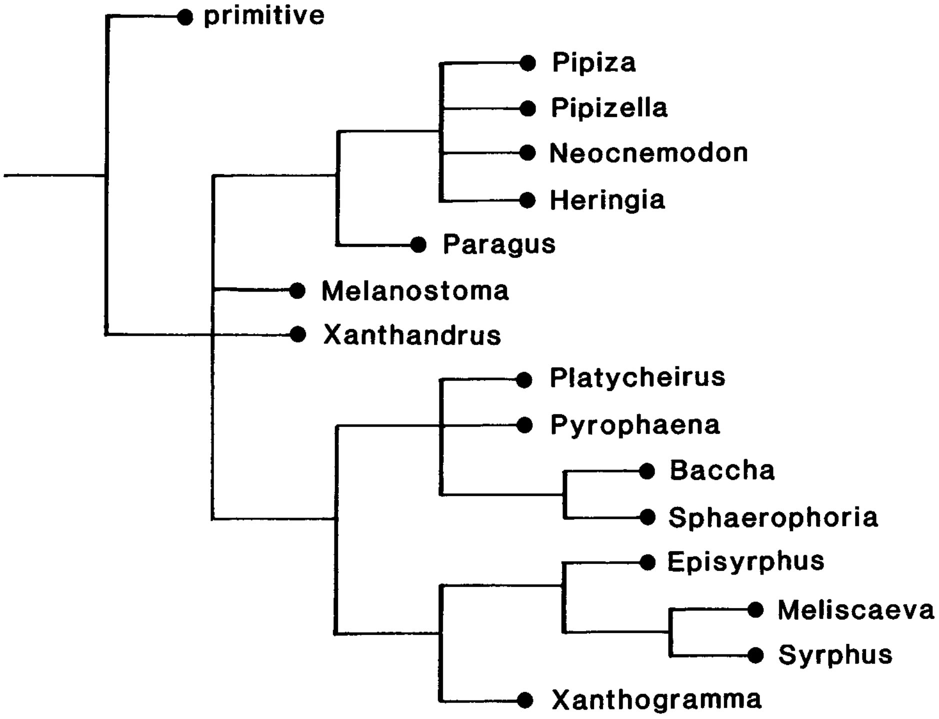


Figure 26. Strict consensus tree for the 100 equally parsimonious trees found for the 16 basal genera. Consistency index (Kluge & Farris, 1969) = 0.667. Length of tree = 60.

and 2 were recoded to show independent loss in *Paragus* (state 2) for the subsequent parsimony analysis.

Parsimony analysis

We checked first to see if recoding the character states of characters 1 (loss of pupal spiracles) and 2 (loss of corresponding cuticular patches) for *Paragus* was reasonable, as indicated by the compatibility analysis. This we did by using the branch-and-bound algorithm (the BANDB option) on the group of 14 genera that are always basal whatever the settings (Pipizini, *Melanostoma*, *Platycheirus*, *Pyrophaena*, *Baccha*, *Sphaerophoria*, *Episyrphus*, *Meliscaeva*, and *Xanthogramma*) plus *Paragus* (with *original* states for characters 1 and 2) and a more advanced genus that appears just above the basal group (*Syrphus*). In compatibility, *Paragus* showed similarities with the *Dasysyrphus* group which is always placed high up on all trees: if *Paragus* is truly an advanced genus of this group it should come out with *Syrphus* in the restricted analysis. One hundred trees were found, all very similar, and all showing *Paragus* as primitive, a sister-group of the Pipizini (Fig. 26). We conclude that parallel evolution has occurred, and that it is reasonable to recode characters 1 and 2 to show independent loss in *Paragus*.

Running PAUP on all taxa with *Paragus* recoded again found the limit of 100 equally parsimonious trees: these were again all very similar, as shown by the 'strict' consensus tree (Fig. 27). The individual trees producing Fig. 27 differ mainly in the branching arrangement of one basal set (Pipizini + *Paragus*,

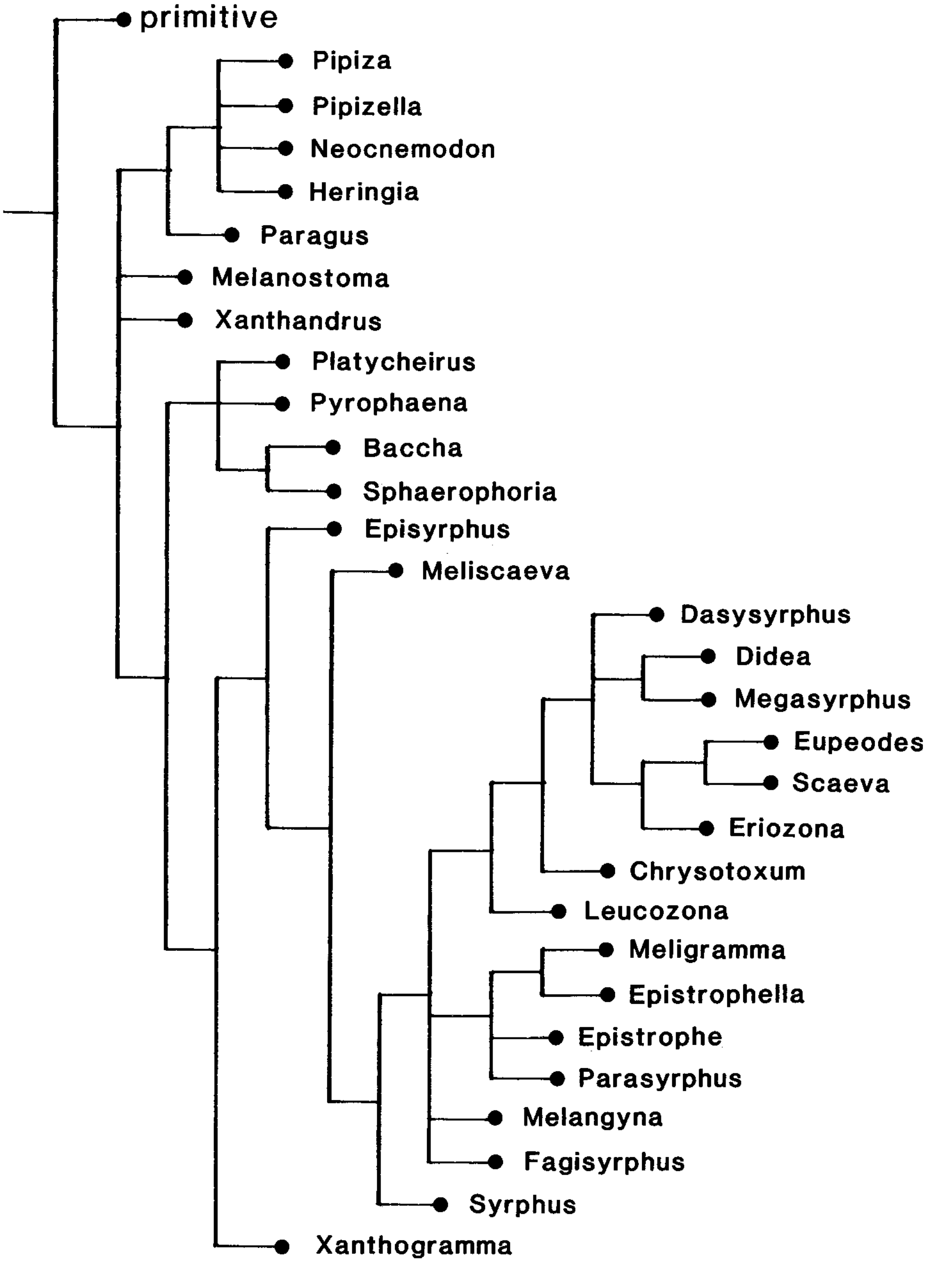


Figure 27. Strict consensus tree for the 100 equally parsimonious trees found for all genera. Consistency index = 0.437. Length = 109.

Melanostoma, *Xanthandrus*, and the rest) and one higher set (*Melangyna*, *Fagisyrphus* the *Epistrophe* group, and the *Leucozona*—upwards group). In the case of the basal set, the same uncertainty is evident in Fig. 26; thus a more restricted analysis fails to resolve these relationships. The same is true for the higher set. In case our recoding of characters 1 and 2 unduly affected the analysis, we checked by giving all other characters (3–35) double importance by assigning them weights of 2; no differences were found in the resulting equally parsimonious trees.

Tribal limits

Some conclusions about the division of the Syrphinae into tribes are obvious from this study. The Pipizini and Paragini are sufficiently different to constitute separate and probably holophyletic tribes. There seems to be little justification for placing *Chrysotoxum* in a separate tribe, as some authors have done (Table 3). The possibly paraphyletic Melanostomini should be restricted to the two genera *Melanostoma* and *Xanthandrus* on account of various characters on the prp, lack of apical setae on papillae bearing sensilla, and type of vestiture (Table 2). Two other aggregates of genera are apparent at the same level in Fig. 27, a group of 4 genera (*Baccha*, *Spaerophoria*, *Platycheirus* and *Pyrophaena* = Bacchini) and the large group comprising the rest (*Xanthogramma* upwards = Syrphini). The division is supported by four characters: 22 (position of spiracular slits, 0 → 1 on *Xanthogramma* line), 23 (colour of spiracular plate, 0 → 2 on *Platycheirus* line), 24 (length of spiracular slits, 0 → 2 on *Xanthogramma* line) and 29 (groove above anal lobes, 0 → 1 on *Platycheirus* line). If this hypothesis of relationships is accepted, *Paragus* is not the only genus to have lost pupal horns (ch 1) and cuticular patches (ch 2) independently of the main group, since *Baccha* and *Sphaerophoria* must have lost pupal horns, and *Sphaerophoria* its cuticular patches as independent evolutionary events.

KEY TO LARVAE AND PUPARIA OF EUROPEAN GENERA OF PREDACIOUS SYRPHIDS

The key is based on character states presented in Table 2. *Doros* is added on the information of M. C. D. Speight (personal communication). It uses prp characters extensively to enable third stage larvae and puparia to be identified in the one key with additional characters added as necessary. Live and parasitized individuals can be identified using it. Identifications should be checked using the sections on generic diagnoses and recognition features which follow the key. Third stage larvae can be distinguished from the first two stages by the fused spiracular plates forming one unit, the prp. In earlier stages these plates are separate.

1 Prp without dorsal spurs 2
1′ Prp with dorsal spurs (Fig. 3A) 19

2 Prp dome-shaped in profile; without a central depression at tip (Fig. 6) 3
2′ Prp angular in profile, not dome-shaped; with a central depression at tip (Figs 3C, 12) 4

3 Prp with wavy spiracular slits (Fig. 6): interspiracular setae (Figs 3B, C) absent or short and inconspicuous. . *Xanthogramma*
3′ Prp with straight or slightly curved spiracles: interspiracular setae long and conspicuous . . . .*Doros*

4 In dorsal view, prp pale brown with spiracular slits on a white or black plate (Fig. 11) 5

4′ In dorsal view, prp pale or dark brown; if pale then spiracular slits not on a white or black plate . . . 8

5 Larva not bright shining green and either with a pair of equally long stripes or 4–5 pairs of 'V'-shaped markings either side of the dorsal mid-line; pupal horns present; puparium convex in profile (Fig. 19) 6
5′ Larva either bright shining green with a pair of inconspicuous longitudinal stripes or larva whitish-brown with one stripe longer than the other; 'V'-shaped markings absent; pupal horns absent; puparium concave in profile 7

6 Sensilla at tip of anal segment with apical setae . *Pyrophaena*
6′ Sensilla at tip of anal segment without apical setae . *Platycheirus*

7 Larva whitish-brown; puparium, from above, with narrow parallel sides which abruptly widen from the front third . *Baccha*
7′ Larva bright shining green; puparium widening gradually from the anal segment. . . . . *Sphaerophoria*

8 Interspiracular setae long and conspicuous, about half as long as the spiracular slits. 9
8′ Interspiracular setae short and inconspicuous, much less than half as long as the spiracles 11

9 Larva very flattened in cross-section, without a pair of rounded projections on the tip of the anal segment; carinae supporting spiracular slits short, about the width of the spiracular slits *Pipizella*
9′ Larva oval or sub-cylindrical in cross-section with a pair of rounded projections on the tip of the anal segment (Fig. 10); carinae supporting spiracular slits tall, more than the width of the spiracular slits 10

10 Vestiture consisting of spines . . . . . *Pipiza*
10′ Vestiture consisting of dome-shaped papillae . . *Heringia*

11 Prp more than 2 × as long as broad at base; larva flattened in cross-section, mottled orange and white . . *Meligramma euchroma*
11′ Prp less than 2 × as long as broad at base; if flattened then coloured otherwise 12

12 Prp at tip with a raised bar connecting the two sides; larva sandy coloured . . . . *Eupeodes neilseni*
12′ Prp at tip without a raised bar connecting the two sides . 13

13 Spiracular slits oval-shaped, less than 2 × as long as broad . 14
13′ Spiracular slits elongate, more than 2 × as long as broad . . 15

14 Apex of prp with a pair of posterior projections (Fig. 8); large larva, more than 10 mm long; in profile, puparium raised sharply in front of prp . . . *Xanthandrus comtus*
14′ Apex of prp without posterior projection; small larva, less than 10 mm long; in profile, puparium not sharply raised in front of prp . . . . *Melanostoma*

15 Vestiture consisting of pointed spicules 16
15′ Vestiture consisting of dome-shaped papillae 17

16 Prp without inwardly sloping spiracular plates; larva subcylindrical with a mid-dorral whitish stripe; puparium with projecting tip (Fig. 21) . . . . . . *Scaeva*
16′ Prp with inwardly sloping spiracular plates; larva flattened without mid-dorsal stripe; puparium without projecting tip *Didea*

17 Prp with a basal rim (Fig. 12); in profile, spiracular plate sloping backwards (*cinctellus*) or not sloping backwards and prp as long as broad (*auricollis*) . . . . *Meliscaeva*
17′ Prp without a basal rim; spiracular plate not sloping backwards and broader than long 18

18 Vestiture consisting of black angular papillae (Fig. 16); prp dark brown or black. . . . . *Eriozona*
18′ Vestiture consisting of translucent dome-shaped papillae; prp pale brown . . . . *Episyrphus*

19 Interspiracular ornamentation ridge-shaped between posterior pair of spiracular slits (Fig. 17). 20
19′ Interspiracular ornamentation cone-shaped between posterior pair of spiracular slits 22

20 Tip of anal segment with a pair of long tapering projections (Fig. 15); prp black or dark brown; bark-coloured larva *Dasysyrphus*
20′ Tip of anal segment without long projections; prp pale brown; green or white and brown larva 21

21 Larva sub-triangular in cross-section; white and brown; more than 0.5 length of the spiracular slits extending over the sides of the prp . . . . *Leucozona*
21′ Larva flattened in cross-section, green; less than 0.5 length of the spiracular slits extending over the sides of the prp . . *Epistrophe*

22 Prp pale-brown about as long as broad and with an orange basal rim (Fig. 12); spiracular slits black-lined; dorsal spurs only weakly indicated, not taller than spiracular slits *Meliscaeva auricollis*
22′ Not entirely as above 23

23 Dorsal spurs as tall as or taller than basally broad; larva and puparium 6–8 mm long . . . . *Paragus*
23′ Dorsal spurs broader than tall; larva and puparium more than 8 mm long 24

24 Tip of anal segment with a pair of short, rounded projections . . . . *Chrysotoxum*
24′ Tip of anal segment without rounded projections . . 25

25 Vestiture consisting of pointed spicules 26
25′ Vestiture consisting of dome-shaped papillae 27

26 Larva without mid-dorsal whitish stripe; spicules grouped into patches on dorsal surface . . *Eupeodes* (*Metasyrphus*)

26′ Larva with mid-dorsal whitish stripe; spicules uniform in distribution on dorsal surface . . . . . . *Scaeva*

27 Sides of the abdomen of larva serrate; tip of anal segment viewed from above transverse, cut straight across; in profile puparium with dorsal and ventral margins almost parallel until anterior bulge (Fig. 22). . . . . *Meligramma*

27′ Sides of the abdomen of larva not serrate; tip of anal segment rounded when viewed from above; in profile puparium without parallel dorsal and ventral margins (Fig. 23) 28

28 Prp broader than long or about as long as broad; spiracular slits more than 6 × as long as broad; larva with three pairs of lobes at tip of anal segment and deep grooves dorsally (Fig. 7) . . . . *Syrphus*

28′ Prp longer than broad; spiracular slits less than 6 × as long as broad; larva with one or two pairs of lobes at tip of anal segment and no deep grooves 29

29 In profile prp continuously broadening towards base (Fig. 23); abdomen of larva widening towards prp and sub triangular in cross-section . . . . *Melangyna*

29′ In profile, prp with straight sides towards base (Fig. 25); abdomen of larva equally narrow at anterior and posterior ends and oval or sub-cylindrical in cross-section . . .*Parasyrphus*

GENERIC DIAGNOSES

These diagnoses are based on 3rd stage larvae, unless otherwise stated.

Pipiza Fallén, 1810

Diagnosis. Up to 9 mm long; oval in cross-section; vestiture of unsclerotized spicules; mid-dorsal projections absent; anal segment with a pair of rounded projections (Fig. 10); prp up to twice as long as broad at tip; spiracular slits short (2–6 × as long as broad), mounted on prominent carinae and not extending over the sides of the prp; interspiracular ornamentation of long setae (more than 0.5 length of a spiracular slit) and mounted on cones; a pair of spots indicating position of pupal horns on the first abdominal segment; pupal horns present; mandibles quadrate (Fig. 2); colour pattern due to haemolymph pigments.

Recognition features. Pipiza larvae are easily recognized by the presence of a pair of rounded projections on the anal segment, vestiture of unsclerotized spicules and prp with short spiracular slits. The larva of *Triglyphus primus* Loew is similar but has not been studied by us. It can be distinguished from *Pipiza* larvae by its smaller size (about 5 mm long) (Sedlag, 1967).

Biology. Pipiza festiva Meigen is associated with *Pemphigus* aphid galls on *Populus* (Dušek & Křistek, 1959). *Pipiza luteitarsis* Zetterstedt has been reared from *Schizoneura* aphid galls on *Ulmus* (Rotheray, 1987a). *Pipiza noctiluca* (Linnaeus) has a wider host range including *Cavariella* aphids on umbelliferous plants (*Pipiza austriaca* Meigen has also been reared on these aphid species, G.E.R.); *Hyalopterus pruni* (Geoffroy) on *Prunus*; *Aphis* sp. on *Cirsium* and *Drepanosiphum platanoidis* (Shrank) on *Acer pseudoplatanus* (L.) (G.E.R.). *Triglyphus primus* is associated with *Cryptosiphum artemisiae* Buckton galls on *Artemisia vulgaris* Linnaeus (Leclercq, 1944; Sedlag, 1967).

Pipizella Rondani, 1856

Diagnosis. Up to 8 mm long; flattened and triangular in cross-section; vestiture of round-tipped papillae; mid-dorsal projections absent; rounded projections on the tip of the anal segment absent; sensilla with club-tipped apical setae; a pair of spots indicating position of pupal horns on the first abdominal segment; pupal horns present; mandibles quadrate; abdominal segments 1–7 with sensilla 5 and 6 reduced to a single pair so that each segment has only 10 pairs of sensilla; prp about twice as long as broad at tip; spiracular slits short (2–6 × as long as broad) and not extending over the sides of the prp; interspiracular ornamentation of long setae (more than 0.5 length of a spiracular slit) and mounted on cones; dark colour pattern due to haemolymph pigments. (Only *Pipizella viduata* (Linnaeus) examined.)

Recognition features. The club shaped setae, the ten pairs of abdominal sensilla and the flattened shape enable this species to be recognized.

Biology. Associated with root-feeding aphids on umbelliferous plants (Heeger, 1858; Dixon, 1959).

Heringia Rondani, 1856

Heringia Rondani, 1856. Type species: *Heringia heringia* Zetterstedt, 1843.

Neocnemodon Geoffe, 1944. Type species: *Cnemodon latitarsis* Egger, 1865. **Syn. nov.** [See generic limits section above.]

Diagnosis. Up to 7 mm long; moderately flattened in cross-section; vestiture of round-tipped papillae; mid-dorsal projections absent; a pair of rounded projections at the tip of the anal segment; a pair of spots indicating position of pupal horns on first abdominal segment; pupal horns present; mandibles quadrate; prp up to 6 × as long as broad at tip; spiracular slit short (2–6 × as long as wide), mounted on prominent carinae and not over the sides of the prp; interspiracular ornamentation of long setae (more than 0.5 length of a spiracular slit) mounted on cones; colour pattern due to haemolymph pigments.

Recognition features. Larvae can be recognized by the pair of rounded projections on the anal segment, vestiture comprising round-tipped papillae and prp with short spiracular slits. The short prp (about 2 × as long as broad) distinguishes *T. primus* from *Heringia* larvae.

Biology. Associated with *Schizoneura* aphids on *Ulmus*, and *Pemphigus* aphids on *Populus* (Dušek & Křistek, 1959; Láska & Starý, 1980), *Dreyfusia piceae* (Ratzeburg) on *Abies* (Delucchi *et al.*, 1957) and *Eriosoma lanigerum* (Hausmann) on *Malus* (Evenhuis, 1959).

Melanostoma Schiner, 1860

Diagnosis. Up to 9 mm long; oval in cross-section; shining translucent green larvae; colour due to haemolymph pigments; vestiture of flat, inconspicuous papillae; sensilla without apical setae; mid-dorsal and anal segment projections absent; a pair of spots indicating position of the pupal horns on the first abdominal segment; pupal horns present; prp broader than long without dorsal spurs and a posterior projection at tip; spiracular slits short (less than 2 × as long as broad) not extending over the sides of the prp and not on a black background; mandibles elongate.

Recognition features. Green colour due to haemolymph pigments, sensilla without apical setae, prp without a posterior projection, short oval-shaped spiracular slits.

Biology. Melanostoma adults are often abundant but larvae are rare at aphid colonies (Rotheray, 1983). Larvae are sometimes found in leaf litter as well as ground layer aphid colonies.

Xanthandrus Verrall, 1901

Diagnosis. Only one European species in this genus, *comtus* Harris, 1780. Up to 12 mm long; oval in cross-section; shining green larva with pale fat bodies; colour due to haemolymph pigments; vestiture of flat, inconspicuous papillae; sensilla without apical setae; mid-dorsal and anal segment projections absent; a pair of spots indicating position of pupal horns on the first abdominal segment; pupal horns present; prp broader than long without dorsal spurs and with a posterior projection just below the tip (Fig. 8); spiracular slits short (less than 2 × as long as broad) not appearing over the sides of the prp and not on a black background; puparium abruptly tapering just in front of prp; mandibles elongate.

Recognition features. The green colour, large size, sensilla without apical setae, short spiracular slits and posterior projection on the prp make this species easy to recognize. The abruptly tapering tip of the puparium is also distinctive.

Biology. A predator of various hyponemeutid and tortricid caterpillars (Chapman, 1906; Lucchese, 1942; Lyon, 1968) but prey range may also include aphids (Lyon, 1968). Non-European species also all seem to be specialized Lepidopteran predators (F. C. Thompson, personal communication).

Platycheirus Lepeletier & Serville, 1828

Diagnosis. Up to 10 mm long; sub-rectangular in cross-section; variously coloured larvae; colour patterns due to fat bodies; particulate fat bodies arranged in the form of chevrons on the dorsal surface; upper and lower lateral fat body stripes; vestiture of dome-like papillae; a pair of spots indicating position of the pupal horns on the first abdominal segment; pupal horns present; sensilla pair 11 on locomotory prominences; tip of anal segment with two pairs of lobes; anal segment with transverse groove behind prp and setae absent from median lobes; prp about as long as broad and lightly nodulated; spiracular slits short (less than 2 × as long as broad) and on a white or black background; dorsal spurs absent, interspiracular ornamentation of short (less than 0.5 length of a spiracular slit) setae mounted on cones; mandibles elongate.

Recognition features. Sub-rectangular shape; dorsally fat body particles aggregated into chevrons; upper and lower lateral stripes; apical setae on sensilla of anal lobes absent; short spiracular slits on a white or black background (faded in occasional specimens); and segment with transverse groove behind prp.

Biology. The most diverse genus within Syrphinae. Larvae are found in the ground layer. Some species are abundant as adults but rarely recorded from aphid colonies e.g. *Platycheirus albimanus* (Fabricius) and *Platycheirus clypeatus* (Meigen). Like *Melanostoma* spp. their larvae may be more common in the leaf litter acting as generalized predators. *Platycheirus manicatus* (Meigen) and *Platycheirus peltatus* (Meigen) may be facultatively aphidophagous (Chandler, 1968a) *Platycheirus fulviventris* (Macquart) is a specialist predator of *Hyalopterus pruni* (Geoffroy) aphids on monocotyledonous food plants in wetland sites (Rotheray & Dobson, 1987). *Platycheirus scutatus* (Meigen) has an obligatory relationship with a wide range of ground layer aphids (Rotheray, 1979).

Pyrophaena Schiner, 1860

Diagnosis. Up to 11 mm long; sub-rectangular in cross-section; pale and dark brown colour pattern due to fat bodies; dorsally particulate fat bodies aggregated into chevrons; upper and lower lateral fat body stripes; vestiture of dome-like papillae; a pair of spots indicating position of pupal horns on the first abdominal segment; pupal horns present; sensilla pair 11 on locomotory prominences; tip of anal segment with two pairs of lobes, median lobes with a pair of setae; and segment with a transverse groove behind prp; prp about as long as broad; spiracular slits short (2–6 × as long as broad) and on a pale or black background; dorsal spurs absent; interspiracular ornamentation of short (less than 0.5 length of a spiracular slit) setae mounted on cones; mandibles elongate.

Recognition features. Similar to *Platycheirus* from which *Pyrophaena* larvae and puparia are most easily distinguished by the presence of a pair of setae on each median lobe of the anal segment in *Pyrophaena* species.

Biology. Larvae have only been found in flood refuse (Lundbeck, 1916). Adults are associated with marshy sites where females have been seen placing eggs on plants low down near the soil (G.E.R.). Larvae are probably generalized predators in leaf litter, although this is not confirmed.

Baccha Fabricius, 1805

Diagnosis. Up to 10 mm long; sub-rectangular in cross-section pale brown and white colour pattern due to asymmetrical dorsal fat bodies; chevrons absent; upper and lower lateral fat body stripes; vestiture of dome-like papillae; a pair of spots indicating position of pupal horns on the first abdominal segment but pupal horns absent; sensilla pair 11 on locomotory prominences; sensilla pair 7 posterior to sensilla pair 8; tip of anal segment with two pairs of lobes, median lobes without setae; anal segment with transverse groove behind prp; prp about as long as broad and lightly nodulated; spiracular slits short (less than 2 × as long as broad) and on a pale or dark background; dorsal spurs absent; interspiracular ornamentation of short (less than 0.5 length of a spiracular slit) setae mounted on cones; mandibles elongate.

Recognition features. Similar to *Platycheirus* except chevrons lacking, sensilla pair 7 posterior to sensilla pair 8 and pupal horns absent.

Biology. Associated with ground layer aphids, particularly those in shaded sites (Rotheray, 1979).

Sphaerophoria Lepeletier & Serville, 1828

Diagnosis. Up to 10 mm long; oval in cross-section; bright green with pale, dorsal stripes; vestiture of dome-like papillae; a pair of spots indicating position of pupal horns on the first abdominal segment and pupal horns absent; sensilla pair 11 on locomotory prominences; tip of anal segment with four lobes; anal segment with transverse groove behind prp; prp up to twice as long as basally broad and lightly wrinkled and nodulated; dorsal spurs absent; spiracular slits short (less than 4 × as long as broad) and on a dark background; interspiracular ornamentation of short (less than 0.5 length of a spiracular slit) setae mounted on cones.

Recognition features. Similar to *Melanostoma* in outward appearance except sensilla with apical setae, transverse groove behind prp and spiracular slits on a dark background (fades in some specimens). Absence of pupal horns and spots on the first abdominal segment of the larval stage distinguishes *Sphaerophoria* larvae and puparia from *Baccha*, *Platycheirus* and other related genera.

Biology. Associated with ground layer aphids (Chandler, 1968c; Rotheray, 1979).

Episyrphus Matsumura & Adachi, 1917

Diagnosis. Up to 12 mm long; oval in cross-section; translucent with asymmetrical dorsal fat bodies and, sometimes conspicuous red malpigian tubules; vestiture of dome-like papillae; spots on first abdominal segment and pupal horns absent; sensilla pair 11 on locomotory prominences; tip of anal segment with four lobes; transverse groove behind prp absent; prp about as long as broad; dorsal spurs absent; spiracular slits long (more than 6 × as long as broad), black lined and extending over the side of the prp; interspiracular ornamentation of short setae (less than 0.5 length of a spiracular slit) mounted on cones.

Recognition features. Translucent colour pattern with asymmetrical dorsal fat bodies either side of a mid-dorsal line; sensilla pair 11 on locomotory prominences; prp about as broad as long; spiracular slits black-lined and tip of anal segment with four lobes.

Biology. Only one European species, *Episyrphus balteatus* (Degeer) which has a wide prey range on ground layer and arboreal aphids. Often very abundant when it occurs.

Meliscaeva Frey, 1946

Diagnosis. Up to 12 mm long; oval in cross-section; translucent; vestiture of dome-like papillae; spots on first abdominal segment and pupal horns absent; sensilla pair 11 on locomotory prominences; anal segment with four lobes and transverse groove absent; prp slightly longer than broad (*Meliscaeva auricollis* (Meigen)) or as long as broad (*Meliscaeva cinctella* (Zetterstedt)); dorsal spurs present; spiracular slits black lined and extending over the side of the prp; prp with a basal rim (Fig. 12); interspiracular ornamentation of short setae mounted on cones.

Recognition features. This is the only syrphine genus in which the colour pattern of the body and shape of the prp differs between species. *Meliscaeva auricollis* is most similar to *E. balteatus* from which it may be distinguished by the longer-than-broad prp and the possession of well developed dorsal spurs. The translucent yellow-to-brown colour of *M. cinctella* is reminiscent of some *Pipiza* species. The form of the prp, which slopes away posteriorly, separates this species from any other known syrphine larva.

Biology. Meliscaeva auricollis is recorded from shrubs such as *Berberis* and *Sarothamus* (Dixon, 1960; Chandler, 1968b), *Cavariella* sp. aphids on *Heracleum sphondylium* L. and from aggregations of the psyllid, *Psylla alni* (L.) on *Alnus glutinosa* (L.) Gaertner (G.E.R.). *Meliscaeva cinctella* is recorded from *Quercus*, *Picea* and *Pinus* (Chandler, 1968b; Kula, 1980; G.E.R.), *Malus*, *Sambucus* (Ward, 1977) and *Cinara* sp. aphids on *Picea* (Kula, 1980).

Paragus Latreille, 1804

Diagnosis. Up to 8 mm long; dorso-ventrally flattened; yellow-brown; vestiture of dome-like papillae; spots on first abdominal segment and pupal horns absent; sensilla pair 11 on locomotory prominences; anal segment with two lobes; first six pairs of sensilla borne on fleshy projections; prp up to 2 × long as broad with dorsal spurs taller than broad; spiracular slits short (up to 2 × long as broad), not extending over the sides of the prp and mounted on dark carinae; prp constricted medically and wrinkled and nodulate; interspiracular setae long (more than 0.5 length of a spiracular slit) and mounted on cones.

Recognition features. The small size of larvae of this genus, the dorsal sensilla borne on projections and the prp with short spiracular slits mounted on tall, dark carinae are the chief distinguishing features. Lack of backwardly directed, tapering projections on the anal segment separate larvae of *Paragus* from small *Dasysyrphus* larvae.

Biology. These are aphidophagous species occurring on ground layer aphids and occasionally trees. *Paragus* (*Pandasyophthalmus*) *haemorrhous* Meigen is recorded from *Sarothamus* (Dixon, 1960) and an undetermined cruciferous plant (W. George, personal communication).

Xanthogramma Schiner, 1860

Diagnosis. Up to 12 mm long; oval in cross-section; off-white colour pattern; vestiture of close-set dome-like papillae; spots on first abdominal segment and pupal horns absent; sensilla pair 11 not on locomotory prominences and anterior to sensilla 10; anal segment with four lobes; prp smooth and rounded and dome-like in profile (Fig. 6); spiracular slits long, wavy and not mounted on carinae; dorsal spurs absent; interspiracular setae small and set in circular pits.

Recognition features. The off-white colour pattern and wavy spiracles distinguish this genus. *Doros* larvae are probably similar in many characters and can be separated from *Xanthogramma* in that the spiracular slits of the former larvae are straight and several interspicular setae are present in each circular pit (see Speight, in press).

Biology. Little known. Recorded from *Lasius* ant colonies (Hoelldobler, 1929; Dixon, 1960) where they may feed on ant-associated aphids (Chandler, 1968b).

Syrphus Fabricius, 1775

Diagnosis. Up to 12 mm long; oval in cross-section anteriorly, broadening posteriorly; translucent with white, yellow or orange chevrons or stripes; vestiture of dome-shaped papillae; spots on first abdominal segment and pupal horns absent; sensilla 11 not on locomotory prominence and anterior to sensilla 10; tip of the anal segment with six lobes; dorsal surface of anal segment with deep grooves (Fig. 18); locomotory prominences oval in outline and well developed; prp broader than long; spiracular slits long (more than 6 × as long as broad), up to 0.5 of their length extending over the side of the prp, mounted on carinae and sometimes black-lined; not taller than broad; interspiracular setae short and mounted on cones.

Recognition features. The translucent colour pattern, the not taller than broad prp and the form of the anal segment with dorsal grooves and six lobes distinguish the larvae of this genus.

Biology. Associated with a wide range of tree, shrub and ground layer aphids (Dixon, 1960; Chandler, 1968b, Rotheray, 1979). *Syrphus ribesii* (L.) is often the dominant species at many aphid colonies (Rotheray, 1979).

Scaeva Fabricius, 1805

Diagnosis. Up to 15 mm long; sub-cylindrical in cross-section; green, brown or pink with pale mid-dorsal and upper lateral stripes; vestiture of evenly and sparsely distributed spicules of uniform size and colour; spots on first abdominal segment and pupal horns absent; sensilla 11 not on locomotory prominence and anterior to sensilla 10; tip of the anal segment with six lobes, median pair greatly enlarged dorsally and ventrally are surrounding the prp which appears, as a result, to be set in a triangular recess; sensilla on ventral surface of metathorax with apical setae; locomotory prominences on abdominal segments 5 and 6 with four lobes and with their tips directed backwards; abdominal sensilla 1 borne on a short projection; prp as broad as long with long spiracular slits mounted on carinae which almost reach down to the base of the prp; dorsal spurs short; interspiracular setae short and mounted on cones; mandibles sub-rectangular distally (Fig. 1).

Recognition features. Sub-cylindrical cross-section with pale mid-dorsal and upper lateral stripes, the backwardly pointing locomotory prominences on abdominal segments 5 and 6, the presence of apical setae on the ventral sensilla of the metathorax and the evenly distributed spicules distinguish the larvae of this genus.

Biology. Scaeva pyrastri (L.) is known from a wide range of ground layer aphids (Dixon, 1960; Rotheray, 1979). *Scaeva selenitica* (Meigen) is recorded from *Pinus* and other coniferous trees (Dixon, 1960; Kula, 1980).

Eupeodes Osten Sacken, 1877

Eupeodes Osten Sacken, 1877. Type species: *Eupeodes volucris* Osten Sacken, 1877.
Metasyrphus Matsumura, 1917. Type species: *Syrphus corollae* Fabricius, 1794. [Synonymized by Vockeroth, 1986.]

Diagnosis. Up to 12 mm long; sub-cylindrical in cross-section; mottled light or dark brown and white; vestiture comprising pointed and blunt-tipped spicules of variable size and colour which on the dorsal surface are crowded together to form dark and light patches; spots on first abdominal segment and pupal horns absent; sensilla 11 not on locomotory prominence and anterior to sensilla 10; tip of anal segment with six lobes, median pair greatly enlarged dorsally and ventrally and surrounding the prp which appears, as a result, to be set in a triangular recess; sensilla on ventral surface of metathorax with apical setae; locomotory prominences on abdominal segments 5 and 6 with four lobes and with their tips directed backwards; sensilla 1 borne on slight projection; prp as broad as long with long spiracular slits mounted on carinae which almost reach down to the base of the prp; dorsal spurs short; interspiracular setae short and mounted on cones; mandibles sub-rectangular distally (Fig. 1).

Recognition features. Similar to *Scaeva* except usually shorter in length, not green or pink and spicules of variable size and colour crowded together to form light and dark patches.

Biology. Eupeodes corollae (Fabricius) and *Eupeodes luniger* (Meigen) are recorded from a wide range of ground layer aphids (Dixon, 1960; Rotheray, 1979). *Eupeodes nielseni* Dušek & Láska, 1976 is probably associated with conifer aphids (Rotheray, 1988). To judge from adult distribution, conifers may be the larval habitat for many other *Eupeodes* species (see Dušek & Láska, 1973; Stubbs & Falk, 1983).

Meligramma Frey, 1946

Meligramma Frey, 1946. Type species: *Scaeva guttata* Fallén, 1817.
Epistrophella Dušek & Láska, 1967. Type species: *Syrphus euchromus* Kowarz, 1885. **Syn. nov.** [See generic limits section above.]

Diagnosis. Up to 12 mm long; dorso-ventrally flattened in cross-section; colour patterns various: orange and white (*Epistrophella euchroma* (Kowarz)), white, black and brown (*Meligramma triangulifera* (Zetterstedt)), black (*Meligramma guttata* (Fallén)); vestiture of dome-shaped papillae; sensilla 11 not on locomotory prominence and anterior to sensilla 10; sensilla 1, 4, 5 and 6 borne on short projections; abdominal segments separated by lateral extensions which together with the projections on sensilla 4, 5 and 6 give the body outline a serrate appearance; tip of anal segment with two lobes; prp broadest basally, nodulate dark and up to 3 × as long as broad at tip; spiracular slits up to 4 × as long as broad and about 0.5 of their length extending over the side of the prp; dorsal spurs present, except *E. euchroma*; interspiracular setae short and mounted on cones; puparia in profile, flattened except anteriorly (Fig. 22).

Recognition features. The serrate outline, deep lateral divisions between the abdominal segments, dorso-ventral flattening and the heavily nodulated prp distinguish larvae of this genus.

Biology. Larvae are mostly arboreal. *Epistrophella euchroma* is recorded from beneath *Prunus* sp. trees (Dušek & Láska, 1959a) and from *Malus* (Goeldlin de Tiefenau, 1974). *Meligramma triangulifera* is commonly associated with *Prunus* spp. but is also recorded from *Betula*, *Rubus* and *Ribes* (Rotheray, 1986b). *Meligramma guttata* is recorded from *A. pseudoplatanus* (Dixon, 1960; F.S.G.).

Parasyrphus Matsumura, 1917

Diagnosis. Up to 12 mm long; hemispherical in cross-section; body narrow so that abdominal segment 1 is about the same width as segment 7; with red, brown and white longitudinal stripes or pairs of spots (chevrons in *Parasyrphus nigritarsis* (Zetterstedt) Schneider, (1953); spots on first abdominal segment and pupal horns absent; sensilla 11 not on locomotory prominence and anterior to sensilla 10; anal segment with two lobes; prp up to 3 × as long as broad, basal half nodular, distally smooth; dorsal spurs about as long as broad; spiracular slits up to 4 × as long as broad, mounted on carinae with more than 0.5 of their length extending over the sides of the prp; interspiracular setae short and mounted on cones.

Recognition features. The narrow, hemispherical shape in cross-section, the striped or spotted body (except *P. nigritarsis* which has chevrons), the anal segment with two lobes and sensilla 11 not on a locomotory prominence distinguish larvae of this genus.

Biology. Larvae are mostly arboreal. *Parasyrphus nigritarsis* is apparently not aphidophagous but is a predator of certain chrysomelid (Coleoptera) larvae, such as *Melasoma* (Schneider, 1953). Larvae of *Parasyrphus annulatus* (Zetterstedt) are recorded in *Picea* woods (Kula, 1980). Eggs and larvae of *Parasyrphus punctulatus* (Verrall) are recorded mostly from *Abies* and *Pinus* (Chandler, 1968b; G.E.R.) but also from *Acer pseudoplatanus* (L.) and *Rosa* sp. (Rotheray, 1987a). *Parasyrphus vittiger* (Zetterstedt) is recorded from *Abies* feeding on an unidentified adelgid (G.E.R.), from *Pinus* feeding on *Eulachnus* (G.E.R.), *Cinara* aphids (Bastian, 1984) and aphids on *Ribes nigrum* L. (Goeldlin de Tiefenau, 1974).

Epistrophe Walker, 1852

Diagnosis. Up to 13 mm long; dorso-ventrally flattened with a smooth outline; green with a pale mid-dorsal stripe; vestiture of dome-like papillae; abdominal sensilla 1 not borne on projection; sensilla 11 not on locomotory prominence and anterior to sensilla 10; tip of anal segment with two lobes; prp up to 2 × as long as broad; spiracular slits up to 6 × as long as broad, mounted on carinae and about 0.5 of their length extending over the side of the prp; dorsal spurs about as long as broad; interspiracular setae short and borne on ridges.

Recognition features. The dorso-ventral flattening, lack of serrate outline and green colour pattern distinguish larvae of this genus.

Biology. Larvae usually found on arboreal aphids but can also occur on shrubs and herbs (Dixon, 1960; Rotheray, 1979). *Epistrophe grossulariae* (Meigen) is known only from *A. pseudoplatanus* (Rotheray, 1986b).

Melangyna Verrall, 1901

Melangyna Verrall, 1901. Type species: *Melanostoma quadrimaculatum* Verrall, 1873.

Fagisyrphus Dušek & Láska, 1967. Type species: *Scaeva cincta* Fallén, 1817. **Syn. nov.** [See generic limits section above.]

Diagnosis. Up to 12 mm long; some dorso-ventrally flattening posteriorly giving the body a sub-triangular cross-section; colour patterns differ between species but are due to arrangements of fat body into stripes, triangles and rectangular blocks; vestiture of domelike papillae; sensilla 11 not on locomotory prominence and anterior to sensilla 10; tip of anal segment with four lobes; prp up to 2 × as long as broad, basally matt, distally shining; spiracular slits up to 3 × as long as broad, mounted on black carinae and about 0.5 of their length extending over the sides of the prp; interspiracular setae short and mounted on cones.

Recognition features. The sub-triangular cross-section with a smooth body outline, two pairs of anal lobes, interspiracular setae mounted on cones and absence of rounded projections on the tip of the anal segment separate larvae of these genera from other syrphines.

Biology. Melangyna artica has been reared from *Pterocallis ulni* (Degeer) aphids on *Alnus glutinosa* Gaertner (Rotheray, 1988) *Melangyna cincta* (Fallén) is particularly associated with *Phyllaphis fagi* (L.) on *Fagus sylvatica* L. (Dušek & Láska, 1962; Rotheray, 1979); it is also recorded from *Quercus*, *Acer*, *Tilia* (Chandler, 1968b; G.E.R.). *Melangyna lasiophthalma* (Zetterstedt) is common on *A. pseudoplatanus* (G.E.R.) and Chandler (1968b) records it from a number of unnamed plants. *Melangyna quadrimaculata* (Verrall) has been found feeding on unidentified adelgids from *Abies* (Rotheray, 1988) and *Melangyna umbellatarum* (Fabricius) from *Heracleum sphondylium* L. (Rotheray, 1986b).

Leucozona Schiner, 1860

Diagnosis. Up to 14 mm long; broadened and flattened posteriorly so appearing sub-triangular in cross-section with a smooth outline; translucent with white chevrons or stripes; vestiture of dome-like papillae; sensilla 1 not borne on projection; sensilla 11 not on locomotory prominence and anterior to sensilla 10; tip of anal segment with 4 lobes and dorsal sensilla mounted on papillae (and apical setae in *Leucozona lucorum* (L.)); prp about as long as broad matt and lightly wrinkled basally more shiny distally; dorsal spurs present; spiracular slits about 6 × as long as broad, mounted on carinae and more than 0.5 of their length extending over the sides of the prp; posterior two pairs of interspiracular setae borne on ridges.

Recognition features. The sub-triangular shape, translucent colour pattern with white stripes or chevrons and anal segment with four lobes and dorsal sensilla borne on basal papillae distinguish the larvae in this genus.

Biology. Leucozona lucorum is associated with arboreal and ground layer aphids (Dixon, 1960; Chandler, 1968b; G.E.R.). *Leucozona* (*Ischyrosyrphus*) *glaucia* (L.) is known from several ground layer aphids (Dušek & Láska, 1962). *Leucozona* (*Ischyrosyrphus*) *laternaria* (Müller) has been reared from *Cavariella* sp. aphids on *Angelica sylvesri's* L. (Rotheray, 1988).

Chrysotoxum Meigen, 1803

Diagnosis. Up to 15 mm long; sub-triangular in cross-section; pale cream; vestiture of unsclerotized spicules; sensilla 11 not on locomotory prominence; sensilla 1–6 borne on projections; tip of anal segment with a pair of short (less than length of the prp) round-tipped projections and four lobes; prp up to 2 × as long as broad, entirely dark in colour, rounded at the apex, nodulate basally and smooth and shining distally; dorsal spurs short and inconspicuous; spiracular slits mounted on slight carinae, more than 6 × as long as broad with up to 0.5 of their length extending over the side of the prp; interspiracular setae short and mounted on cones.

Recognition features. The pair of rounded projections on the anal segment and the prp with long spiracular slits over the side of the prp distinguish larvae of this genus.

Biology. The feeding habits of *Chrysotoxum* larvae have yet to be determined. However larvae and puparia seem to be associated with ant nests where they possibly feed on root aphids (see Speight, 1976). A larva of *Chrysotoxum bicinctum* (Linnaeus) has been reared on pea aphids in the laboratory (J. C. Hartley, personal communication). A female *C. bicinctum* has been seen to oviposit repeatedly about a *Lasius* nest (G.E.R.).

Dasysyrphus Enderlein, 1938

Diagnosis. Up to 12 mm long; sub-triangular in cross-section; dark larvae, mottled grey, black, yellow and white; vestiture of patchily distributed spicules; sensilla 1, 4, 5 and 6 borne on tall projections giving the body a serrate outline; sensilla 2 and 3 not borne on projections or projections slight; sensilla 11 not on a locomotory prominence and separated from sensilla 9 and 10 and only slightly anterior to sensilla 10; tip of the anal segment with a pair of long (more than length of the prp) tapering projections and with two lobes; prp dark in colour, up to 2 × as long as broad, wrinkled sometimes patchily nodular in the basal half and smooth at tip; spiracular slits up to 6 × as long as broad and with up to 0.5 of their length extending over the sides of the prp; dorsal spurs present; interspiracular setae mounted on cones.

Recognition features. The sub-triangular shape, serrate outline, vestiture of spicules and the long pair of tapering projections on the anal segment distinguish larvae of this genus.

Biology. Larvae mostly arboreal on both coniferous and broad-leaved trees (Chandler, 1986b; Rotheray, 1979, 1987a). *Dasysyrphus tricinctus* (Fallén) is recorded as rejecting aphids in favour of lepidopterous and hymenopterous larvae (Gabler, 1939; Friedrichs *et al.*, 1940). However it regularly occurs as a predator of *Drepanosiphon platanoidis* (Shrank) aphids on *A. pseudoplatanus* in Scotland (G.E.R.).

Eriozona Schiner, 1860

Diagnosis. Up to 15 mm long; rectangular in cross-section; truncate posteriorly; black; vestiture of shiny, black angular papillae; sensilla 1–6 on projections; sensilla 3 on projection larger than those supporting sensilla 2 and 4; body outline serrate; transverse folds deep in resting larva, so that projections supporting sensilla 1 borne on a dorsal ridge; prp black, broader than long, lightly wrinkled basally, tip with recticulate pattern of carinae; spiracular plates more or less level; dorsal spurs weakly indicated; spiracular slits mounted on orange carinae with more than 0.5 of their length over the sides of the prp; interspiracular ornamentation apparently lacking setae.

Recognition features. The large size, serrate outline, black angular papillae and lack of inwardly sloping spiracular plates characterize this genus.

Biology. Eriozona syrphoides (Fallén) is recorded from *Picea* feeding on *Cinara pineae* (Panzer) aphids (Kula, 1983).

Didea Macquart, 1834

Didea Macquart, 1834. Type species: *Didea fasciata* Macquart, 1834.
Megasyrphus Dušek & Láska, 1967. Type species: *Scaeva annulipes* Zetterstedt,

1838. **Syn. nov.** [See generic limits section above.]

Diagnosis. Up to 15 mm long; sub-rectangular in cross-section; truncate posteriorly; mottled brown and white or yellow; vestiture of long tapering spicules sensilla 1–6 on projections; body outline serrate; transverse folds deep in resting larva so that projections supporting sensilla 1 borne on a dorsal ridge; prp black, up to 2 × as long as broad, wrinkled and patchily nodulate; dorsal spurs absent; spiracular plates sloping towards each other; spiracles mounted on orange carinae with up to 0.75 of their length extending over the sides of the prp; interspiracular ornamentation apparently lacking setae.

Recognition features. The serrate outline, vestiture of long, tapering spicules and inwardly sloping spiracular plates distinguish larvae of these genera.

Biology. Associated with *Schizolachnus* and probably other aphids on *Pinus* (Evenhuis, 1978; Kula, 1980).

DISCUSSION

The history of syrphine classification is largely one of attempts to divide the large genus *Syrphus sensu lato*. The unsatisfactory nature of these attempts was signalled by their abandonment by Coe (1953), who thought that genera could not usefully be distinguished. However, despite this, three studies independently come to a fairly high level of agreement on divisions within *Syrphus sensu lato* (Dušek & Láska, 1967; Hippa, 1968; Vockeroth, 1969). These generic boundaries have been tested using larval characters in this study. The results confirm most of the genera and suggest solutions to some remaining problems that, on adult characters alone, were difficult to resolve. The major difference between this study and the currently accepted classification is that the Pipizini belong in the subfamily Syrphinae and thus carnivory arose only once in syrphid phylogeny. Accepting Fig. 27, it seems clear that delimiting tribal boundaries beyond the basal groups: Pipizini, Melanostomini, Paragini, Bacchini and Syrphini is not particularly useful. Most genera above the Bacchini form a chain of gradual change without fundamental divisions.

Having established a plausible phylogeny, trends in morphology, ecology and behaviour can often be recognized. Without a phylogeny such features are difficult to verify or recognize as part of a pattern, and interpretation is arbitrary. Furthermore, hypotheses about how such features came about can then be formulated and tested (Andersen, 1979). Based on our phylogeny some morphological and biological trends in syrphine evolution can be identified.

Morphological evolution

A variety of morphological trends are evident in the evolution of syrphine genera, from *Melanostoma* to *Didea*.

All Syrphini lack both pupal horns and cuticular patches, which have also been lost independently in the Paragini, *Sphaerophoria* and partially in *Baccha* in which patches are present but pupal horns are absent. All Pipizini, Melanostomini, *Platycheirus* and *Pyrophaena* possess both features.

Locomotory prominences become more differentiated and cone-like rather than bar-shaped. This seems to result from their innermost edges, on which sensilla 11 occurs, becoming part of the flat ventral surface and not part of a locomotory prominence. The result is two lines of locomotory prominences running along the lateral borders of the ventral surface, as seen in the genera above *Episyrphus*/*Meliscaeva* in the tree of Fig. 27. The primitive condition, in which sensillum 11 is part of the locomotory prominence, occurs in the Pipizini, Paragini, Melanostomini and genera up to and including *Episyrphus* and *Meliscaeva*.

Locomotory prominences reach their most complex development in *Scaeva* and *Eupeodes* at the top of the tree. In these genera, there are backwardly directed locomotory prominences which provide a grasping structure that works most effectively on narrow cylindrical substrates such as stems and leaf petioles (Rotheray, 1987b). In this respect, the preponderance for *Eupeodes* and *Scaeva* species to occur around conifers on which their larvae presumably feed suggests that these specialized locomotory organs are particularly useful in overcoming locomotion problems on pine needles and branches.

There is an increase in size from Melanostomini to Syrphini. Pipizini, Melanostomini, Paragini and Bacchini are about 6–9 mm long. Syrphini are about 8–15 mm long. Below *Episyrphus* in Fig. 27, larvae are usually oval or spherical in cross-section and do not widen posteriorly. In contrast, above and including *Episyrphus*, larvae are flattened to varying degrees and widened posteriorly. The only exceptions appear to be *Pipizella* and *Paragus*, which are dorso-ventrally flattened, and *Parasyrphus*, which is hemispherical in cross-section and does not widen posteriorly. *Parasyrphus* larvae are strongly associated with conifer aphids where their narrow spherical shape may be part of a cryptic adaptation to life among pine needles (Rotheray, 1986b).

The prp tends to increase in morphological complexity from Melanostomini to Syrphini. In particular the spiracular slits increase in length and tend to run down the sides of the prp to varying degrees. The apex of the prp tends to be enlarged and not parallel or tapering.

Finally the derivation of colour patterns is different. In Pipizini and Melanostomini they are derived from pigments in the haemolymph. In the Bacchini and Syrphini they result from various arrangements of adipose tissue into particles, stripes, bars and other shapes which are variously coloured (Rotheray, 1986b).

Biological trends

There is a pronounced trend from generalized to specialized predation and this occurs in both main arms of the phylogenetic tree (Fig. 27).

Melanostoma, most *Platycheirus* and probably *Pyrophaena* species appear to be generalized facultative aphid predators, living in the leaf litter or on plants close to the ground, and have a relatively long larval growth period (Chandler, 1968a; Rotheray, 1983). Chandler (1968a) found distinct oviposition differences between these and other syrphine genera, interpreting them as a fundamental orientation towards plants ('phytozetic') rather than aphids ('aphidozetic'). There have been suggestions that detritus feeding could also occur (see Rotheray, 1983; Gilbert, 1986) but this now seems unlikely: the larvae may feed on leaf-litter arthropods as an alternative to the preferred aphid prey.

In the main evolutionary sequence most generalists are low on the tree: *Baccha*, *Sphaerophoria*, *Episyrphus* and *Syrphus* species all eat a very wide variety of aphids and have shorter larval growth periods. Nearly all the upper half of the tree contain more specialized genera that exploit a narrow range of mostly arboreal aphids.

In the pipizine + paragine line, a parallel specialization has occurred. *Paragus* is a generalized herb-layer genus occasionally found on trees. *Pipizella* is also a ground-layer species on root-aphids so far as is known. The remaining pipizine genera are mostly arboreal and are commonly specialized predators of aphids in galls and aphids that produce flocculence.

Thus there appears to have been a dramatic change during the evolution of the predatory habit in Syrphinae. Without a specific sampling programme it is difficult to substantiate this trend further: collation of data from the literature is inadequate (Fox & Morrow, 1981). Despite this, it is obvious that syrphine genera have gradually concentrated upon aphids and then narrowed their prey range to fewer and fewer aphid species; some are nearly monophagous. Correlated with this is a shift from ground-layer to arboreal habitats.

Another trend appears to be the elaboration of increasingly complex and substrate-specific cryptic colour patterns (Rotheray, 1986b). Amongst the generalists, colour patterns are simple. *Melanostoma* and *Sphaerophoria* species are all green, for example. Other generalists use translucence with white adipose tissues to disguise the black hind gut: for example *Syrphus*, *Baccha* and *Episyrphus*. Translucence as a camouflage has the advantage that it works on many different substrates (Rotheray, 1986b). Further up the phylogenetic tree more specialist colour patterns occur which are suited to particular backgrounds: for example, the white larva of *Melangyna umbellatarum* lives among the white flowers of *Heracleum sphondylium* L.; *Parasyrphus vittiger* has brown and red longitudinal stripes that disguise it on the pine needles among which it occurs; *Dasysyrphus* larvae are modified in shape as well as colour pattern to resemble bark; *Epistrophe* larvae are also modified in shape and colour pattern for disguise on leaves; the larvae of *Meligramma triangulifera* resembles a bird dropping (Rotheray, 1986b).

Correlated with aphid prey specialization is a trend towards decreasing abundance. In most studies reporting relative abundance of syrphines, by far the commonest genera are *Melanostoma*, *Platycheirus*, *Episyrphus*, *Sphaerophoria*, and *Syrphus* (e.g. Owen, 1981). Genera higher up on the tree are nearly always much rarer, and form a small part of the syrphid community. This is probably connected with the trend towards specialization, but the ecological relationships between species within communities and their relative abundance remains an unsolved problem. In syrphids there is the confounding factor of mimicry of wasps and bees by the adult flies which theoretically should influence patterns of abundance; the implications of this phylogeny for ideas about the evolution of mimicry in the subfamily are currently being assessed.

Interpreting trends

Most of the morphological trends considered above can be correlated with the development of an obligate relationship with arboreal aphids. The increase in overall size and shorter larval growth period may have resulted from a more efficient utilization of the aphid biomass as the specialized relationship developed. However, the hypothesis that specialization results in increased efficiency of resource use as a pay-off against reduced resource abundance has failed to be confirmed in phytophagous insects (Slansky & Scriber, 1985), but little is known of specialization in carnivores (Tauber & Tauber, 1987). The trend towards increasing size is accompanied by an increase in the relative size of the spiracular slits, possibly reflecting some physiological need.

A major hurdle for plant-dwelling insects is developing efficient locomotory and attachment mechanisms to prevent falling off (Southwood, 1973) and this may account for the greater development of locomotory prominences seen in genera high up the phylogenetic tree: Rotheray (1987b) describes these specializations in more detail. Moving about on plant surfaces, particularly in arboreal environments, possibly entails a greater risk of predation: cryptic colour and shape patterns are more complex and varied in arboreal than ground-dwelling genera (Rotheray, 1986b).

The development of a plant-dwelling way of life probably accounts for the gradual loss of pupal horns seen in predacious syrphids. Their occurrence is a feature shared with non-predacious groups of syrphid larvae. However, pupal horns in predacious syrphids are very small and do not occur in genera high up the phylogenetic tree. Most non-predacious syrphid larvae pupate either in the soil or in association with a variety of wet situations (see Hartley, 1961). Here, with the spiracular openings, on vertically projecting pupal horns, they are less likely to become inundated with fluids. Predacious syrphids, however, pupate either on plants or in the upper layer of the leaf litter where inundation may be less of a problem.

The Pipizini have long prps and their spiracular slits are borne on tall carinae. Most pipizines are specialized predators of gall and root aphids, where the long prp may represent an adaptation to avoid the spiracular slits becoming coated with honeydew which, in the confined spaces in galls and around roots, tends to build up in large quantities.

It is clear from this study that larval stages of predacious Syrphidae contain a great deal of phylogenetic information. The morphological and biological trends evident in the proposed phylogeny are a valuable means of generating hypotheses. The hypothesis that increased specialization on aphids has occurred has been tested, for example, by comparing feeding behaviour in species high and low on the phylogenetic tree. Species higher up should be more efficient than those lower down. On the basis of quantitative differences in some key aspects of prey catching and handling behaviour this seems to be the case in *Syrphus ribesii* and *Melanostoma scalare.* The former species is a more effective predator of *Aphis fabae* (Scopoli) aphids (Rotheray, 1983).

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APPENDIX

List of syrphid species studied: l = larva, p = puparium, m = mouthparts; material at the Royal Museum of Scotland unless otherwise indicated. G = type species of the genus or subgenus.

Nomenclature according to Stubbs & Falk (1983)	OTU's employed in this study, for explanation see Table 2 & section on generic relationships	Names considered valid
Baccha elongata (Fabricius)^{G} l	*Baccha*	*Baccha*
Baccha obscuripennis Meigen l,p,m	*Baccha*	*Baccha*
Melanostoma mellinum (Linnaeus)^{G} p,m	*Melanostoma*	*Melanostoma*
Melanostoma scalare (Fabricius) l,p,m	*Melanostoma*	*Melanostoma*
Platycheirus		
S. *Pachysphyria ambiguus*^{G} p,m	*Plaaycheirus*	*Platycheirus*
Platycheirus albimanus (Fabricius) l,p	*Platycheirus*	*Platycheirus*
Platycheirus angustatus (Zetterstedt) l	*Platycheirus*	*Platycheirus*
Platycheirus clypeatus (Meigen) l,p	*Platycheirus*	*Platycheirus*
Platycheirus fulviventris (Macquart) l,p,m	*Platycheirus*	*Platycheirus*
Platycheirus manicatus (Meigen) l,p,m	*Platycheirus*	*Platycheirus*
Platycheirus scambus (Meigen) l	*Platycheirus*	*Platycheirus*
Platycheirus scutatus (Meigen)^{G} l,p,m	*Platycheirus*	*Platycheirus*
Pyrophaena granditarsa (Forster)^{4} p,m	*Pyrophaena*	*Pyrophaena*
Pyrophaena rosarum (Fabricius)^{5G} p,m	*Pyrophaena*	*Pyrophaena*
Xanthandrus comtus (Harris)^{6G} p,m	*Xanthandrus*	*Xanthandrus*
Paragus		
S. *Pandasyopthalmus haemorrhous* Meigen p,m	*Paragus*	*Paragus*
Chrysotoxum verralli Collin l,p,m	*Chrysotoxum*	*Chrysotoxum*
Dasysyrphus albostriatus (Fallén)^{G} l,p,m	*Dasysyrphus*	*Dasysyrphus*
Dasysyrphus lunulatus (Meigen) p,m	*Dasysyrphus*	*Dasysyrphus*
Dasysyrphus tricinctus (Fallén) l,p,m	*Dasysyrphus*	*Dasysyrphus*
Dasysyrphus venustus (Meigen) l,p	*Dasysyrphus*	*Dasysyrphus*
Didea fasciata Macquart^{G} l,m	*Didea*	*Didea*
Epistrophe eligans (Harris) l,m,p	*Epistrophe*	*Epistrophe*
Epistrophe grossulariae (Meigen)^{G} l,m,p	*Epistrophe*	*Epistrophe*
Epistrophe nitidicollis (Meigen) l,m,p	*Epistrophe*	*Epistrophe*
Epistrophe		
S. *Epistrophella euchroma*^{G} (Kowarz)	*Epistrophella*	*Meligramma*
Episyrphus balteatus (Dageer)^{G} l,m,p	*Episyrphus*	*Episyrphus*
Eriozona syrphoides (Fallén)^{1G} l,p,m	*Eriozona*	*Eriozona*
Leucozona		
S. *Ischyrosyrphus laternaria* (Müller) l,p,m	*Leucozona*	*Leucozona*
Leucozona lucorum (Linnaeus)^{G} l,p,m		
Megasyrphus annulipes (Zetterstedt)^{2G} l,p,m	*Megasyrphus*	*Didea*
Melangyna artica (Zetterstedt) l,p,m	*Melangyna*	*Melangyna*
Melangyna lasiophthalma l,p,m	*Melangyna*	*Melangyna*
Melangyna quadrimaculata (Verrall) l,p	*Melangyna*	*Melangyna*
Melangyna umbellatarum (Fabricius) l,p,m	*Melangyna*	*Melangyna*

APPENDIX *Continued*

Nomenclature according to Stubbs & Falk (1983)	OTU's employed in this study, for explanation see Table 2 & section on generic relationships	Names considered valid
Melangyna		
S. *Meligramma cincta* (Fallén)^{G} l,p,m	*Fagisyrphus*	*Melangyna*
Melangyna		
S. *Meligramma guttata* (Fallén)^{G} l,p,m	*Meligramma*	*Meligramma*
Melangyna		
S. *Meligramma triangulifera* (Zetterstedt) l,p,m	*Meligramma*	*Meligramma*
Meliscaeva auricollis (Meigen) l,p,m	*Meliscaeva*	*Meliscaeva*
Meliscaeva cinctella (Zetterstedt)^{G} l,p	*Meliscaeva*	*Meliscaeva*
Metasyrphus corollae (Fabricius)^{G} l,p,m	*Eupeodes*	*Eupeodes*
Metasyrphus latilunulatus (Collin) p,m	*Eupeodes*	*Eupeodes*
Metasyrphus luniger (Meigen) l,p,m	*Eupeodes*	*Eupeodes*
Metasyrphus nielseni Dušek & Láska l,p	*Eupeodes*	*Eupeodes*
Parasyrphus punctulatus (Verrall) l,p,m	*Parasyrphus*	*Parasyrphus*
Parasyrphus vittiger (Zetterstedt) l,p,m	*Parasyrphus*	*Parasyrphus*
Scaeva pyrastri (Linnaeus)^{G} l,p,m	*Scaeva*	*Scaeva*
Scaeva selenitica (Meigen) l,p,m	*Scaeva*	*Scaeva*
Sphaerophoria menthastri (Linnaeus) l,p,m	*Sphaerophoria*	*Sphaerophoria*
Sphaerophoria scripta (Linnaeus)^{G} l,p,m	*Sphaerophoria*	*Sphaerophoria*
Syrphus ribesii (Linnaeus)^{G} l,p,m	*Syrphus*	*Syrphus*
Syrphus torvus Osten-Sacken l,p,m	*Syrphus*	*Syrphus*
Syrphus vitripennis Meigen l,p,m	*Syrphus*	*Syrphus*
Xanthogramma pedissequum (Harris) p,m	*Xanthogramma*	*Xanthogramma*
Heringia heringia (Zetterstedt)^{G} p,m	*Heringia*	*Heringia*
Neocnemodon vitripennis (Meigen)^{3} p,m	*Neocnemodon*	*Heringia*
Pipiza austriaca Meigen l,p,m	*Pipiza*	*Pipiza*
Pipiza luteitarsis (Zetterstedt) l,p,m	*Pipiza*	*Pipiza*
Pipiza noctiluca (Linnaeus)^{G} l,p,m	*Pipiza*	*Pipiza*
Pipizella varipes (Meigen) l,p,m	*Pipizella*	*Pipizella*

European genera and subgenera not available for study with their type species
Paragus sensu stricto Latreille, 1802
    Syrphus bicolor Fabricius, 1794
Doros Meigen, 1803
    Syrphus conopeus Fabricius, 1775
Metasyrphus (Lapposyrphus) Dušek and Láska, 1967
    Scaeva lapponica Zetterstedt, 1838
Trichopsomyia Williston, 1888
    Trichopsomyia polita Williston, 1888 (from Brazil, see Thompson, 1981)
Triglyphus Loew, 1840
    Triglyphus primus Loew, 1840

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