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Phylogenetic relationships and the larval head of the lower Cyclorrhapha (Diptera)

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We examined final-stage larvae of all currently recognized lower cyclorrhaphan (= Aschiza) families, except Ironomyiidae and Sciadoceridae, and those of the higher cyclorrhaphan (= Schizophora) families Calliphoridae, Conopidae, Lonchaeidae, Muscidae, and Ulidiidae, and compared them with larvae of two out-group families, Rhagionidae and Dolichopodidae, paying particular attention to structures of the head. A set of 86 morphological characters were analysed phylogenetically. The results show that the lower Cyclorrhapha is paraphyletic in relation to the higher Cyclorrhapha. The monophyly of the Cyclorrhapha is strongly supported. The lower Cyclorrhapha is resolved into two clades, based on the Lonchopteridae. Within the Syrphidae the traditional three-subfamily system is supported, based on the Microdontinae. Within the lower Cyclorrhapha, the larval head is variable in form and arrangement of components. In Lonchopteridae, the mouth lies at the back of an open trough or furrow, comprising ventrally an elongate labium and laterally the maxilla. This arrangement of components appears to facilitate scooping food in water films. In Platypezoidea there is no furrow, and the dorsolateral lobes bearing the antennae are connected by a dorsal extension of the pseudocephalon. The main food-gathering structure is the hooked apex of the labium, but in Phoridae the mandibles may also be important. In Eumuscomorpha the mandibles are at the apex of the head skeleton. The pseudocephalon is extended and infolded dorsally to form an oral pocket over the mouth. In the Pipunculidae, and the Microdontinae and Syrphinae of the Syrphidae, ventrally it forms a V-shaped groove or guide along which the mandibles project. The labium is sclerotized apically, and forms a plate or tapered projection. This arrangement of components facilitates holding, piercing and extracting prey tissues. In Eristalinae the pseudocephalon is attached to the mandibles and is formed into a pair of cirri bearing mandibular lobes that lie either side of the mouth. Furthermore, the epipharynx is produced anteriorly in relation to the hypopharynx, and the labium is attached to the anterior part of the epipharynx to form a cavity or atrium. This arrangement is suited to fragmenting and imbibing solid food in Eristalinae with hooked mandibles, and when the mandibles are reduced and the mandibular lobes are inverted and sclerotized, these structures form a filter for separating fluid-suspended particulate food. In higher Cyclorrhapha an atrium is present as in Eristalinae, but a connection between the pseudocephalon and the mandibles is absent. Instead, the pseudocephalon is bifurcate dorsally and forms a pair of cephalic lobes that ventrally ensheath each mandible. The surface of the sheath may be coated in cirri and other food-gathering structures. The cephalic lobes, mandibular sheaths and the head skeleton are maneuverable and retractile to a higher degree than in lower Cyclorrhapha. This arrangement of components facilitates feeding on both solid food, in which the mouthooks may extend from the sheath to break the food up, and particulate and suspended food, in which the food-gathering structures of the sheath scoop up the food. In many higher Cyclorrhapha, maneuverability is enhanced by a break between the labium and the basal sclerite, to which it is fused in all lower Cyclorrhapha. Intermediate characters and states for the structures of the higher cyclorrhaphan larval head are present in out-groups, and lower Cyclorrhapha and homologies are discussed. Liquidity of the food is an important factor explaining the structure of the larval head in Cyclorrhapha. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **153**, 287–323.

ADDITIONAL KEYWORDS: head skeleton – morphology – predation – saprophagy.

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INTRODUCTION

Recent attempts using both morphological and molecular characters to resolve relationships between families of the lower Cyclorrhapha (Diptera) (= Aschiza; Yeates & Wiegmann, 1999) have resulted in conflicting hypotheses (Collins & Wiegmann, 2002). The lack of agreement is partially explained by the varying ways in which morphological homologies have been inferred (Collins & Wiegmann, 2002). For example, much disagreement exists over how to interpret male genitalia (Yeates & Wiegmann, 1999).

Taxon sampling is also a problem. With the limits and monophyly of families not fully resolved, e.g. the Microdontinae within the Syrphidae (Skevington & Yeates, 2000; Ståhls *et al*., 2003), and poor understanding of groundplan characters, the method of exemplar selection that must be used cannot preclude using taxa with derived character states that may either poorly resolve or conflate relationships.

Despite these difficulties, confidence is gained where several studies using different taxa, character sets, or methods of analysis converge on the same result. For example, one major consensus emerging from several recent studies based on morphological and molecular characters is that the lower Cyclorrhapha are paraphyletic with respect to the higher Cyclorrhapha (= Schizophora) (Griffiths, 1972; Wada, 1991; Cumming, Sinclair & Wood, 1995; Zatwarnicki, 1996; Collins & Wiegmann, 2002).

In this paper we give results of a morphological analysis of final-instar larval characters, particularly of the head. A review of some aspects of the immense structural diversity in the dipteran larval head was made by Teskey (1981) and was updated by Courtney, Sinclair & Meier (2000), the changes of which represent a major evolutionary development across the Diptera. However, Teskey (1981) points out that difficulties exist in tracing the homology of individual characters in the Cyclorrhapha because of an apparent lack of intermediates. But the problem could be lack of knowledge. As Courtney *et al*. (2000) point out, in terms of larval characters, there is a lack of information about lower cyclorrhaphan larvae, such as those of the Platypezidae. Recent studies have begun to fill this gap (e.g. Rotheray, Chandler & Gilbert, 2004). One aim of the investigation reported here was to determine whether intermediate character states exist within the lower Cyclorrhapha, and hence whether a set of homologies can reasonably be proposed for the higher cyclorrhaphan larval head.

MATERIAL AND METHODS

TAXON SAMPLING

We obtained larval characters from 27 taxa (Appendices 1 and 2), including two Brachyceran out-group families, all lower cyclorrhaphan families, except Ironomyiidae and Sciadoceridae, and six higher cyclorrhaphan families. The choice of these families was based on relationships in McAlpine (1989) and the availability of material. They included relatively basal families, such as Lonchaeidae and Conopidae, and representatives of nonbasal families, such as Calliphoridae and Muscidae. We also included representatives of three of the four subfamilies of the Platypezidae, and representatives of all three subfamilies of the Syrphidae. We also included the Pipizini (Syrphidae), the phylogenetic relationship of which is unresolved (Vockeroth & Thompson, 1987; Rotheray & Gilbert, 1999; Ståhls *et al*., 2003).

MORPHOLOGICAL ANALYSIS

Larvae were collected in the field, fixed in hot water, and preserved in 70% alcohol, or, to confirm identity, were reared through to the adult stage. To examine the morphology of the head a number of approaches were taken, as described previously by Rotheray *et al*. (2004). A binocular microscope was used to examine the external morphology of the thorax and head. Larvae were either placed in alcohol or were examined dry. Integumental detail was confirmed where necessary by staining with methylene blue.

Additional detail and functional relationships between the components of the head were obtained by cutting through the metathorax of a preserved larva, and clearing the cut section in cold KOH for about 1 h or in hot KOH for 10–15 min. Where necessary, excess tissue was removed with pins. When placed in a watch glass with alcohol or glycerol, the resulting translucent preparation enabled clear, *in situ* views of the head skeleton, head, and thorax. Functional relationships between the various parts were suggested by pushing down and forward on the rear of the preparation with a pin, which opened the mouth, and enabled the relative positions and movements of the component parts to be seen. This is possible because of impressed lines and folds present in the integument of the head and thorax. These lines and folds were retained in preparations, and represent places where the integument characteristically bends or collapses when the larva moves (Rotheray & Gilbert, 1999).

Head skeletons, i.e. the sclerotized mouthparts, were examined by dissecting them from preserved larvae and clearing in KOH, or removing them from puparia after soaking in KOH for about 1 h. When extracting head skeletons from puparia, care was taken to remove any attached but membranous and translucent structures, such as oral ridges, maxillary palpi, and antennae. Head skeletons were examined by placing them in a watch glass containing glycerol and using a binocular microscope. Apart from removing attached membranous tissue where necessary to obtain clear views, head skeletons were neither further dissected nor slide mounted. This was because more information was available by being able to rotate the whole head skeletons in glycerol. Such all-round views were particularly helpful in tracing translucent parts of the head skeleton, and those that are in more than one plane.

For morphological analyses, we determined the status of characters and character states using the standard criteria of general resemblance, spatial relationships, parsimony, and presence of landmark features such as sensilla and points of muscle attachment. Landmark features are assumed to be part of the groundplan of higher, more inclusive groups than the taxa considered here, and hence are fixed in the same relative positions, with little modification across both in- and out-groups. For the nomenclature of components of the larval head we followed Roberts (1969), Hartley (1963), and in particular Courtney *et al*. (2000).

Drawings were made using a drawing tube attached to the microscope. Measurements were made using a measuring eyepiece. Except where noted, larval material examined in this study is deposited in the National Museums of Scotland (NMS).

PHYLOGENETIC ANALYSIS

To investigate phylogenetic relationships, a set of 86 characters were obtained from the larva and/or puparium of 25 lower cyclorrhaphan species (Appendices 1 and 2), and were scored on an out-group consisting of the brachyceran species *Rhagio scolopaceus* (Linnaeus, 1758) (Rhagionidae) and *Systenus pallipes* (von Roser, 1840) (Dolichopodidae).

We used PAUP v4.0 to analyse these data. All characters were unordered and had equal weight. Three characters were parsimony uninformative. Trees were obtained using the 'Bandb' command with the default options of addition sequence ('furthest') and Multrees. The tree was drawn using out-group rooting, and characters were optimized by accelerated transformation. The bootstrap analysis used the Bandb method and reported all branches appearing in more than 50% of bootstrap replicates (Conlevel = 50, the default). Bremer support values were also calculated using PAUP. Repeat runs of Bandb were made, each time increasing the length of the maximum retained tree by one step, accepted as equally 'short' as the minimum step tree. A strict consenus tree was then run between the retained trees, and when a clade disappeared from the concensus tree, the difference between the minimum length tree and the maximum retained length tree is taken as the Bremer support for that clade.

RESULTS

MORPHOLOGY OF THE LARVAL HEAD

Rhagio scolopaceus (Linnaeus, 1758) (Rhagionidae) (Figs 1–4)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold (Fig. 3); base membranous, infolded anteriorly, and continuous with the labrum, labium, and maxillomandibles; cranium present as a rectangular dorsal plate with heavily sclerotized margins; antennae on anterolateral margins of the cranium; tentorial phragma present, from which extends a pair of tentorial arms with crescent-shaped apices ventroposteriorly and a pair of metacephalic rods anteroposteriorly (Fig. 1).

Atrium: absent, i.e. enclosed cavity incorporating the labium not present.

Position of mouth: between the apices of the epipharyngeal plate and the hypopharynx; surrounded by labrum dorsally, mandibles laterally, and labium ventrally (Fig. 3).

Labrum: sclerotized, base attached to the tentorial phragma, and tapering anteriorly to project free above the opening of the mouth (Fig. 2); anterodorsal margin serrated; ventrally attached to the epipharynx.

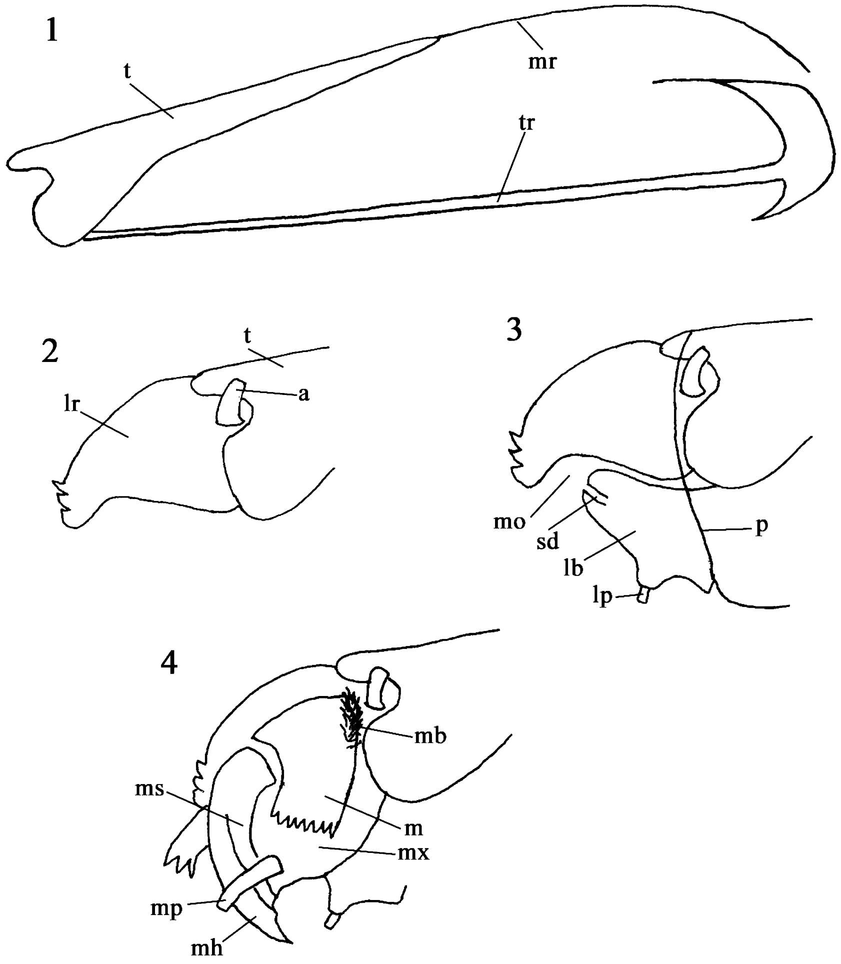
Labium: a square-shaped, fleshy lobe attached basally to the hypopharynx bearing, at its apex, a pair of labial papillae and sensilla (Fig. 3).

Mandible: consisting of two sclerites, with a U-shaped, posterior sclerite that overlies the labrum and extends to the floor of the mouth, and that bears a serrated ventral margin; dorsum with a mandibular brush of rows of setae; anterior mandibular sclerite consisting of a narrow, downwardly projecting hook that lies in a fleshy fold of the maxilla, and articulates with the anterodorsal margin of the tentorial phragma (Fig. 4).

Maxilla: fleshy, rectangular in shape with maxillary palpi on long basal projections on the apical margin (Fig. 4); one half of the maxilla and one apical mandibular hook lie on either side of the apex of the labrum.

Material examined: One larva, Scotland, Perthshire, Fungarth Wood nr Dunkeld; 1 April 1998, ex. wet decayed birch branch (*Betula*) lying in a seepage, identification confirmed by comparison with reared material in collections of the NMS, G. E. Rotheray.

Previous descriptions: Roberts (1969); Rotheray *et al*. (2004).



Figures 1–4. Head skeleton of final-stage larva of *Rhagio scolopaceus* (Linnaeus, 1758) (Rhagionidae): 1, head skeleton, lateral view, anterior end to the left; 2, apex of the tentorial phragma showing attachment of labrum; 3, apex with labrum and labium; 4, apex with labrum, labium, and maxillomandibles. Abbreviations: a, antenna; lb, labium; lp, labial palp; lr, labrum; m, mandible, basal sclerite; mb, mandibular brush; mh, mouthook, apical sclerite; mo, mouth; mp, maxillary palp; mr, metacephalic rods; ms, maxillary sheath for the mouthook; mx, maxilla; p, pseudocephalon, anterior limit; sd, salivary duct; t, tentorial phragma; tr, tentorial rods.

Systenus pallipes (von Roser, 1840) (Dolichopodidae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold; base membranous, infolded anteriorly, and continuous with the labrum, labium, and maxillomandibles; cranium reduced to a narrow, crescent-shaped plate; tentorial phragma present, from which extends a pair of tentorial arms ventroposteriorly and a pair of metacephalic rods anteroposteriorly, which are separated from the tentorial phragma by a gap; antennae on short, basal projections on lateral margins of the cranium.

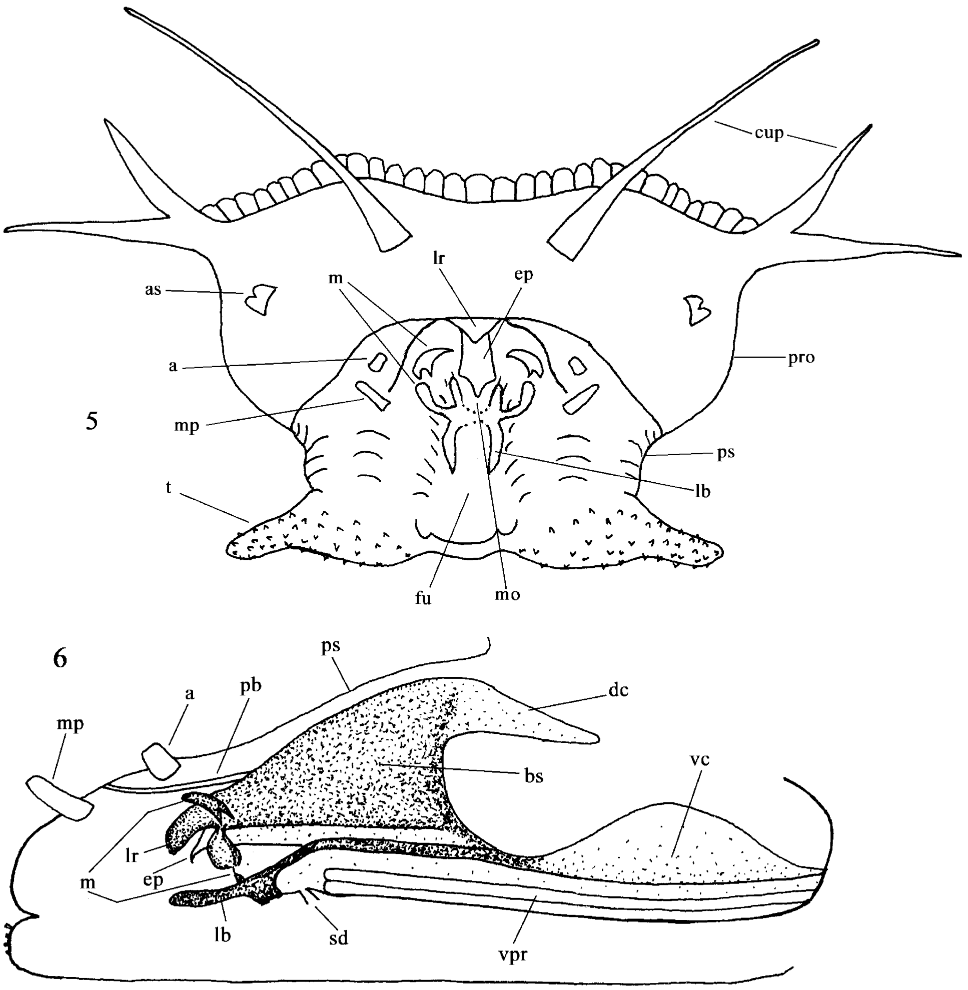
Position of mouth: between the apices of the epipharyngeal plate and the hypopharynx; surrounded by labrum dorsally, mandibles laterally, and labium ventrally.

Atrium: absent, i.e. enclosed cavity incorporating the labium not present.

Labrum: sclerotized, base attached to the tentorial phragma, and tapering anteriorly to project free above the opening of the mouth; anterodorsal margin smoothly tapered and inclined downwards; ventrally attached to the epipharynx.

Labium: a longer than wide, fleshy lobe, bearing, at its apex, a pair of sensilla; the internal skeleton comprises a pair of curved, sclerotized rods, the labial rods; labial rods taper from base to apex, with their extreme apices toothed and free of the fleshy apex of the labium; basally attached to the hypopharynx.

Mandible: consisting of four articulated sclerites; anterior mandibular sclerite consisting of a narrow, inclined hook that lies in a fleshy fold of the maxilla.



Figures 5–6. Final-stage larva of *Lonchoptera lutea* Panzer, 1809 (Lonchopteridae): 5, head, apicodorsal view; 6, head, lateral view, anterior end to the left. Abbreviations: a, antenna; as, anterior spiracle; bs, basal sclerite; cup, cuticular projections; dc, dorsal cornu; ep, epipharynx; fu, furrow; lb, labium, anterior rods; lr, labrum; m, mandible; mo, mouth; mp, maxillary palp; pb, parastomal bar; pro, prothorax; ps, pseudocephalon; sd, salivary duct; t, triangular lobes; vc, ventral cornu; vpr, ventral pharyngeal ridges (= cibarial ridges).

Maxilla: fleshy, rectangular in shape, each half with a crescent-shaped sclerite surrounding a maxillary palpus that is mounted on a short, basal projection on the apical margin; one half of the maxilla and one apical mandibular hook lie on either side of the apex of the labrum.

Material examined: One larva, Scotland, Perthshire, Dalguise nr Pitlochry; 26 April 1995, ex. sap run on horse chestnut (*Aesculus hippocastanum* L.), identification confirmed by comparison with reared material in collections of the NMS, G. E. Rotheray.

Previous descriptions: Krivosheina (1973); Rotheray *et al.* (2004).

Lonchoptera lutea Panzer, 1809 (Lonchopteridae) (Figs 5, 6)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold (Fig. 5); membranous, infolded apically, and continuous with the labrum, labium, and maxilla; cranium absent; anterodorsally not as produced as the ventral and lateral margins, so that the apex of the head forms a wedge-shaped furrow (Fig. 5); ventral margin greatly developed, being rounded, coated in triangular-shaped setae, and with conspicuous, tapering, lobes similarly coated in setae on the apicolateral margins; dorsocentrally this rim folds to meet the apex of the labium; anterolateral margins of the head continuous with the maxilla; antennae on dorsolateral margins (Fig. 5).

Atrium: absent, i.e. enclosed cavity incorporating the labium not present.

Position of mouth: between the apices of the epipharyngeal plate and the hypopharynx; surrounded by labrum dorsally, mandibles laterally, and labium ventrally (Fig. 5).

Basal sclerite (= pharyngeal sclerite): present, consisting ventrally of the hypopharynx, which is supported on each side by modified tentorial bars, the ventral cornua, the hypopharynx bears on its upper surface longitudinal, crenulated ridges, the cibarial ridges (Fig. 6); anteriorly, the tentorial bars are fused to and supported by the tentorial phragma, which is a vertical, U-shaped plate; anteriorly, the two halves of the vertical plate are joined by a translucent strip, except for a narrow region of sclerotization, the dorsal bridge; a pair of tapering projections extends from the posterodorsal margin of the vertical plate, the dorsal cornua, and the labrum extends from the anterodorsal margin below the dorsal bridge; from the anterolateral margins of the vertical plate, a pair of diverging, sclerotized bars, the parastomal bars, extend into and support the maxilla.

Labrum: sclerotized, base attached to the vertical plate, and tapering anteriorly to project free above the mouth; ventrally attached to the epipharynx.

Labium: a longer than wide, fleshy lobe, attached at its base to the hypopharynx, and bearing, at its apex, a pair of sensilla and three pairs of fleshy lobes; the internal skeleton comprises a pair of parallel labial rods; rods interrupted medially by an articulation point with the mandibles; articulation point heavily sclerotized, but not forming a complete transverse bridge across the floor of the labium; posterior rods fused at base with the vertical plate; anterior rods ensheathed in and supporting the fleshy labium.

Mandible: consisting of two or more sclerites; articulating at base with the labial rods and apically with the dorsolaterally inclined mouthhook; ensheathed in the maxilla (Fig. 6).

Maxilla: fleshy, divided dorsoventrally into two halves, each half inclining anteriorly and fused posteriorly with the pseudocephalon and ventrally with the labium; maxillary sclerite internal and attached to the basal sclerite, and extending to the maxillary palpus; anterodorsal margin of each maxilla with a maxillary palpus on a short projection, approximated with an antenna.

Material examined: Five larvae, England, Devon, Whiddon, 18 October 1991, M. Drake; one puparium, Scotland, Edinburgh, Leith, 25 November 1993, on fallen *Acer* leaf, D. M. Robertson.

Previous descriptions: de Meijere (1900); Brauns (1954); Hennig (1976).

Melanderomyia kahli (Kessel, 1960) (Platypezidae) (Figs 7–11)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold (Fig. 7); membranous and incorporating the fleshy maxilla on the lateral margins; infolded apically, and continuous with the labrum and labium; cranium absent; tapering in shape; dorsum with membranous connection between the antennae and maxillary palpi; this connection delimited laterally by a pair of impressed longitudinal lines on the inside margins of the antennae (Fig. 10); antennae and maxillary palpi approximated on the anterolateral margins of the head, and both on short projections; oral ridges and cirri absent.

Atrium: not developed, i.e. enclosed cavity incorporating the labium and epipharynx very short.

Position of mouth: between the labrum and labium at the base of the mandibles (Fig. 10).

Basal sclerite: similar in basic form to that of *L. lutea*, except dorsal bridge and parastomal bars indistinct; mouth more or less directed anteriorly and narrow, with the labrum and labium approximated close together (Figs 9, 11).

Labrum: translucent, with a tapered apex over the mouth (Figs 8, 10).

Labium: fleshy apical lobe absent, with posterior and anterior rods free and exsheathed; articulation point forming anteriorly directed epicondyles, articulating and supporting the mandibles; anterior rods fused at apex into a downwardly directed hook, which is the foremost part of the head (Figs 8, 10).

Mandible: consisting of one mostly translucent, subrectangular sclerite (Fig. 9); anterior margin inclined forwards ventrally and bearing a series of rounded teeth; mandibular base widened to form an articulation point with the epicondyle of the labium; mandible free, not embedded in a fleshy maxilla, directed anteriorly and lying each side of the tapered end of the labrum.

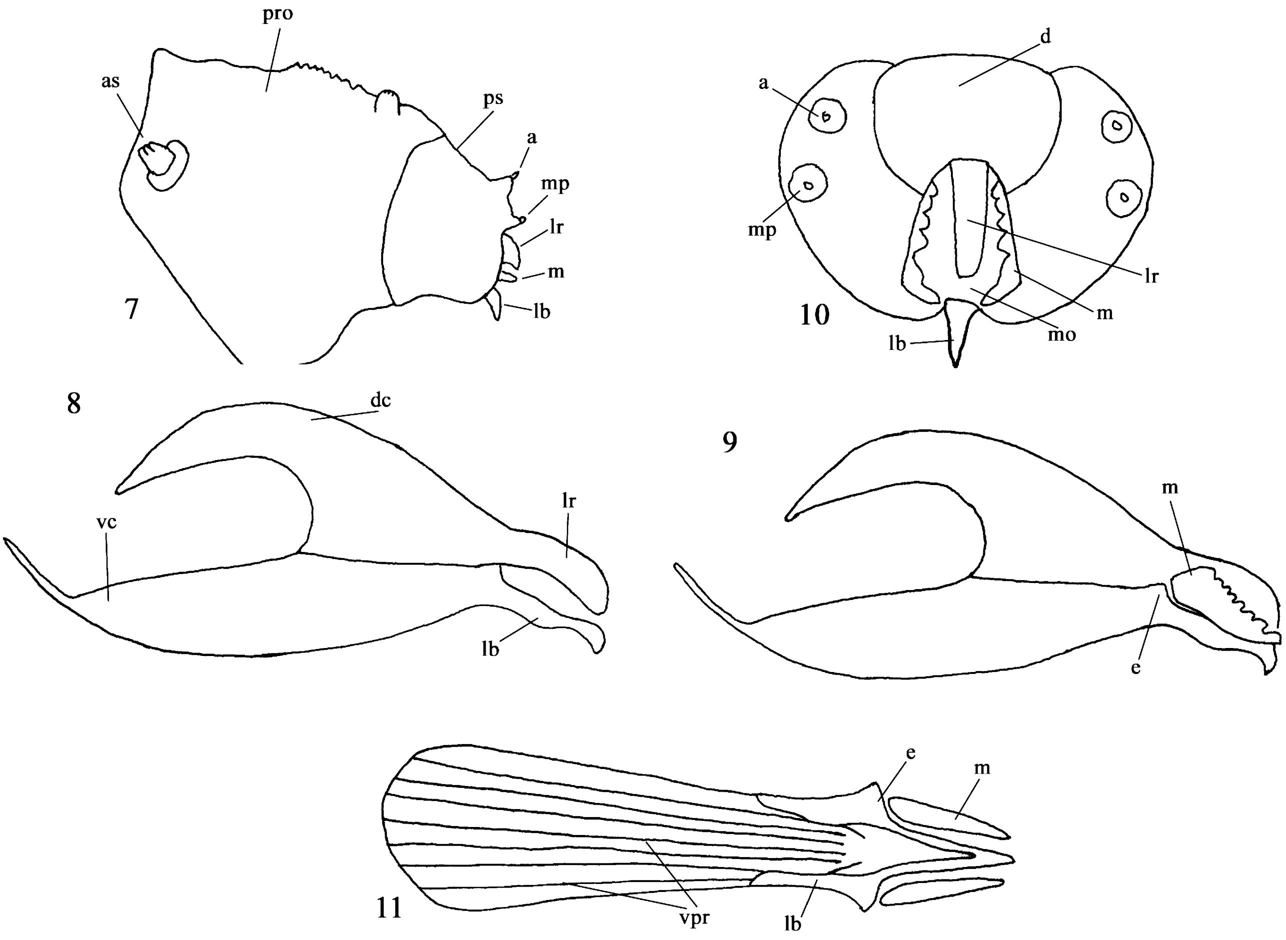
Maxilla: not distinct.

Material examined: Nine larvae, USA, Georgia, Tifton, 16 March 1969, from Stinkhorn fungus (Phallaceae), J. A. Payne, Canadian National Collections, two larvae retained in NMS.

Previous descriptions: Kessel, Buegler & Keyes (1973), Sinclair (1992), Rotheray *et al*. (2004).

Callomyia amoena Meigen, 1824 (Platypezidae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous; infolded apically and continuous with the labrum and labium; cranium absent; tapering in shape; dorsum with membranous connection between the antennae and



Figures 7–11. Final-stage larva of *Melanderomyia kahli* (Kessel, 1960): 7, head, lateral view; 8, head skeleton, lateral view, anterior end to the right, minus mandibles; 9, head skeleton, ventral view, anterior end to the left with mandibles; 10, head, apical view, 11, head skeleton, ventral view, anterior end to the right. Abbreviations: a, antenna; as, prothoracic spiracle; d, dorsal connection of pseudocephalon; dc, dorsal cornu; e, epicondyle; lb, labium; lr, labrum; m, mandible; mo, mouth; mp, maxillary palp; pro, prothorax; ps, pseudocephalon; vc, ventral cornu; vpr, ventral pharyngeal ridges (= cibarial ridges).

maxillary palpi; this connection not delimited laterally by a pair of impressed longitudinal lines on the inside margins of the antennae; mouth opening more or less directly anteriorly; antennae and maxillary palpi approximated on the anterolateral margins of the head, and both on short projections; oral ridges and cirri absent.

Atrium: not developed, i.e. enclosed cavity incorporating the labium and epipharynx very short.

Position of mouth: between the labrum and labium at the base of the mandibles.

Basal sclerite: heavily sclerotized, dorsal bridge present; parastomal bars and cibarial ridges absent; narrow dorsoventrally, with the labrum and labium approximated; dorsal and ventral cornua short and diverging.

Labrum: translucent with a tapered apex over the mouth.

Labium: fleshy lobe absent, with heavily sclerotized posterior and anterior rods free and exsheathed; articulation point forming anteriorly facing epicondyles, articulating and supporting the mandibles; anterior rods separated from the rest of the labium by a narrow gap, and with three large downwardly facing hooks that are joined ventrally by narrow, sclerotized strips; labial lobe absent.

Mandible: consisting of one mostly scleroteized, subrectangular sclerite; base widened to articulate with the labium; mandible free, not embedded in a fleshy maxilla, directed anteriorly and lying each side of the tapered end of the labrum.

Maxilla: not distinct.

Material examined: One puparium, England, Berkshire, Windsor Forest, 20 June 1968, ex decayed wood of *Fagus* stump, A. E. Stubbs.

Previous descriptions: Chandler (2001), Kessel *et al*. (1973), Rotheray *et al*. (2004).

Bolophus furcata (Fallén, 1826) (Platypezidae)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold; membranous, and incorporating the fleshy maxilla on the lateral margins; infolded apically, and continuous with the labrum and labium; cranium absent; tapering in shape; dorsum with membranous connection between the antennae and maxillary palpi; this connection delimited laterally by a pair of impressed longitudinal lines on the inside margins of the antennae; antennae and maxillary palpi approximated on the anterolateral margins of the head, and both on short projections; oral ridges on lateral margins.

Atrium: not developed, i.e. enclosed cavity incorporating the labium and epipharynx very short.

Position of mouth: between the labrum and labium at the base of the mandibles.

Basal sclerite: dorsal bridge present; ventral cornu with an apodeme; dorsal and ventral cornua approximated; cibarial ridges absent.

Labrum: translucent with a tapered apex over the mouth.

Labium: fleshy lobe absent, with posterior and anterior rods free and exsheathed; articulation point forming anteriorly directed epicondyles, articulating and supporting the mandibles; anterior rods with three large hooks separated from the rest of labium by an interruption; apex with a sclerotized plate below the hooks; labial lobe absent.

Mandible: consisting of one, mostly translucent, subrectangular sclerite; base widened to articulate with the labium; mandible free, not embedded in a fleshy maxilla, directed anteriorly and lying on each side of the tapered end of the labrum.

Maxilla: not a distinct structure.

Material examined: Five larvae, England, Sussex, Rogate in *Polyporus squamosus* Huds. (Polyporaceae), June 1979, P. J. Chandler; 15+ larvae, England, Lancashire, Whalley, ex *P. squamosus*, 14 July 1963, A. Brindle, Natural History Museum, London (NHM).

Previous descriptions: Kessel *et al*. (1973), Chandler (2001), Rotheray *et al*. (2004).

Agathomyia falleni (Zetterstedt, 1819) (Platypezidae)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold; membranous, and incorporating the fleshy maxilla on the lateral margins; infolded apically, and continuous with the labrum and labium; cranium absent; tapering in shape; dorsum with membranous connection between the antennae and maxillary palpi; this connection delimited laterally by a pair of impressed longitudinal lines on the inside margins of the antennae; antennae and maxillary palpi approximated on the anterolateral margins of the head, and both on short projections; oral ridges and cirri absent.

Atrium: not developed, i.e. enclosed cavity incorporating the labium and epipharynx very short.

Position of mouth: between the labrum and labium at the base of the mandibles.

Basal sclerite: vertical plate heavily sclerotized; dorsal bridge present; dorsal and ventral cornu approximated; cibarial ridges absent.

Labrum: translucent with a tapered apex over the mouth.

Labium: fleshy lobe absent, with posterior and anterior rods free and exsheathed; articulation point forming anteriorly directed epicondyles, articulating and supporting the mandibles; anterior rods with three hooks separated from the rest of labium by an interruption; apex with a sclerotized plate below the hooks; labial lobe absent.

Mandible: consisting of one, mostly translucent, subrectangular sclerite; base widened to articulate with the labium; mandible free, not embedded in a fleshy maxilla, directed anteriorly, and lying on each side of the tapered end of the labrum.

Maxilla: not distinct.

Material examined: Four larvae, England, Kent, Chislehurst, Pond Wood in *Bjerkandera adusta* (Willd.) P. Karst (Coriolaceae), 7 October 1971, P. J. Chandler.

Previous descriptions: Chandler (2001); Rotheray *et al*. (2004).

Platypeza consobrina (Zetterstedt, 1844) (Platypezidae)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold; membranous, and incorporating the fleshy maxilla on the lateral margins; infolded apically, and continuous with the labrum and labium; cranium absent; tapering in shape; dorsum with membranous connection between the antennae and maxillary palpi; this connection delimited laterally by a pair of impressed longitudinal lines on the inside margins of the antennae; antennae and maxillary palpi approximated on the anterolateral margins of the head, and both on short projections; oral ridges on lateral margins.

Atrium: not developed, i.e. enclosed cavity incorporating the labium and epipharynx very short.

Position of mouth: between the labrum and labium at the base of the mandibles.

Basal sclerite: vertical plate heavily sclerotized; dorsal bridge, cibarial ridges, and apodeme present; dorsal and ventral cornua diverging.

Labrum: translucent with a tapered apex over the mouth.

Labium: fleshy lobe absent, with posterior and anterior rods free and exsheathed; anterior rods with four small hooks separated from the rest of labium by an interruption; labial lobe absent.

Mandible: consisting of one, mostly translucent, subrectangular sclerite; supported by parastomal bar; mandible free, not embedded in a fleshy maxilla, directed anteriorly, and lying on each side of the tapered end of the labrum.

Maxilla: not distinct.

Material examined: Two larvae, England, Hertfordshire, Ashridge, ex *Armillaria mellea* (Wahl.) Kummer (Tricholomataceae), P. J. Chandler.

Previous descriptions: Kessel *et al*. (1973), Chandler (2001), Rotheray *et al*. (2004).

Megaselia rufipes (Meigen, 1804), Megaselia scalaris (Loew, 1866), Spinifera bergenstammi (Mik, 1864), and Triphelba minuta (Fabricius, 1787) (Phoridae)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold; membranous and tapering in shape; oral ridges and cirri absent, but two pairs of oval-shaped lateral lobes surround the mouth; pseudocephalon not extending over the mouth; antennae and maxillary palpi approximated on the anterolateral margins of the head, and connected by a medial extension of the pseudocephalon; antennae, but not maxillary organs, on short projections.

Atrium: not developed, i.e. enclosed cavity incorporating the labium and epipharynx very short.

Position of mouth: between the labrum and labium at the base of the mandibles.

Basal sclerite: similar in basic form to that of *L. lutea*; cibarial ridges, dorsal bridge, and parastomal bars present; parastomal bars extending to base of mandibles.

Labrum: translucent with a tapered apex over the mouth; approximated dorsoventrally with the labium.

Labium: fleshy lobe absent, with posterior and anterior rods free and exsheathed; articulation point extended laterally to form epicondyles, articulating and supporting the mandibles; anterior rods fusing at apex into a single, large, downwardly facing hook, which is the foremost part of the head; ventral bridge V-shaped and directed anteriorly, incomplete, and not sclerotized medially; labial lobe absent.

Mandible: consisting of one sclerotized, red-brown, elongate sclerite with teeth on apicoventral margin (subrectangular and lacking teeth in *S. bergenstammi*); mandible free, not embedded in a fleshy maxilla, directed anteriorly, and lying on each side of the tapered apex of the labrum.

Maxilla: not distinct.

Material examined: M. rufipes, seven larvae, Wales, Caernarvon, ex *Helix aspersa* (Mollusca), W. R. Wright, NHM; *M. scalaris*, four larvae, East Nigeria, NHM *S. bergenstammi*, ten+ puparia, Scotland, Edinburgh, Blackford, ex empty shells of *Helix aspersa* (Mollusca), collected 21 March 2001, adults emerged 18–25 April 2001, K. P. Bland; *T. minuta*, five larvae, England, Hampshire, New Forest, ex fungus, NHM.

Chalarus sp. and Verrallia sp. (Pipunculidae)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous; atrium and pre-oral cavity present, i.e. pseudocephalon extends beyond the mouth, which is between the bases of the mandibles; short, with each antenna and set of maxillary organs on a shared, cyclindrical projection, and projections approximated across the atrium; antennae and maxillary organs blunt-tipped; a fleshy V-shaped lobe, the dorsal lip, present above the mandibles and below, the projections bearing the antennae and maxillary organs; oral ridges absent; oral setae, a group of conspicuous, spicule-like, setae, present at each side of the mouth; not attached to the mandible.

Atrium: present, but short, i.e. an enclosed cavity incorporating the posterior rods of the labium laterally, the epipharyngeal plate dorsally, and the connecting membrane laterally.

Position of mouth: between the base of the mandibles, with dorsally the apex of the labrum, and ventrally the labial plate and sclerites.

Basal sclerite: with dorsal bridge; not strongly sclerotized; ventral and dorsal cornu short, so that the basal sclerite is higher than long; cibarial ridges absent; weakly indicated parastomal bars at the margins of the epipharyngeal plate.

Labrum: translucent, with tapered apex ending between the bases of the mandibles.

Labium: sclerotized and elongate; posterior rods broad and fused with the basal sclerite; epicondyles at apex, which articulate with the mandibles, and below and slightly behind this apex the short, broad anterior rods arise from an incompletely sclerotized articulation point, the ventral bridge; between the anterior rods is a broad, square-shaped sclerite that is longer than the anterior rods, the labial sclerite; labial sclerite possibly hinged basally; smooth at apex and upper surface, with spicules.

Mandible: comprising a single sclerite that is the most anterior part of the head skeleton; not attached to opposing mandibular sclerite; apex hook-like; ventral margin not serrated; base subrectangular.

Maxilla: not distinct.

Material examined: Chalarus sp., eight+ larvae, Scotland, Midlothian, Newbattle Abbey, September 1990, ex leafhopper on *Urtica dioica* Linnaeus (Urticaeae), G. E. Rotheray; *Verrallia* sp., one larva, England, Surrey, Addington, 12 August 1965, ex *Philaenus spumarius* (Linnaeus) (Hemiptera, Ceropidae), R. L. Coe, NHM.

Nephrocerus sp. (Pipunculidae)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous; atrium and pre-oral cavity present, i.e. pseudocephalon extends beyond the mouth, which is between the bases of the mandibles; short, with each antenna and set of maxillary organs on a shared, cyclindrical projection, and projections approximated across the atrium; antennae and maxillary organs blunt-tipped; a fleshy V-shaped lobe, the dorsal lip, present above the mandibles and below, the projections bearing the antennae and maxillary organs; oral ridges absent; oral setae, a group of conspicuous, spicule-like, setae, present at each side of the mouth; not attached to the mandible.

Atrium: present but short, i.e. an enclosed cavity incorporating the posterior rods of the labium laterally, the epipharyngeal plate dorsally, and the connecting membrane.

Position of mouth: between the base of the mandibles, with the apex of the labrum dorsally and the labial plate and sclerites ventrally.

Basal sclerite: with dorsal bridge; not strongly sclerotized; ventral and dorsal cornu short, so that basal sclerite is higher than long; cibarial ridges absent; weakly indicated parastomal bars at the margins of the epipharyngeal plate.

Labrum: translucent, with tapered apex ending between the bases of the mandibles.

Labium: sclerotized and elongate; posterior rods broad and fused with the basal sclerite; epicondyles at apex, which articulate with the mandibles, below and slightly behind this apex the short, broad anterior rods arise from an incompletely sclerotized articulation point, the ventral bridge; between the anterior rods is a broad, square-shaped sclerite longer than the anterior rods, the labial sclerite; labial sclerite possibly hinged basally; smooth at apex, and upper surface with spicules.

Mandible: comprising a single sclerite that is the most anterior part of the head skeleton; not attached to opposing mandibular sclerite; apex hook-like; ventral margin not serrated; base subrectangular.

Maxilla: not distinct.

Material examined: One larva, USA, Pennsylvania, Allegheny County, Boyce Regional Park, 14 July 2003, ex *Tipula* sp., female, C. W. Young.

Previous description: Koenig & Young (2007).

Microdon analis (Macquart, 1842) and
Microdon mutabilis (Linnaeus, 1758)
(Microdontinae, Syrphidae) (Figs 12–14)
Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous (Fig. 12); atrium and pre-oral cavity present, i.e. pseudocephalon extends beyond the mouth, which is between the bases of the mandibles; narrow, almost cyclindrical; each antenna and set of maxillary organs on a shared, cyclindrical projection, and projections approximated across the atrium; antennae and maxillary organs tapered; a fleshy, triangular-shaped lobe, the dorsal lip, present above the mandibles and below, the projections bearing the antennae and maxillary organs with a medial groove; oral ridges and setae absent; not attached to the mandible.

Atrium: present but short, i.e. an enclosed cavity incorporating the posterior rods of the labium laterally, the epipharyngeal plate dorsally, and the connecting membrane.

Position of mouth: between the base of the mandibles, with the apex of the labrum dorsally and the labial plate and sclerites ventrally.

Basal sclerite: with dorsal bridge; not strongly sclerotized; cibarial ridges absent; weakly indicated parastomal bars at the margins of the epipharyngeal plate.

Labrum: translucent, with tapered apex ending between the bases of the mandibles (Figs 12, 14).

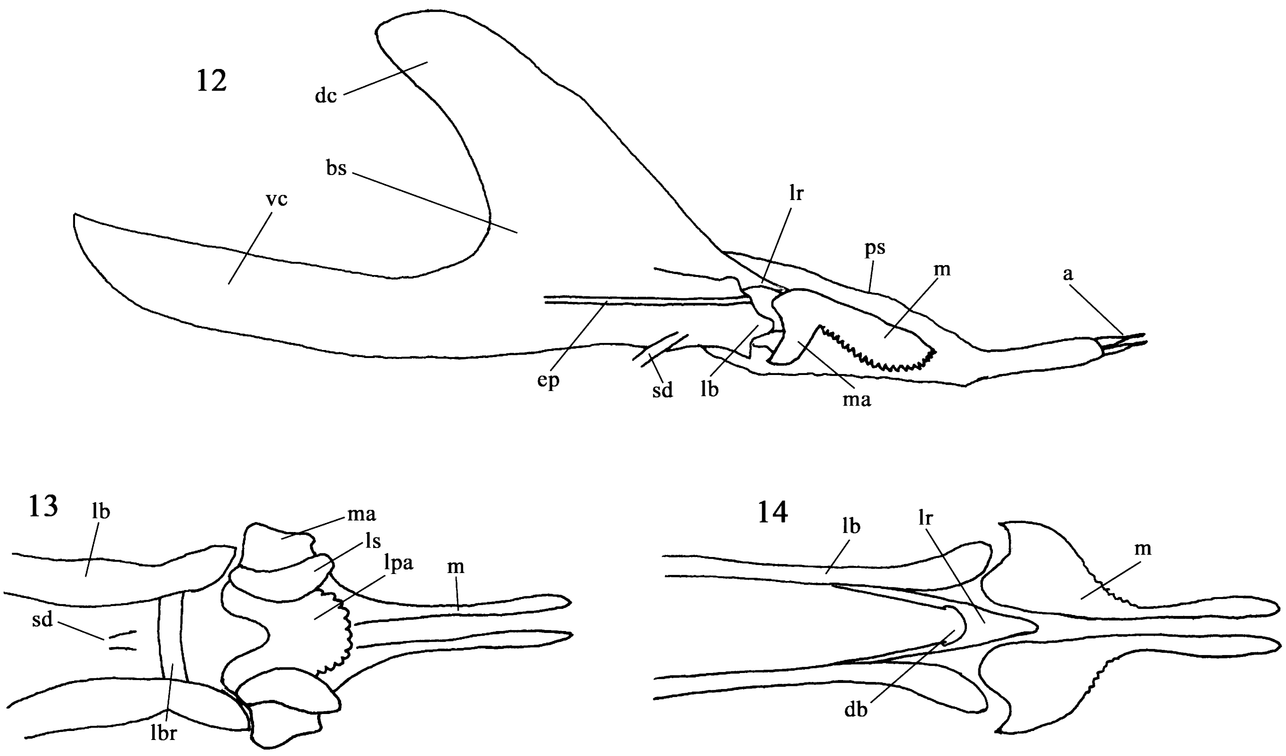
Labium: sclerotized and elongate; posterior rods broad, expanded at apex, and articulating with the mandible, below and slightly behind this apex, the short, broad anterior rods arise from an incompletely sclerotized articulation point; anterior rods articulating with the mandibular apodeme; between the anterior rods is a broad, scoop-shaped sclerite, as long as the anterior rods, the labial sclerite; labial sclerite indented and possibly hinged basally; blunt-toothed at apex, and upper surface with spicules (Fig. 13).

Mandible: one sclerite, which is the most anterior part of the head skeleton and separate from the opposing mandibular sclerite; ventral margin serrated; basal apodeme present.

Maxilla: not distinct.

Material examined: Five+ larvae per species, Scotland, *M. mutabilis*, Isle of Mull, B. Barr, *M. analis*, Sutherland, Glen Shin, G. E. Rotheray.

Previous descriptions: Hartley (1963); Barr (1994); Rotheray & Gilbert (1999).



Figures 12–14. Final-stage larva of *Microdon mutabilis* (Linnaeus, 1758) (Microdontinae, Syrphidae); 12, head skeleton and pseudocephalon, lateral view, anterior end to the right; 13, apex of head skeleton, ventral view, anterior end to the right, 14, apex of head skeleton, dorsal view, anterior end to the right. Abbreviations: a, antennomaxillary process; bs, basal sclerite; db, dorsal bridge; dc, dorsal cornu; ep, epipharyngeal plate; lb, labium; lbr, labial bridge; lpa, labial plate; lr, labrum; ls, labial sclerite (= anterior labial rods); m, mandible; ma, mandibular apodeme; ps, pseudocephalon; sd, salivary duct; vc, ventral cornu.

Pipizella viduata (Linnaeus, 1758) (Pipizini) and Platycheirus scutatus (Meigen, 1822) (Syrphinae) (Syrphidae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous; atrium and pre-oral cavity present, i.e. pseudocephalon extends beyond the mouth, which is between the labrum and labium; narrow but widening basally with each antenna and set of maxillary organs on a shared, cyclindrical projection, and projections approximated across the atrium; antennae and maxillary organs blunt-tipped; a fleshy, triangular-shaped lobe, the dorsal lip, present above the mandibles and below, the projections bearing the antennae and maxillary organs; oral ridges and setae absent; not attached to the mandible.

Basal sclerite: narrow and elongate; dorsal bridge and cibarial ridges absent; parastomal bars short, at the margins of the epipharyngeal plate below the labrum.

Atrium: present but short, i.e. an enclosed cavity incorporating the posterior rods of the labium laterally, the epipharyngeal plate dorsally, and the connecting membrane.

Position of mouth: between the base of the mandibles and the base of the labrum.

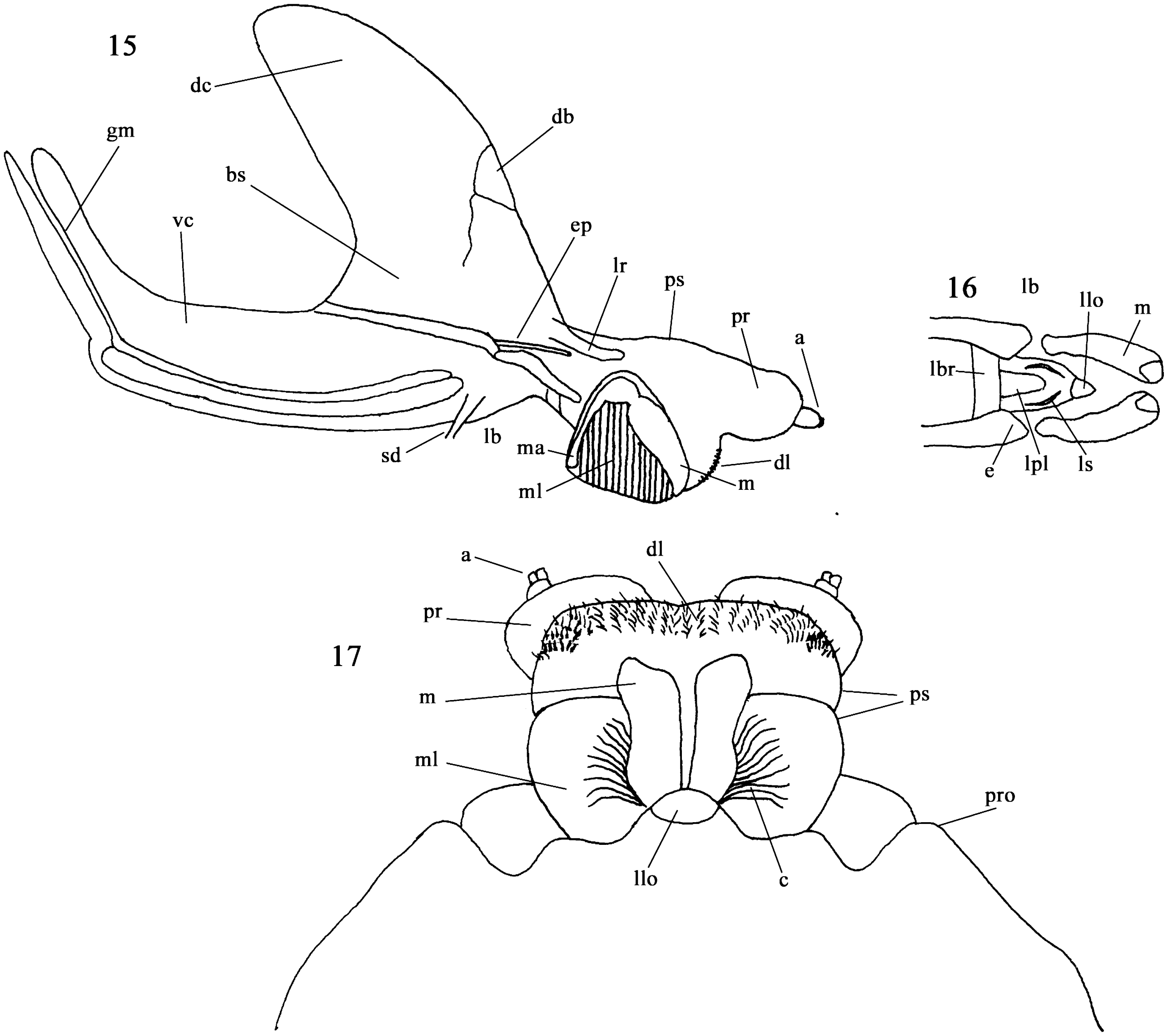
Labrum: heavily sclerotized, and extremely narrow, elongate, and tapered; apex free.

Labium: posterior rods similar in size and shape to those of *Microdon*, and articulating with the mandible (narrower and shorter in *P. scutatus*); below and slightly behind the articulation point the short, broad anterior rods arise; anterior rods elongate, narrow, and tapered, and project forward free under the slightly longer labrum; fused ventrally with the similarly elongate labial plate forming the ventral floor of the labium.

Mandible: one sclerite; narrow and rod-like without an apical hook or apodeme, and separate from the opposing mandible; not strongly sclerotized (longer and more heavily sclerotized in *P. scutatus*); directed forwards and articulating with the posterior rods.

Maxilla: not distinct.

Material examined: P. viduata, ten+ larvae, England, Berkshire, Ascot, ex ant-attended root aphids, T. J. Dixon; *P. scutatus*, two larvae, Scotland, Midlothian,



Figures 15–17. Final-stage larva of *Eumerus funeralis* Meigen, 1822 (Eristalinae, Syrphidae): 15, head skeleton and pseudocephalon, lateral view, anterior end to the right; 16, apex of head skeleton, ventral view, anterior end to the right, 17, apex of head, ventral view. Abbreviations: a, antennomaxillary process; bs, basal sclerite; c, cirri; db, dorsal bridge; dc, dorsal cornu; dl, dorsal lip; e, epicondyle; ep, epipharyngeal plate; gm, grinding mill; lb, labium (= posterior labial rods); lbr, labial bridge; llo, labial lobe; lpl, labial plate; lr, labrum; ls, labial sclerite; m, mouthook; ma, mandibular apodeme; ml, mandibular lobe; pr, projection supporting antennomaxillary organs; pro, prothorax; ps, pseudocephalon; sd, salivary duct; vc, ventral cornu.

Newbattle Abbey, ex aphids on *Heracleum sphondylium* L. (Umbelliferaceae), G. E. Rotheray.

Previous descriptions: P. viduata, Dixon (1960); *P. scutatus*, Bhatia (1939), Dixon (1960).

Alipumilio femoratus Shannon, 1927 and Eumerus funeralis Meigen, 1822 (Eristalinae, Syrphidae) (Figs 15–17)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous (Fig. 15); atrium and pre-oral cavity present, i.e. pseudocephalon extends beyond the mouth, which is between the the bases of the mandibles; broad, with each blunt-tipped antenna and set of maxillary organs on a cyclindrical projection, and with these projections on a dome-shaped projection about as high as basally broad; a fleshy, triangular-shaped lobe, the dorsal lip, present above the mandibles and below, the projections bearing the antennae and maxillary organs, dorsal lip bilobed and coated in rows of cirri; oral ridges present on raised mandibular lobes that are attached to the mandibular apodeme (Fig. 17).

Atrium: present and elongate, i.e. an enclosed cavity present, incorporating the epipharyngeal plate dorsally, the posterior rods, connecting membrane, and epicondyles of the labium laterally, and the labial plate, sclerites and lobe, and connecting membrane ventrally.

Position of mouth: between the base of the mandibles, with the truncate apex of the labrum dorsally and the labial lobe ventrally (Fig. 17).

Basal sclerite: dorsal bridge and cibarial ridges present; parastomal bars not distinct; grinding organ at apex of ventral cornu (Fig. 15).

Labrum: transluscent and apex truncate between bases of mandibles.

Labium: posterior rods elongate and narrow; articulation point lightly sclerotized ventrally and forming a bridge, epicondyles narrow, not developed strongly; labial sclerite forming the ventral floor of the labium beyond the articulation point, lacking spines, and not free; anterior rods forming a narrow pair of sclerites projecting forward beyond the labial sclerite; apex of labium enlarged into a fleshy lobe, which is free at the posterior margin of the mouth (Figs 15, 16).

Mandible: one sclerite, which is the most anterior part of the head skeleton, articulating with apex of posterior rods of the labium; mandible with one main hook, and sometimes with smaller teeth and a basal apodeme (Figs 15–17); both mandibles separate, but attached to each mandibular hook and to each apodeme are the mandibular lobes, which are fleshy, coated in cirri, and attached to the dorsal lip.

Maxilla: not distinct.

Material examined: A. femoratus, 20 larvae, Ecuador, past Puyo, 29 January 1979, ex *Psychotria* sp. sap (Rubiaceae), N. Whitten, Smithsonian Institution (SI); *E. funeralis*, ten+ larvae, imported from Europe into the USA, intercepted at El Paso, Texas, 4 November 1962, ex *Iris* bulbs, SI.

Previous descriptions: A. femoratus: Rotheray *et al*. (2000); *E. funeralis*: Hodgson (1927, 1932), Dixon (1960); Roberts (1970).

Lonchaea fugax Becker, 1895 (Lonchaeidae) (Figs 18–21) and Homalocephala biumbrata (Wahlberg, 1838) (Ulidiidae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous (Fig. 18); elongate atrium present; cephalic lobes and pre-oral cavity present, i.e. pseudocephalon bilobed beyond the mouth at the base of the mandibles (Fig. 21); each lobe with an antenna and maxillary palpus on the dorso-apical surface, and oral ridges on the ventral surface, which radiate from the inner margin of the base of the mandibles; ventrally, the inner margin of each lobe forms a narrow sheath for the mouthhook; dorsal lip absent (Fig. 18).

Atrium: present and elongate, i.e. an enclosed cavity present, incorporating the epipharyngeal plate dorsally, the posterior rods, connecting membrane, and epicondyles of the labium laterally, and the labial plate, sclerites and lobe, and connecting membrane ventrally.

Position of mouth: between the base of the mandibles, with the truncate apex of the labrum dorsally and the labial lobe ventrally.

Basal sclerite: narrow and elongate, i.e. basal sclerite about as high as broad, and shorter than the dorsal cornu, not strongly sclerotized, i.e. pale; dorsal bridge weakly sclerotized; cibarial ridges present; dorsal cornu shorter than ventral cornu, and parallel with each other; parastomal bars elongate, i.e. reaching from vertical plate to the base of mandibles.

Labrum: transluscent with truncate apex between the base of the mandibles (Figs 18, 19).

Labium: H-shaped sclerite present and separated from the mandibles and the vertical plate, comprising tapering posterior rods that articulate with a ventral extension of the vertical plate; bridge weakly indicated, and anterodorsal epicondyles about equally as long as posterior arms, strongly sclerotized, and articulating with the mandibles; labial plate and labial sclerites fused into floor of the labium, which extends to the base of the mandibles and ends in a fleshy brown labial lobe (Figs 18, 20).

Mandible: one sclerite, which is the most anterior part of the head skeleton articulating with the epicondyles of the labium; mandibles approximated, but not fused; base of mandible produced and subrectangular with a separate dental sclerite below.

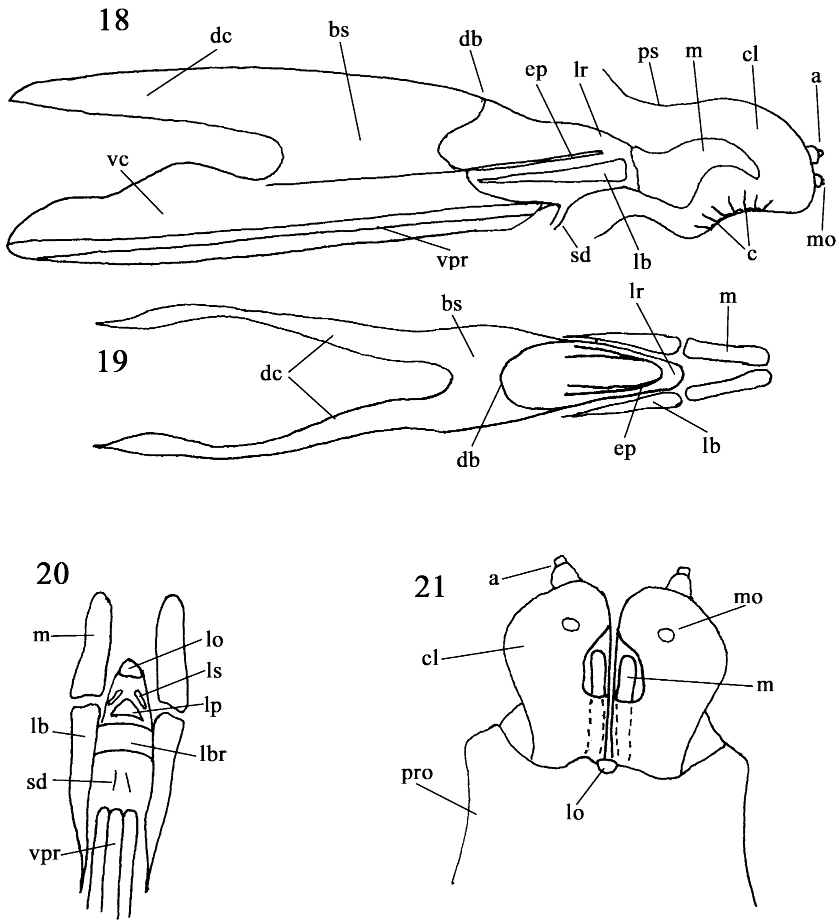
Maxilla: not distinct.

Material examined: L. fugax, ten+ larvae, Scotland, Inverness-shire, Aviemore, Ord Ban, 25 May 1990, under bark of fallen *Populus tremula* Linnaeus (Salicaeae), G. E. Rotheray; *H. biumbrata*, three larvae, Scotland, Inverness-shire, Aviemore, Ord Ban, 25 May 1990, under bark of fallen *P. tremula*, G. E. Rotheray.

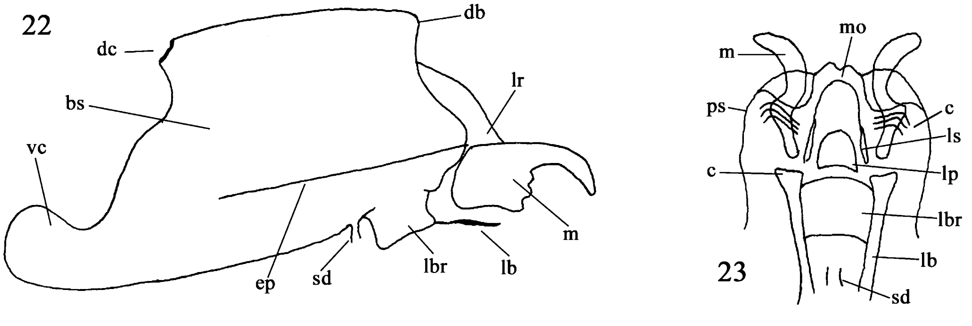
Previous descriptions: L. fugax: Krivosheina (1976); *H. biumbrata*: Rotheray & Robertson (1998).

Physocephala sp. (Conopidae) (Figs 22, 23)

Diagnosis: Pseudocephalon: narrow and cyclindrical; delimited from the thorax by an impressed fold and



Figures 18–21. Final-stage larva of *Lonchaea fugax* Becker, 1895 (Lonchaeidae): 18, head skeleton and pseudocephalon, lateral view, anterior end to the right; 19, head skeleton, dorsal view, anterior end to the right, 20, apex of head skeleton, ventral view; 21, head, ventral view. Abbreviations: a, antenna; bs, basal sclerite; c, cirri; cl, cephalic lobe; db, dorsal bridge; dc, dorsal cornu; ep, epipharyngeal plate; m, mandible; mo, maxillary organs; lb, labium (= posterior labial rods); lbr, labial bridge; lo, labial lobe; lp, labial plate; lr, labrum; ls, labial sclerite (= anterior labial rod); pro, prothorax; ps, pseudocephalon; sd, salivary duct; vc, ventral cornu; vpr, ventral pharyngeal ridges (= cibarial ridges),



Figures 22–23. Final-stage larva of *Physocephala* sp. (Conopidae): 22, head skeleton, lateral view, anterior end to the right; 23, apex of head, ventral view. Abbreviations: bs, basal sclerite; db, dorsal bridge; c, cirri; dc, dorsal cornu; ep, epipharyngeal plate; m, mandible; mo, mouth; lb, labium (= posterior labial rods); lbr, labial bridge; lp, labial plate; lr, labrum; ls, labial sclerite (= anterior labial rod); ps, pseudocephalon; sd, salivary duct; vc, ventral cornu.

membranous; pre-oral cavity not strongly developed; cephalic lobes present.

Basal sclerite: vertical plate transluscent and rectangular shaped (Fig. 22); higher than broad, and dorsal and cornu little developed; dorsal bridge, cibarial ridges, and parastomal bars absent.

Atrium: present, but short, i.e. an enclosed cavity present, incorporating the epipharyngeal plate dorsally, the posterior rods, connecting membrane, and epicondyles of the labium laterally, and the labial plate, sclerites, and connecting membrane ventrally.

Position of mouth: between the base of the mandibles, with the tapered apex of the labrum dorsally and the tapered apex of the labium ventrally (Fig. 23).

Labrum: strongly developed, with free apex reaching to the base of the mandibles.

Labium: H-shaped sclerite not present, but a square-shaped sclerite that has slight epicondyles articulating with the mandibles is present instead (Fig. 22); posteroventrally, this sclerite extends to create an opening for the salivary duct; anteroventrally, the anterior arms of the labium extend forward under the base of the mandibles, and taper apically, reaching forward about as far as the labrum; labial plate and sclerites fused together to form part of the floor of the labium, which lacks a fleshy labial lobe, and has a free apex underlying the labrum.

Mandible: one sclerite, which is the most anterior part of the head skeleton, articulating with the epicondyles of the square-shaped base of the labium; mandibles approximated, but not fused, and mouthhook out-turned; base of mandible subrectangular, without a separate dental sclerite below (Figs 22, 23).

Maxilla: not distinct.

Material examined: Three larvae, Canada, Alberta, Calgary, ex workers of *Bombus* sp. (Hymenoptera, Apidae), T. L. Whidden.

Scatophaga stercoraria (Linnaeus, 1758) (Scatophagidae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold, and membranous; cephalic lobes and pre-oral cavity present; dorsal lip absent.

Atrium: present and elongate, i.e. an enclosed cavity present, incorporating the epipharyngeal plate dorsally, the posterior rods, connecting membrane, and epicondyles of the labium laterally, and the labial plate, sclerites and lobe, and connecting membrane ventrally.

Position of mouth: between the base of the mandibles, with the truncate apex of the labrum dorsally and the labial lobe ventrally.

Basal sclerite: vertical plate higher than broad, and shorter than dorsal cornu, not strongly sclerotized, i.e. red-brown; dorsal bridge and cibarial ridges present; dorsal cornu shorter than ventral cornu and diverging; parastomal bars not indicated.

Labrum: transluscent, with truncate apex between the base of the mandibles.

Labium: H-shaped sclerite present and separated from the mandibles and the vertical plate comprising posterior rods that articulate with a ventral extension of the vertical plate; bridge weakly indicated, and anterodorsal epicondyles about equally as long as posterior arms, strongly sclerotized, and articulating with the mandibles; labial plate and labial sclerites fused into floor of the labium, which extends to the base of the mandibles and ends in a fleshy labial lobe.

Mandible: one sclerite, which is the most anterior part of the head skeleton, articulating with the epicondyles of the labium; mandibles approximated, but not fused; base of mandible produced and subrectangular, with a separate dental sclerite below; oral ridges strongly indicated and attached to the base of the mandibles.

Maxilla: not distinct.

Material examined: Five puparia, Scotland, Highland Region, Coire an t′ Sneachda, 20 June 1987, ex sheep dung, M. Nelson.

Previous descriptions: Cotterell (1920), Sasaki (1980).

Phaonia gobertii (Mik, 1881) (Muscidae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous; cephalic lobes and pre-oral cavity present; dorsal lip absent.

Atrium: present and elongate, i.e. an enclosed cavity present, incorporating the epipharyngeal plate dorsally, the posterior rods, connecting membrane and epicondyles of the labium laterally, and the labial plate, sclerites and lobe, and connecting membrane ventrally.

Position of mouth: between the base of the mandibles, with the truncate apex of the labrum dorsally and the labial lobe ventrally.

Basal sclerite: narrow and elongate, i.e. vertical plate about as high as broad, and about as long as dorsal cornu, not strongly sclerotized, i.e. red-brown; dorsal bridge not sclerotized; cibarial ridges present; dorsal and ventral cornu about equally produced and parallel with each other; parastomal bars apparently absent.

Labrum: transluscent, with truncate apex between the base of the mandibles.

Labium: H-shaped sclerite present and separated from the mandibles and the vertical plate comprising posterior rods that articulate with a ventral extension of the vertical plate; bridge weakly indicated, and anterodorsal epicondyles about equally as long as posterior arms, strongly sclerotized, and articulating with the mandibles; labial plate and labial sclerites fused into floor of the labium, which extends to the base of the mandibles and ends in a fleshy, but reduced, labial lobe.

Mandible: one sclerite, which is the most anterior part of the head skeleton, articulating with the epicondyles of the labium; mandibles approximated but not fused; base of mandible produced and broad, with a large separated dental sclerite, and beneath the mouthhooks, a pair of narrow sclerites, the assessory oral sclerites; mandibles retractile.

Maxilla: not distinct.

Material examined: Two larvae, Scotland, Stirlingshire, Falkirk, Avon Gorge, under bark of fallen *Fraxinus*, 3 September 1995, G. E. Rotheray.

Previous descriptions: Skidmore (1985).

Calliphora vomitoria (Linnaeus, 1758)
(Calliphoridae)

Diagnosis: Pseudocephalon: delimited from the thorax by an impressed fold and membranous; cephalic lobes and pre-oral cavity present; dorsal lip absent; antennae on a short projection, and maxillary organs without a projection, both sets of structures each on a dome-shaped projection, below which is a flat and smooth dorsal lip.

Atrium: present and elongate, i.e. an enclosed cavity present, incorporating the epipharyngeal plate dorsally, the posterior rods, connecting membrane, and epicondyles of the labium laterally, and the labial plate, sclerites and lobe, and connecting membrane ventrally.

Position of mouth: between the base of the mandibles, with the truncate apex of the labrum dorsally and the labial lobe ventrally.

Basal sclerite: vertical plate higher than wide, strongly sclerotized, i.e. black; dorsal bridge and cibarial ridges present; dorsal cornu more elongate than ventral cornu; parastomal bars distinct, but short, not reaching and articulating with the mandibles.

Labrum: transluscent, with truncate apex between the base of the mandibles.

Labium: H-shaped sclerite separated from the mandibles and the vertical plate comprising short and broad, but tapering, posterior rods that articulate with a ventral extension of the vertical plate below the parastomal bars; ventral bridge strongly sclerotized and black; anterodorsal extensions to the bridge inflated apically into epicondyles, which articulate with the mandibles; labial plate narrow and labial sclerites short and broad, both appearing and overlapping just anterior to the bridge, with anterior arms produced further forward than labial plate; a new structure, the V-shaped lignoid arch (Erzinçlioğlu 1984), in front of the anterior arms at the base of the fleshy labial lobe.

Mandible: one sclerite, which is the most anterior part of the head skeleton, articulating with the epicondyles of the labium; mandible subrectangular at base, and both mandibles separate but not independent of each other; dental sclerite below base of mandible; mouthooks outurned and connected by a U-shaped sclerite, the oral sclerite (Erzinçlioğlu 1984), which connects anteriorly via a sclerotized bar to the dorsal lip, and infolds posteriorly into the mouth.

Maxilla: not distinct.

Material examined: Ten+ larvae, Scotland, Fife, St Andrews, ex Bell-Pettigrew Museum, NMS.

Previous descriptions: Erzinçlioğlu (1984).

Cladistic analysis

Based on a set of 86 larval characters (Appendices 1 and 2) the analysis found 36 equally short trees, the strict consensus tree of which is shown in Figure 24. The stability of the characters in the matrix and support for the nodes were revealed by a bootstrap analysis, which obtained group frequencies in 50% and above of 100 replicates and calculated Bremer support values (Fig. 25). The results show that the lower Cyclorrhapha is paraphyletic in relation to the higher Cyclorrhapha, but that the monophyly of the Cyclorrhapha is strongly supported (bootstrap 100%, Bremer support value 9). The lower Cyclorrhapha divides into two clades based on the Lonchopteridae: one fairly well-supported clade includes the Platypezidae + Phoridae (bootstrap 63%, Bremer support value 3), and the other better supported clade is the Eumuscomorpha (Pipunculidae + Syrphidae + higher Cyclorrhapha) (bootstrap 100%, Bremer support value 9). Within the Syrphidae, the traditional three-subfamily system is supported based on the Microdontinae.

DISCUSSION

RELATIONSHIPS WITHIN THE LOWER CYCLORRHAPHA

This analysis of relationships between lower cyclorrhaphan families is based on the morphology of the final stage larva. The analysis was rooted on the Brachyceran families, Rhagionidae and Dolichopodidae. To test the monophyly of the lower Cyclorrhapha, we included representative families of the higher Cyclorrhapha. We also tested the three sub-

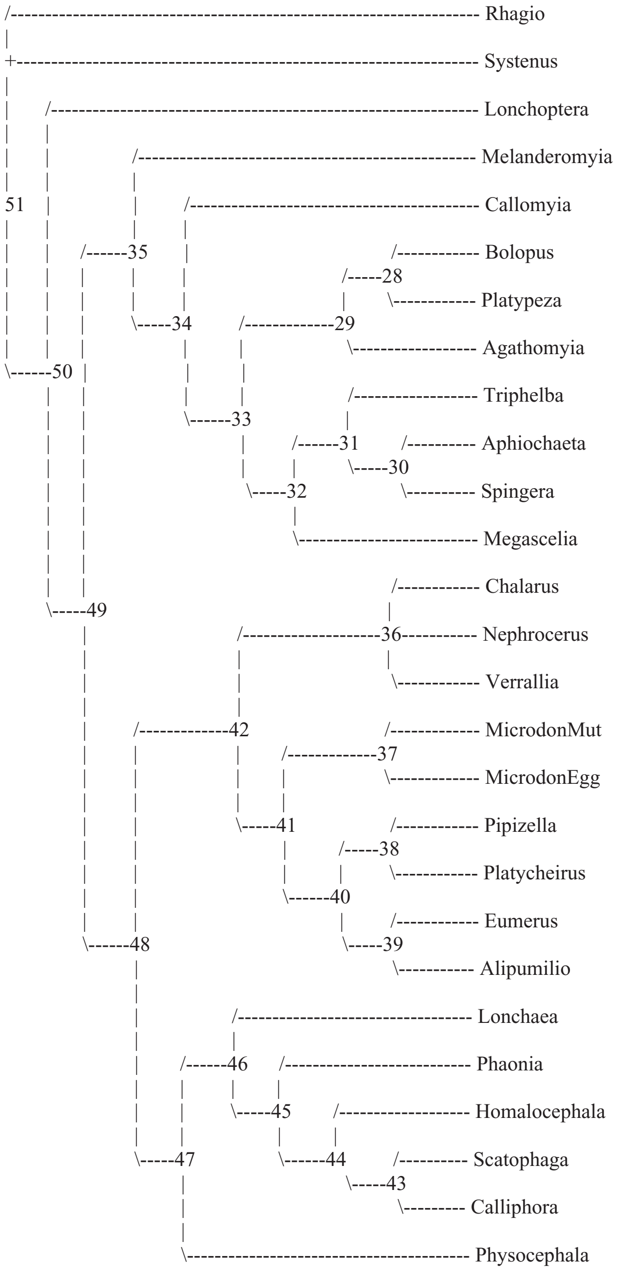


Figure 24. The strict consensus of 36 trees revealed by parsimony analysis using PAUP v4.0 (details in text) of cyclorrhaphan larvae based on a set of 86 characters (Appendix 1) scored on a Brachyceran out-group (Appendix 2) [length = 103, consistency index, (*CI*) = 0.73, retention index (RI) = 0.9]. Apomorphies supporting numbered nodes are listed in Appendix 3.

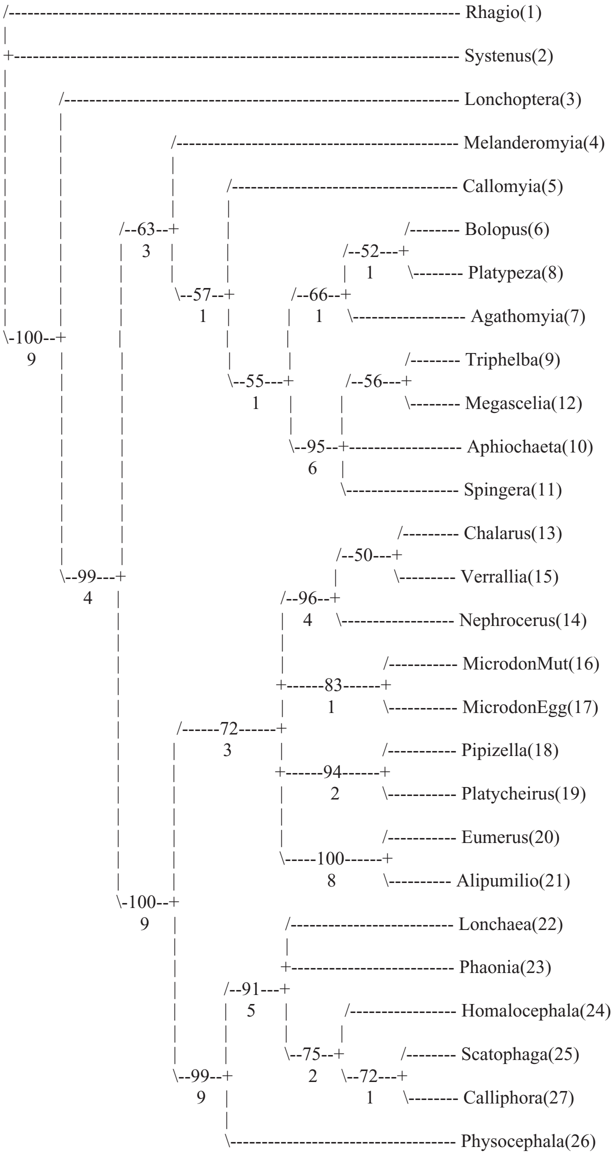


Figure 25. Bootstrap 50% majority-rule consensus tree generated from 100 replicate searches. Upper numbers refer to branches appearing in more than 50% of bootstrap replicates, and numbers below are Bremer support values.

families of the Syrphidae, Eristalinae, Microdontinae, and Syrphinae, and the enigmatic syrphid tribe, the Pipizini (Vockeroth & Thompson, 1987).

The relationships we recovered that were also found previously include: the paraphyly of the lower Cyclorrhapha and the monophyly of the Cyclorrhapha (Wada, 1991; Zatwarnicki, 1996; Collins & Wiegmann, 2002), the monophyly of the Eumuscomorpha (Pipunculidae + Syrphidae + higher Cyclorrhapha) (Wada, 1991; Collins & Wiegmann, 2002) and the Platypezoidea (Platypezidae + Phoridae) (McAlpine, 1989; Collins & Wiegmann, 2002), but our analysis excluded the Lonchopteridae (Fig. 24). The position of the Lonchopteridae has not yet been settled by previous studies, and our results support those of Zatwarnicki (1996) and Collins & Wiegmann (2002) for a basal position within the Cyclorrhapha for this family.

Within the Syrphidae the Pipizini was associated with the Syrphinae, as we have found previously (Rotheray & Gilbert, 1999; Ståhls *et al*., 2003). The Microdontinae were basal with respect to the rest of the Syrphidae. This position was suggested by Skevington & Yeates (2000) and Ståhls *et al*. (2003), but not by our previous study (Rotheray & Gilbert, 1999). In this study, we gained an improved understanding of transluscent and sclerotized components in a much wider range of taxa, and consequently rescored characters of the head. This is the reason why our data now support a basal position of the Microdontinae relative to the rest of the Syrphidae.

A problem limiting our results is taxon sampling. For example, we were unable to include larvae of the Opetiidae, which may be important for resolving the base of the Cyclorrhapha (Yeates & Wiegmann, 1999; Chandler, 2001; Collins & Wiegmann, 2002). Opetid larvae remain unknown. Our attempts to find them in decaying wood, the presumed breeding site (Chandler, 2001; Ståhls & Kahanpää, 2006), were unsuccessful. Few phorid larvae and only one representative of the Melanderomyinae + Microsaniinae were available to us. The latter are important because they are basal within the Platypezidae (Chandler, 2001; Rotheray *et al*., 2004). The apparent paraphyly of the Platypezidae with respect to the Phoridae (Fig. 24) could be resolved by analysing additional basal platypezids, more phorids, and also larvae of the two lower cyclorrhaphan families not studied here, the Ironomyiidae and the Sciadoceridae. The latter two families are related to the Phoridae (Brown, 1992). However, by raising both the Melanderomyinae + Microsaniinae and the Callomyinae to family status, the paraphyly of the Platypezidae with respect to the Phoridae would be resolved, and there exists support for such proposals from adult morphology (P. J. Chandler, pers. comm.).

LARVAL MORPHOLOGY

Changes in the larval head represent a major evolutionary development across the Diptera (Teskey, 1981). But, within the lower Cyclorrhapha, such changes are poorly understood due mainly to lack of study (Courtney *et al*., 2000). One of our aims was to fill this gap in knowledge. We discovered great diversity in the lower cyclorrhaphan larval head, and each taxon in Figure 24 had a distinctive arrangement of structures. On the basis of these structures alone, each taxon can be recognized and identified. All components were modified to some extent, and some such as the maxilla are indistinct, but the greatest changes were to the labium and the pseudocephalon (Table 1). The main features characterizing the major nodes in Figure 24 are summarized below.

Out-groups vs. Cyclorrhapha (node 51)

A major difference between out-groups and the Cyclorrhapha is desclerotization of the cranium, which in out-groups appears as a dorsal, curved sclerite above an articulated tentorial phragma. Furthermore, in out-groups the labrum, labium, and maxillomandibles articulate with the tentorial phragma, and are easily distinguished from it either by groove-like impressions or differences in sclerotization. In Cyclorrhapha, the tentorial phragma, hypopharynx, epipharynx, labrum, maxillary sclerite (= parastomal bars in Cyclorrhapha), and labial rods are fused to varying degrees to form the basal (= pharyngeal) sclerite. The labium is elongate in Cyclorrhapha, relative to out-groups, and the mandibles articulate with it. Finally, in many lower Cyclorrhapha, the hypopharynx bears cibarial ridges. Other proposed synapomorphies supporting the Cyclorrhapha (Table 2) are dealt with below.

Lonchopteridae vs. remaining nodes (node 50)

The main differences between Lonchopteridae and its sister group (the remaining nodes) are that anterior to the mouth in Lonchopteridae there is an open furrow or trough created by the labium (ventral) fused on either side to the divided maxilla. The mandibles are at the back of this trough next to the labrum (Figs 5, 6). They retain the out-group state of more than one sclerite and ensheathment within a fleshy maxilla, but share the cyclorrhaphan synapomorphy of articulating with the labium. Posterodorsally in Lonchopteridae, the fleshy maxilla is fused seamlessly with anterodorsal projections of the pseudocephalon, as indicated by the approximated positions of the antennae and maxillary palpi (Fig. 6). The pseudocephalon is elongate ventrally and laterally and, as indicated by infolds, is attached to the labium and maxilla just behind their apices. Anterolaterally it is developed into autapomorphic triangular lobes (Fig. 6). In the remaining nodes, the mandibles are separate from the maxilla and consist of a single sclerite. The fleshy part of the maxilla is absent, and is incorporated into the pseudocephalon and into the sides of the labium as a translucent membrane. An open trough anterior to the mouth is absent, and varying arrangements of labrum, labium, mandibles, and pseudocephalon surround the mouth. The head and head skeleton are narrowed apically and the antennae are not on separate lobes, but are connected by a dorsal extension of the pseudocephalon.

Platypezoidea vs. Eumuscomorpha (node 49)

The most conspicuous difference between these taxa is the position of the mandibles. In Platypezoidea they appear on either side of the mouth (Fig. 10),

Table 1. Changes in components of the larval head of in-group Cyclorrhaphan taxa and two out-group Brachyceran families (Diptera)

		Cranium	Tentorial phragma	Epipharynx	Hypopharynx	Labrum	Labium	Maxilla	Mandible	Pseudocephalon	Mouth
Outgroup:	Rhagionidae	Present	Present	Aligned anteriorly with the epipharynx, forming roof of the mouth	Without ridges	U-shaped tapered sclerite at apex of mouth attached posteriorly to the tentorial phragma	Fleshy plate	Fleshy and forming a sheath for the mandible	Comprising two sclerites, not anterior to labrum and labium	Not developed	At apex of hypopharynx and epipharynx with labrum overhead, labium underneath, and maxilla-mandibles on either side
	Dolichopodidae	Reduced	Present	Similar	Without ridges	Similar	Fleshy with sclerotized rods	Similar but with internal supporting sclerites	Similar, but four sclerites	Similar	Similar
Ingroup:	Lonchopteridae	Absent	Modified into a basal sclerite	Slightly anterior to the hypopharynx	Ridges present	U-shaped tapered sclerite at apex of mouth fused seamlessly to the basal sclerite	Similar but rods interrupted at articulation point with mandibles; posterior rods fused with basal sclerite; anterior rods parallel and not extended to apex	Divided dorso-ventrally with each half attached to the labium and sclerite fused to the basal sclerite	Similar, but two sclerites	Bilobed antero-dorsally with lateral margins fused seamlessly with maxilla and ventral margin produced anteriorly almost to apex of labium	Similar, but at the back of an open trough or furrow formed by the elongate labium and maxilla
Lower Cyclorrhapha:	Platypezidae	Absent	Similar	Similar	Ridges present	Similar	Similar but anterior rods fused apically into downwardly projecting hooks	Not a distinct structure; sclerite forming parastomal bars supporting the hypopharynx; fleshy part attached to the labium modified as a transluscent membrane	Similar, but one sclerite	Similar but antero-dorsal lobes connected, infolded and attached to the labrum	At apex of hypopharynx and epipharynx with labrum overhead, labium underneath and maxilla-mandibles on either side
	Phoridae	Absent	Similar	Similar	Ridges present	Similar	Similar, but anterior rods fused apically into downwardly projecting hooks	Similar	Similar	Similar	Similar
	Pipunculidae	Absent	Similar	Similar	Without ridges	Similar but transluscent	Reduced to short labial sclerites supporting the medial labial plate	Similar	Similar, but anterior to labrum and labium	Similar, but apical infold produced to form an oral pocket anterior to the mouth with a guiding groove for the mandibles before attachment to the labrum	Similar, but with mandibles in front of the mouth
Syrphidae:	Microdontinae	Absent	Similar	Similar	Without ridges	Similar, but transluscent	Similar	Similar	Similar	Similar	Similar
	Syrphinae	Absent	Similar	Similar	Without ridges	Similar, but sclerotized and elongate	Similar, but fused with the labial plate, elongate and aligned with the similarily elongate and tapered labrum	Similar	Similar, but lateral to labrum and labium	Similar	Similar

Table 1. *Continued*

		Cranium	Tentorial phragma	Epipharynx	Hypopharynx	Labrum	Labium	Maxilla	Mandible	Pseudocephalon	Mouth
	Eristalinae	Absent	Similar	Greatly anterior to the hypopharynx; forming roof of the atrium	Ridges present	Similar, but translucent	Similar, but labial sclerites anterior to the labial plate and connected by transluscent membrane, truncate apically and terminating in a fleshy labial lobe; forming the floor of the atrium; ventrally rods connected by a bridge and posterior bars attached to the basal sclerite and extended beyond bridge to form epicondules supporting the mandibles	Similar	Similar, but anterior to labrum and labium	Similar, but forming a dorsal lip instead of a groove and attached to the mandibles	Similar
Higher Cyclorrhapha:	Conopidae	Absent	Similar	Similar	Ridges present	Similar, but sclerotized	Similar, but without fleshy labial lobe	Similar	Similar	Similar, but infold enveloping and forming a sheath for each mandible	Similar
	Lonchaeidae	Absent	Similar	Similar	Ridges present	Similar, but translucent	Similar, but labial sclerites anterior to the labial plate and connected by transluscent membrane, truncate apically and terminating in a fleshy labial lobe; forming the floor of the atrium; ventrally rods connected by a bridge and posterior bars separated from basal sclerite and extended beyond bridge to form epicondules supporting the mandibles	Similar	Similar	Similar	Similar
	Ulidiidae	Absent	Similar	Similar	Ridges present	Similar, but translucent	Similar	Similar	Similar	Similar	Similar
	Muscidae	Absent	Similar	Similar	Ridges present	Similar, but translucent	Similar	Similar	Similar	Similar	Similar
	Scatophagidae	Absent	Similar	Similar	Ridges present	Similar, but translucent	Similar	Similar	Similar	Similar	Similar
	Calliphoridae	Absent	Similar	Similar	Ridges present	Similar, but translucent	Similar	Similar	Similar	Similar	Similar

Table 2. Proposed larval and puparial synapomorphies supporting the monophyly of the Cyclorrhapha (Diptera)

Proposed synapomorphy	References	Status in this study
Head desclerotized and membanous	Teskey (1981); McAlpine (1989); Courtney *et al*. (2000)	Confirmed
Antennae and maxillary palpi approximated	Teskey (1981); McAlpine (1989)	Confirmed
Presence of an internal head skeleton	Hennig (1973); Teskey (1981); McAlpine (1989); Courtney *et al*. (2000)	Confirmed
Presence of cibarial ridges	Sinclair (1992)	Confirmed
Mandible articulating with the H-shaped sclerite	Krivosheina (1969); McAlpine (1989)	Modified
Anterior spiracles on a stalk	Teskey (1981); McAlpine (1989)	Confirmed
Posterior spiracles with interspiracular setae	Hennig (1973); Teskey (1981); McAlpine (1989)	Confirmed
Pattern of segmental sensilla	Rotheray & Gilbert (1999)	Confirmed
Pupa with pupal spiracles	McAlpine (1989)	Confirmed
Labium attached to basal sclerite	Courtney *et al*. (2000)	Confirmed
3 larval stages instead of 4 or more	Hennig (1973); McAlpine (1989)	Not investigated
Presence of an atrium	Hennig (1973); Teskey (1981); McAlpine (1989); Courtney *et al*. (2000)	Invalid
Labrum absent in final stage larva	Hennig (1973); McAlpine (1989)	Invalid
Single component mandible	Hennig (1973); Teskey (1981); McAlpine (1989); Sinclair (1992); Courtney *et al*. (2000)	Invalid
Presence of an H-shaped intermediate sclerite	Teskey (1981); McAlpine (1989)	Invalid
Presence of cephalic lobes	Teskey (1981); Courtney *et al*. (2000)	Invalid

whereas in Eumuscomorpha the mandibles are at the apex of the head skeleton, directly in front of the mouth (Fig. 12). The Syrphinae of the Eumuscomorpha superficially appear to be an exception, because the mandibles lie on either side of the autapomorphic elongated, and sharply tapered, labrum and labium. However, the mouth in Eumuscomorpha is between the hypopharynx and the base of the mandibles. The mandibles in syrphines are in this same position relative to the hypopharynx, but the mouth is obscured by the elongation of the labrum and labium: when feeding, the mandibles extend to the front of the head skeleton.

The labium in Platypezoidea is tapered apically into one or more hooks, which project beyond the ventral margin of the pseudocephalon (Figs 8, 10). In Eumuscomorpha the apex of the labium takes various forms, but is not fused into apical hooks. A pair of shortened anterior labial rods, the labial sclerites, are usually present, and either between or posterior to them lies a new structure, the labial plate (Fig. 13). Furthermore, in Eumuscomorpha the anterodorsal margin of the pseudocephalon is developed anteriorly over and beyond the mouth, to form the oral pocket. The antennae and maxillary organs are on the outer, dorso-apical margin of the oral pocket, and the inner, infolded margin is greatly developed and supports the mandibles in various ways, and often plays a direct role in food gathering. In Platypezoidea the anterodorsal margin of the pseudocephalon is simply infolded above the labrum. It does not form an oral pocket over the mouth; neither does it support the mandibles nor play a role in food gathering.

Pipunculidae + Syrphidae vs. higher Cyclorrhapha (node 48)

The main difference between these taxa is in the form of the oral pocket. In Pipunculidae + Syrphidae the antennae and maxillary organs are at the apex of a pair of fleshy projections arising from the apico-dorsal margin of the oral pocket (Fig. 12). In higher Cyclorrhapha, each antenna and set of maxillary organs is at the apex of a separate basal projection (Fig. 18). Furthermore, in Pipunculidae + Syrphidae, except Eristalinae, the infolded margin of the oral pocket has a V-shaped groove, which acts as a guide for the retractable mandibles (Rotheray & Gilbert, 1999). In Eristalinae, the mandibular guide is replaced by the autapomorphic dorsal lip (Rotheray & Gilbert, 1999). The dorsal lip is usually coated in cirri or setae. Furthermore, the oral pocket is attached directly to the mandibles in Eristalinae (Roberts, 1970), where it forms a pair of raised lobes bearing cirri that lie on either side of the mouth (Fig. 17): the mandibular lobes of Hartley (1961). In higher Cyclorrhapha, the infolded margin of the oral pocket neither forms a dorsal lip nor is attached to the mandibles. Instead it envelops each mandible to form a supporting sheath, from the apex of which the retractable mouthooks can project (Figs. 21, 23). Radiating from the part of the sheath that envelops the base of the mandibles are systems of food-gathering cirri.

Another conspicuous difference is the atrium. In Eristalinae and higher Cyclorrhapha the epipharynx (and overlying labrum) project much further forward than the hypopharynx. The anterior position of the latter is landmarked by the salivary duct (Roberts, 1969). In Eristalinae and higher Cyclorrhapha, the elongate apical section of the epipharynx is fused with the labium to form a cavity beyond the hypopharynx: the atrium. In Pipunculidae, Microdontinae, and Syrphinae, the epipharynx is about as developed anteriorly as in out-groups, and the labium is barely fused with it so that an atrium is either absent or little developed.

HOMOLOGIES AND SUPPORT FROM EMBRYOLOGY

Historically, interpretation of the cyclorrhaphan larval head has not been easy, leading Teskey (1981) to conclude that its characters cannot be homologized because intermediate character states are unrecognizable. We found little support for this notion. The basal sclerite incorporates elements of the Brachyceran tentorial phragma, as has been revealed by spatial similarity and resemblance, and embryological evidence from *Drosophila* (Drosophilidae) (Jürgens *et al*., 1986; Jürgens & Hartenstein, 1993). It also includes elements of the maxilla, revealed both by embryology (Jürgens *et al*., 1986; Jürgens & Hartenstein, 1993) and morphology via the parastomal bars, which by spatial similarity and resemblance are homologized with the sclerotized element of the maxilla in empidoid out-groups, and which are fused to the basal sclerite in Cyclorrhapha. The fleshy part of the maxilla is incorporated into both the lateral margins of the pseudocephalon and the labium, as the approximated positions of the antennae and maxillary organs indicate in lower Cyclorrhapha, and as revealed by embryological evidence (Jürgens *et al*., 1986; Jürgens & Hartenstein, 1993).

In out-groups, the labrum is attached posteriorly to the tentorial phragma, dorsally to the pseudocephalon, and ventrally to the epipharynx. It has this position and attachments in Cyclorrhapha, but is fused seamlessly with the basal sclerite. In many Eumuscomorpha it is transluscent and inconspicuous. In empidoid out-groups the labium is fleshy with an internal skeleton of a pair of sclerotized rods. It is attached posteriorly to the tentorial phragma and ventrally to the pseudocephalon, and is continuous with the hypopharynx. It has this position and attachments in Cyclorrhapha, but is greatly modified across the lower Cyclorrhapha.

In Lonchopteridae the labium is similarly fleshy with internal labial rods, but they are separated into posterior and anterior sections by the attachment point with the mandibles. The attachment point is strengthened by an incomplete sclerotized strip across the floor of the labium, which is homologized with the ventral bridge in higher Cyclorrhapha. Above the Lonchopteridae and *Melanderomyia* at the base of the Platypezoidea (node 34 of Fig. 24), the posterior labial rods are connected by the ventral bridge, and beyond the bridge, the rods develop epicondyles that articulate with the mandibles. The posterior rods, ventral bridge, and epicondyles are homologized with the H-shaped sclerite of higher Cyclorrhapha. On embryological evidence, the membrane connecting these components contains elements of the maxilla, but this is not obvious from morphology. The anterior rods take various forms. In the Lonchopteridae they are short and parallel and ensheathed within the elongate and fleshy labium. In Platypezoidea they are elongate and fused apically into freely projecting hooks. In Pipunculidae and Microdontinae they are also free, but are short, lack hooks, and support a new structure, the labial plate. In Syrphinae, Eristalinae, and higher Cyclorrhapha the anterior rods and the labial plate are fused into the floor and sides of the labium. By resemblance, the labial sclerites of higher Cyclorrhapha are homologous with the anterior rods. In Eristalinae and higher Cyclorrapha the labium is fused dorsally with the epipharynx to form a cavity in front of the hypopharynx: the atrium.

In out-groups, the mandible consists of more than one sclerite, is ensheathed in the fleshy maxilla, and articulates with the tentorial phragma (Roberts, 1969). In Lonchopteridae the mandible is similar, but articulates with the labium, and in remaining Cyclorrhapha the mandible consists of a single sclerite that is not associated with the maxilla. In Platypezoidea the mandibles lie lateral or just above the apex of the labrum. In Eumuscomorpha, except Syrphinae, the mandibles are at the apex of the head skeleton.

The similarities of the Eristaline and higher Cyclorrhaphan head result, according to Figure 24, from convergence. However, the clade containing the Eristalinae includes the predatory groups Pipunculidae, Microdontinae, and Syrphinae. Larval heads in predatory cyclorrhaphans are often simplified in relation to saprophages (Ferrar, 1987; Courtney *et al*., 2000), implying derived reductions and losses. Hence, the ancestor of these groups probably resembled Eristalinae and higher Cyclorrhapha in larval head structure, and the similarities are homologous.

SYNAPOMORPHIES SUPPORTING THE CYCLORRHAPHA

Sixteen larval synapomorphies supporting the monophyly of the Cyclorrhapha have been proposed by previous authors. Ten were confirmed in this study, one was not investigated, and five were invalid (Table 2). Some of the confirmed synapomorphies are modified in nonbasal cyclorrhaphans. The head skeletons of predatory pipunculid, microdontine, and syrphine larvae, for example, lack cibarial ridges. Platypezidae, higher syrphines (Rotheray & Gilbert, 1989), and many higher Cyclorrhapha lack pupal spiracles. Most higher Cyclorrhapha have inconspicuous sensilla or lack segmental sensilla altogether. Synapomorphies considered invalid in this study are explained below.

Presence of an atrium

In Cyclorrhapha, according to Hennig (1973), invagination of the head creates a new cavity anterior to the cibarium, the atrium or oral pocket that is considered a synapomorphy for the Cyclorrhapha (Table 2). In out-groups, the mouth is at the apex of the cibarium. The cibarium comprises the epipharynx dorsally and the hypopharynx ventrally. Surrounding the mouth are the apex of the labrum dorsally, the apex of the maxillomandibles laterally, and the labium ventrally (Roberts, 1969). The labrum and maxillomandibles articulate with the tentorial phragma and the labium articulates with the hypopharynx, the boundary of which is determined by the entry point of the salivary duct (Roberts, 1969).

The mouth is unaltered in these positions in Lonchopteridae according to landmark and associated features. The difference between Lonchopteridae and out-groups is that the labium and maxilla have elongated anteriorly to form an open trough or furrow in front of the mouth. Hence, in Lonchopteridae, no atrium exists beyond the mouth, which is retained in a plesiomorphic position at the apex of the epipharynx and the hypopharynx (de Meijere, 1900; Brauns, 1954; Hennig, 1976).

In higher Cyclorrhapha, the position of the landmark and associated features of the mouth have altered. The mandibles are now at the front of the head skeleton, and the apices of the labrum and the epipharynx lie between the bases of the mandibles, indicating the position of the mouth. However, the entry point of the salivary duct is posterior to these structures (Figs. 12, 15, 18, 22), and the epipharynx extends proportionately much further forward compared with most of the lower Cyclorrhapha. Ventrally, the section of the cibarium anterior to the salivary duct is the labium, which is fused with the epipharynx to form an atrium. The apex of the labium is a fleshy lobe bearing sensilla, the ventral lip (Fig. 17) (Hartley, 1963), or labial lobe (Fig. 21) (Snodgrass, 1953), which lies just posterior to the base of the mandibles, and is a ventral landmark for the mouth in these taxa. This is the atrium recognized by Hennig (1973) and others. Anterior to the atruim is an oral pocket formed by the infolded pseudocephalon. However, the absence of an atrium in Lonchopteridae, Platypezoidea, Pipunculidae, Microdontinae, and Syrphinae means it is not a valid synapomorphy for the Cyclorrhapha.

Absence of labrum in final-stage larva

In out-groups, the labrum is a heavily sclerotized structure attached posteriorly to the tentorial phragma. Ventrally it is attached to the epipharynx. The apex, however, is free, tapered, and projects over the mouth (Roberts, 1969). In final stage cyclorrhaphan larvae, the absence of a labrum was considered by Hennig (1973) and McAlpine (1989) to be a synapomorphy supporting the monophyly of the Cyclorrhapha. In the platypezid, *M. kahli*, Sinclair (1992) found an exception in that the final-stage larva had a labrum with a tapered apex. A tapered labrum is also known in syrphine larvae (Hartley, 1961; Roberts, 1969). Rotheray *et al*. (2004) found that a tapered labrum was generally characteristic of platypezid larvae. A similar tapered labrum was also found in this study in lonchopterid, microdontine, phorid, pipunculid, and conopid larvae (Figs 6, 12, 22). Posteriorly, it is fused with the vertical plate of the basal sclerite. The vertical plate has its origin in the tentorial phragma and associated structures (Courtney *et al*., 2000). As with out-groups, the labrum projects over the mouth anteriorly, is attached to the pseudocephalon dorsally, and is continuous with the epipharyngeal plate ventrally. In all Eumuscomorpha, except Syrphinae and Conopidae, the labrum is a transluscent membrane, and in Eristalinae and higher Cyclorrhapha, the apex is truncate not tapered. Hence, the absence of the labrum is invalid as a synapomorphy for the Cyclorrhapha.

Single-component mandible

In orthorrhaphous Brachycera the mandible consists of two sclerites (Roberts, 1969). Sinclair (1992) has shown that a four-component mandible is a synapomorphy for the Empidoidea, and proposes, with others (Table 1), that a single-component mandible is a synapomorphy for the Cyclorrhapha. However, the gross morphology of the mandible of Lonchopteridae suggests two or more sclerites are present. The basal one is attached to the labium. At the distal end is a hook-shaped sclerite that is directed anterolaterally in relation to the longitudinal axis of the head (Fig. 6). All other cyclorrhaphan larvae examined in this study had a single-component mandible, based on the position of landmark sensilla and attachment points of muscles (Sinclair, 1992). The lonchopterid mandible makes a single-component structure invalid as a synapomorphy for the Cyclorrhapha according to Figure 24.

Presence of an H-shaped intermediate sclerite

The intermediate sclerite in higher Cyclorrhapha lies between the basal and the mandibular sclerites of the head skeleton and, in many taxa, is separated from them by narrow gaps. The two halves of the intermediate sclerite are connected by a sclerotized strip, the ventral bridge behind the point where the mandibles articulate, and in front of where the salivary duct enters the cibarium. In dorsal and ventral view, the gaps and the bridge give the intermediate sclerite its characteristic 'H' shape. In out-groups and lower Diptera, the salivary duct enters the cibarium between the hypopharynx and the labium, and because of this the bridge is assumed to be primarily of labial origin (Hartley, 1963; Courtney *et al*., 2000).

The labium is the most altered component of the cyclorrhaphan larval head. In Rhagionidae the labium is a simple, undifferentiated, square-shaped, fleshy lobe that articulates with the hypopharynx and has a pair of papillae with sensilla at its apex (Fig. 3) (Roberts, 1969). In Dolichopodidae and other empidoids a similar lobe is present, but it has the internal support of a pair of curved, sclerotized bars: the labial rods or V-shaped sclerite (Vaillant, 1952; Sinclair, 1992). These rods arise from the base of the labium at the junction with the hypopharynx, and they taper and project from its distal margin, with the labial sensilla just below on the fleshy part of this margin.

In Lonchopteridae the labium is similar to the Dolichopodidae, and does not form an H-shaped sclerite intermediate between the mandibles and basal sclerite. In all taxa above Lonchopteridae in Figure 24, the labium is not fleshy and consists of sclerotized components and a connecting membrane. In Platypezoidea, Pipunculidae, and Syrphidae a ventral bridge is often present, but the posterior labial rods are attached to the basal sclerite, and a separated H-shaped sclerite is not present. Only in higher Cyclorrhapha are the posterior labial rods sometimes separated to form this sclerite. However, in many higher Cyclorrhapha, e.g. *Stegana* (Drosophilidae) (Rotheray & Robertson, 1998), *Loxocera* (Psilidae) (Bland & Rotheray, 2002), and *Platyparea* (Tephritidae) (Rotheray & Bland, 2003), the posterior rods are attached to the basal sclerite.

Another exception is Conopidae. The posterior rods of the labium are short and not separated from the basal sclerite. The bridge is exceptionally wide, with small epicondyles on the dorsoventral margins that articulate with the labium (Figs. 22, 23). The labial sclerites extend forward, taper, and are free between the bases of the mandibles. The labial plate is fused into the floor of the labium between the bases of the anterior rods, but a fleshy labial lobe is absent. The head skeleton is also unusual in that the basal sclerite is subrectangular in profile, the mandibles are out-turned apically, and a prominent, tapered projecting labrum is present (Fig. 23).

In summary, an H-shaped, intermediate sclerite is a feature of certain higher, not lower, Cyclorrhapha, and it is therefore not a synapomorphy supporting the monophyly of the Cyclorrhapha. However, the attachment of the mandibles to the labium (Table 2) is a valid synapomorphy for the Cyclorrhapha.

Presence of cephalic lobes

In both out-groups and in-groups studied here, the membranous head (= pseudocephalon; Courtney *et al*. (2000) is invaginated apically, and attached to the labrum dorsally and to the labium ventrally. According to Teskey (1981) and Courtney *et al*. (2000), the pseudocephalon of the cyclorrhaphan head is bilobed apically, forming a pair of cephalic lobes that have an antenna and maxillary palpus on the dorsal surface and, in saprophagous larvae but simplified in parasitic and predatory larvae, have particle-gathering organs such as oral ridges, cirri, or facial combs (crenulated ridges) and sensilla on the ventral surface. As pointed out by Rotheray *et al*. (2004), a bilobed head is, however, absent in Platypezidae, and it is also absent in other lower Cyclorrhapha.

In Lonchopteridae the apex of the head is bilobed dorsally but is attached to the maxilla that, together with the fleshy labium, forms an open furrow anterior to the mouth, and not a pair of cephalic lobes. In Platypezoidea the lobes bearing the antennae are connected dorsally by an extension of the pseudocephalon, but the apex does not overlie the mouth and is truncate, not bilobed (Fig. 10). In Pipunculidae and Syrphidae the pseudocephalon overlies the mouth, but in these taxa, it is also truncate apically.

Only in higher Cyclorrhapha is the pseudocephalon in the form of lobes as described by Teskey (1981) and Courtney *et al*. (2000) (Fig. 21). Ventrally, the cephalic lobes diverge from the base of the mandibles, except in *C. vomitoria* (Calliphoridae), where the lobes diverge from the apex of the mandibles. The pseudocephalon has a different relationship with the head skeleton than in the otherwise similar Eristalinae. The dorsal lip that is characteristic of Eristalinae, is absent in higher Cyclorrhapha. Also, the pseudocephalon envelops the mandibular hooks and forms a narrow sheath from which they can project. Unlike Eristalinae, the pseudocephalon is not attached directly to the mandibles, but instead curves round their bases, which in many higher Cyclorrhapha are enlarged, subrectangular, and sometimes have a separate sclerite below them, the dental sclerite, to which muscles are attached (Teskey, 1981). The presence of cephalic lobes is thus a feature of higher not lower Cyclorrhapha, and is invalid as a synapomorphy for the Cyclorrhapha.

FUNCTIONAL MORPHOLOGY

Lonchopterid larvae are detritivores feeding on algal and fungal mats in moist-to-watery films coating the surfaces of fallen leaves, stones, etc. (Ferrar, 1987; M. Drake, pers. comm.). The morphology of the head is explicable in terms of this feeding mode. The head, prothorax, and mesothorax are retractile, and can be directed downwards at angles to the longitudinal axis of the body. Such flexibility facilitates scooping food, and the sclerotized dorsal plate comprising the fused dorsum of the metathorax and first abdominal segment provides rigid support for the musculature. The ventro-apical margin of the head, with its autapomorphic triangular lobes and coating of stout setae, probably loosen and gather food into the fleshy furrow formed by the elongate labium and maxilla. The tapered end of the labrum, which projects at the back of the furrow, and the hook-like apical mandibular sclerites, which are sited just anterior to it, may also help loosen and guide food into the mouth. The mouth is wide, as revealed by the extent to which the labrum is separated from the labium dorsoventrally, and this optimizes the amount of food that can be processed. Food is strained and concentrated by the cibarial pump and ridges in the basal sclerite in the manner described for other cyclorrhaphan larvae (Hartley, 1963; Dowding, 1967; Roberts, 1970).

This type of feeding and pumping action almost certainly imposes mechanical strains on the head skeleton, and the formation of the basal sclerite, in which the various parts are fused, adds strength and stability. The fleshy maxillomandibles and labium have internal sclerotized rods that are fused to the vertical plate of the basal sclerite, and the mandibles are attached to the labium adding strength and stability to the entire trophic apparatus.

Platypezid larvae are mycophagous on fungal fruiting bodies (Chandler, 2001). From observations of *Polyporivora* larvae feeding on *Trametes* fungus, the mechanism for gathering food is rasping and tearing using the hooked labium. The mandibles and labrum play relatively minor roles, mainly guiding loosened fragments into the mouth. Within the Platypezidae, modifications exist related to the type of fungal tissue used as food. One group of genera is specialized for feeding on firm, fungal tissues such as polypore fungi, whereas another is specialized for feeding on softer, gill fungi (Rotheray *et al*., 2004).

The larva of *Callomyia* (Platypezidae) shares many head skeleton features with the former group, but it surface-feeds on firm fungi encrusting decaying wood (Chandler, 2001). Larvae of this genus are dorsoventrally flattened and have a fringe of marginal projections. These features probably enhance crypsis. As with lonchopterid larvae, those of *Callomyia* also have a flexible thorax supported by a dorsal plate comprising a fused and sclerotized dorsum of the metathorax and first abdominal segment, and it probably functions in the same way, i.e. the head can be bent sharply and thereby purchase can be gained on the food. According to Figure 23, these similarities are convergent. Except for the larva of *Melanderomyia*, all platypezid larvae studied share an interrupted labium at a point just posterior to the apical hooks. This break probably enhances the range of movement of the labial hooks and the efficiency with which fungi are fragmented.

Phorid head skeletons are poorly known, but the species studied here and those described elsewhere (Ferrar, 1987; Brown, 1993; Robinson & Brown, 1993; Brown & Buck, 1998) have an arrangement of components similar to the Platypezidae. Oral ridges were absent in the species examined, and the mandibles are usually sclerotized, and not translucent, as in platypezids (except *Callomyia*). The mandibles are also diverse in size, shape, and number of teeth, and they play presumably a greater role in food gathering in the Phoridae. Also, the apex of the labium bears one hook rather than three or more as is usual in platypezids, and breaks in the labium may also be present but are closer to the base of the posterior rods. In feeding modes and breeding sites, phorid larvae are more diverse than platypezids (Disney, 1994). Correlations between head skeleton structure, feeding mode, and liquidity of food probably exist in Phoridae, but have yet to be demonstrated.

In the Eumuscomorpha the mandibles are at the front of the head skeleton and replace the labium as the main food-gathering structures. The labium has two roles: it supports the mandibles and it helps guide food into the mouth. In Pipunculidae and Microdontinae, the labium is sclerotized, and the labial plate has spines on the dorsal surface and may aid in holding prey or extracted tissues while the mandibles break them up. In the Syrphinae the narrow, elongate, and highly sclerotized labrum and labium meet at the margin of the mouth and are organs for piercing prey. The mandibles are chisel-like for cutting up prey tissues (Hartley, 1963). In Eristalinae and higher Cyclorrhapha the labium consists of labial sclerites, plate, lobe, and connecting membrane. It is fused to the epipharynx to form the atrium: a tube-like cavity behind the mandibles.

In the Eumuscomorpha the pseudocephalon is attached to or closely ensheathes an enlarged mandibular base, and at this point, it is usually coated in food-gathering ridges and cirri. Functionally, this combined set of structures, the pre-oral cavity or oral pocket (Courtney *et al*., 2000), forms a highly flexible means of gathering particulate or fluid-suspended food. The hooked apices of the mandibles can be extended from their sheaths to tear, rasp, and fragment food. With the mandibles retracted, the surrounding mandibular or oral lobes scoop and gather fragmented or fluid-suspended food into the mouth. The angled, labial lobe at the apex of the labium, which lies between the bases of the mandibles, helps guide food into the mouth. In addition, manoeuvrability of the head and thorax is enhanced in Eumuscomorpha in relation to other Cyclorrhapha. They are retractile to a greater degree and can be directed in multiple directions: up, down, or sideways. Such freedom of movement is enhanced by breaks in the labium, which reach their most derived state in higher Cyclorrhapha where two breaks are frequent: posterior and anterior to the labial bridge, forming the separated H-shaped sclerite.

In Eristalinae, food gathering is supported by other modifications to the head and prothorax (Rotheray & Gilbert, 1999). The dorso-apical margin of the prothorax is curved down towards the head, the anterior fold (Rotheray & Gilbert, 1999), and is coated in setae or sclerotized spicules. The latero-apical margins of the prothorax are formed into a pair of opposing lobes lying on either side of the mouth: the lateral lobes (Hartley, 1963; Rotheray & Gilbert, 1999). They are usually coated in short, broad setae at the base and tufts of long, fine setae apically. The anterior fold and the lateral lips begin the process of straining the food. Between the projections bearing the antennae and maxillary organs and the mandibles is another pair of lobes coated in cirri or setae, the dorsal lip, which along with the mandibular/oral lobes help to guide loosened food into the mouth.

In higher Cyclorrhapha few of these structures are present, or if they are present they play roles other than feeding. For example, the anterior fold is often present and coated in setae or ridges, but they appear to be more involved in preventing wear and tear than in feeding. The lateral lobes and the dorsal lip are replaced by cephalic lobes, which scoop and guide loosened food into the cibarium.

Within the Eristalinae there is a wide array of changes in relation to feeding mode and particular breeding sites (Rotheray & Gilbert, 1999). In phytophagous taxa the mandibular lobes are sometimes sclerotized, which adds strength and size to the mandible in species that feed on firm plant tissues, e.g. the stem- and root-tunnelling larva of *Cheilosia grossa* (Fallén, 1817) (Rotheray, 1988). In saprophagous eristalines the mandible is not a protruding hook for fragmenting food, but forms a support bar for enlarged mandibular lobes that filter food in oily liquids such as decaying tree sap or watery fluids in freshwater bodies (Hartley, 1963; Rotheray & Gilbert, 1999). Within the Xylotini, many of which are saproxylic, the thorax is armoured with genus- and sometimes species-specific arrangements of sclerotized hooks and spicules that help larvae move through and fragment decaying wood to locate new sources of food (Rotheray & Gilbert, 1999).

An even more diverse set of changes occurs in the higher Cyclorrhapha. Ferrar (1987) discusses correlations between feeding mode and morphology, such as the absence of cibarial ridges in predatory larvae. Rotheray & Robertson (1998) found a correlation between large, fused mandibles and small, inconspicuous, separated mandibles, and feeding on relatively firm versus semiliquid materials, respectively. Furthermore, in species feeding on firm material, not only are the mandibles large and sometimes fused, but the H-shaped sclerite is enlarged to the extent that it is often smoothly continuous and attached without a break to the basal sclerite, e.g. *Stegana* (Drosophilidae) (Rotheray & Robertson, 1998), *Loxocera* (Psilidae) (Bland & Rotheray, 2002), and *Platyparea* (Tephritidae) (Rotheray & Bland, 2003).

A relationship between head skeleton morphology and liquidity of food is thus apparent in the Cyclorrhapha, where large, sclerotized head skeletons with fused components are correlated with solid food, and where small, lightly sclerotized head skeletons are associated with either soft or liquid food. However, as the examples in platypezids, eristalines, and higher cyclorrhaphans show, gross similarities in head skeletons in response to the liquidity of the food exist across these groups, but when studied component by component, diverse morphological solutions are revealed. Hence, cyclorrhaphan larval heads encompass numerous independent changes within shared trophic environments. Such diversity is invaluable because of its potential to distinguish lineages and resolve their phylogenetic relationships. To dismiss these similarities as simply functional (Ferrar, 1987) is to seriously underestimate a major evolutionary development. As emphasized by Courtney *et al*. (2000), larval stages in Cyclorrhapha are superficially understood. We hope that the details presented here have demonstrated their value and have indicated their potential in studies of cyclorrhaphan evolution.

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APPENDIX 1

Characters used for scoring and phylogenetic analysis. Numbers in parentheses after character states show polarity based on out-group comparison, (0) = primitive, (1) (2) (3) = derived, 9 = unscorable.

Pseudocephalon

1. *Cranium* present (0); absent (1).
2. *Apex of pseudocephalon* symmetrical, dorsal and ventral margins equally produced (0); ventral margin more produced (1); dorsal margin more produced (2).
3. *Rear section of pseudocephalon* longer behind than in front of antennae (0); about as long as in front of antennae (1); shorter behind than in front of antennae (2).
4. *Connection between lateral margins* conection absent (0); connection present and delimited by longitudinal impressed lines (1); connection present without impressed lines (2).
5. *Antennae and maxillary organs* not on the same basal projection (0); sharing the same basal projection (1).
6. *Basal projection of antennae and maxillary organs* short, not as long as broad (0); longer than broad (1).
7. *Approximation of antennae and maxillary organs* separated by more than width of antennae (0);

approximated, closer together than width of antennae (1).

8. *Distance between both antennae and both maxillary organs across the pseudocephalon* same distance apart (0); maxillary organs closer then antennae (1).
9. *Position of antennae and maxillary organs on the pseudocephalon* on the dorso-lateral margins (0); at the apex (1).
10. *Basal projection of maxillary organs* on basal projection (0); without a projection (1).
11. *Presence of oral ridges* absent (0); present (1).
12. *Size of oral ridges* uniform size (0); varying size (1).
13. *Oral papillae (fleshy projections) at sides of pseudocephalon* absent (0); present (1).
14. *Pseudocephalon relationship to mandibular sclerite* no connection (0); connected (1); ensheathed (2).
15. *Presence of dorsal lip* absent (0); present (1).
16. *Lobes of dorsal lip* single lobe (0); two lobes (1).
17. *Sculpture of dorsal lip* absent, smooth (0); ridges (1).
18. *Cephalic lobes (bifurcated apex of pseudocephalon)* absent (0); present (1).

Head skeleton

19. *Basal sclerite (= pharyngeal sclerite)* absent (0); present (1).
20. *Length of head skeleton in relation to length of prothorax* not longer (0); longer (1).

Basal Sclerite

21. *Parastomal bars* absent (0); present (1).
22. *Cibarial ridges (= ventral pharyngeal ridges)* present (0); absent (1).
23. *Dorsal bridge (area of sclerotization connecting the two halves of the basal sclerite at the apex* present (0); absent (1).
24. *Ventral cornu of basal sclerite* dorsal apodeme absent (0); present (1).
25. *Shape of basal sclerite* basal sclerite U-shaped (0); basal sclerite narrow with the dorsal and ventral cornua approximated (1); ventral and dorsal cornua diverging (2).
26. *Length of basal sclerite* truncate, as long as tall (0); longer than tall (1).
27. *Relative width of dorsal and ventral cornua* dorsal cornua as wide as ventral cornua (0); narrower (1); wider (2).
28. *Relative length of dorsal and ventral cornua* dorsal cornua as long as ventral cornua (0); dorsal cornua shorter (1); dorsal cornua longer (2).

Labrum

29. *Apical margin of labrum* rounded (0); tapered (1).
30. *Length of labrum* reaching into oral cavity (0); apex free at front of mouth (1); apex not free, fused with cibarium (2).
31. *Sclerotization of apex* light pale brown sclerotization (0); transluscent (1); heavily sclerotised, dark brown or black (2).

Labium

32. *Sclerotization* fleshy (0); fleshy with internal sclerotization (1); with complete sclerotization (2); fleshy at apex only (3).
33. *Position relative to the mouth* at front of mouth (0); anterior to mouth (1); posterior to mouth (2).
34. *Articulation with mandibles* articulation absent (0); articulation present (1).
35. *Sclerotization at mandibular articulation point* sclerotisation absent (0); lightly sclerotised bridge (1); heavily sclerotised bridge (2).
36. *Epicondules at mandibular articulation point* absent (0); present (1).
37. *Posterior rods in relation to basal sclerite* attached (0); separated (1).
38. *Anterior rods in relation to mandibular articulation point* attached (0); separated (1).
39. *Approximation of anterior rods* tapered (0); fused (1); parallel (2).
40. *Apex of anterior bars* without hooks (0); one hook (1); > one hook (2).
41. *Labial plate* absent (0); present (1).
42. *Labial plate in relation to anterior rods* between anterior rods (0); anterior to rods (1).
43. *Teeth on labial plate* absent (0); present (1).
44. *Lobe at apex of labium* absent (0); present (1).
45. *Labial lobe* spherical (0); flattened (1).
46. *Atrium* absent (0); present (1).
47. *Length of atrium* short (0); long (1).

Mandibular sclerite

48. *Maxillary sheath for mandible* present (0); absent (1).
49. *Position of mandibles in relation to the mouth* in the same plane as the mouth (0); posterior to mouth (1); directly anterior to mouth (2).
50. *Retractability of mandible* partial (0); complete (1).
51. *Sclerites of mandible* two sclerites (0); > two sclerite (1); one sclerite (2).
52. *Mandible with secondary sclerites* absent (0); present (1).
53. *Sclerotisation of apex of mandibles* sclerotised (0); not sclerotised (1).
54. *Apex of mandibular sclerite* hooked (0); toothed (1); chiselled (2).
55. *Base of mandible enlarged* absent (0); present (1).

56. *Separation of enlarged base* attached (0); separated (1).
57. *Size of mandibular base in relation to mouthook* shorter than width of mouthook (0); as long as width of mouthook (1); wider (2).

Prothorax

58. *Infold of prothorax at junction with mesothorax* absent (0); present (1).
59. *Lateral lobes (= lateral lips, Hartley (1963)) on antero-lateral margins of prothorax* absent (0); present (1).
60. *Shape of lateral lips* tapered (0); spherical (1).
61. *Longitudinal grooves on dorsum of prothorax* absent (0); present (1).
62. *Number of sensilla on dorsum of prothorax* none (0); < 2 pairs (1); > 2 pairs (2).
63. *Size and shape of prothorax in relation to mesothorax* same (0); shorter and not tapered (1); shorter and tapered (2)
64. *Anterior fold at apex of prothorax* little developed (0); well developed (1).
65. Surface vestiture of anterior fold setae present (0); smooth (1); spicules present (2).
66. *Number of openings of the anterior spiracles* 1–2 (0); 3–4 (1); > 4 (2); spiracles absent (3).

Abdominal segments 1–7

67. *Sensilla on abdominal segments* absent (0); present (1).
68. *Projection bearing dorsal abdominal sensilla* present (0); absent (1).
69. *Size and density of vestiture coating the dorsum of the abdomen* absent (0); equal size and density (1); varying size and density (2).
70. *Spicules on locomotory organs* absent (0); present (1).
71. Shape of abdomen in cross-section as broad as high (0); broader than high (1); dorso-ventrally flattened (2).
72. *Position of locomotory organs* on anterior margin (0); medial position (1); posterior margin (2).
73. *Impressed lines on integument of the abdomen* absent (0); few (1); many (2).
74. *Intrasegmental folds on the dorsum* absent (0); 2 folds (1); 3 folds (2).
75. *Borders of abdominal segments* not interrupted (0); interrupted (1).

Anal segment

76. *Grasping bar at apex of anal segment* absent (0); present on ventral surface only (1); encompassing entire apex (2).
77. *Lappets (fleshy projections) on anal segment* up to 2 pairs (0); 3–4 pairs (1); absent (2).
78. *Length of lappets* as long as vestiture (0); longer (1).
79. *Posterior breathing tubes* separate (0); approximated (1); fused at base (2).
80. *Posterior breathing tubes in relation to surface of anal segment* within depression (0); mounted on projection (1); flush (2).
81. *Number of spiracular openings of each posterior breathing tube* more than 5 (0); 3–5 (1); 3 (2).
82. *Interspiracular setae* absent (0); 3 pairs (1); 4 pairs (2).
83. *Base of posterior breathing tubes* absent, flush with integument of anal segment (0); on fleshy projection (1); on sclerotised projection (2); with sclerotised base plate (3)
84. *Position of anus* separate from anterior margin (0); at anterior margin (1).
85. *Sensilla on ventral surface of anal segment beyond anus* absent (0); present (1).
86. *Pupal spiracles* absent (0); present (1).

APPENDIX 2

Character states of Cyclorrhaphan in-group taxa and Brachyceran out-group.

	Outgrp		Lon	Platypezidae					Phoridae				Pipunc			Microdo		Syrphinae		Eristal		Schizo					
Character number	Rhagio	Systenus	Lonchoptera	Melanderomyia	Callomyia	Bolopus	Agathomyia	Platypeza	Triphelba	Aphiochaeta	Spingera	Megascelia	Chalarus	Nephrocerus	Verrallia	Microdon mut	Microdon egg	Pipizella	Platycheirus	Eumerus	Alipumilio	Lonchaea	Phaonia	Homalocephala	Scatophaga	Physocephala	Calliphora
1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	0	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
3	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	0	0	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
5	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1
6	9	9	9	9	9	9	9	9	9	9	9	9	1	0	1	1	1	1	1	1	1	9	9	9	9	9	0
7	1	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
8	9	9	9	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	9	9	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
10	0	0	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
11	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
12	9	9	9	9	9	1	9	1	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2
15	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1
16	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	1	1	9	9	9	9	9	0
17	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	1	1	9	9	9	9	9	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
19	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	9	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1
21	9	9	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1
22	9	9	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1
23	9	9	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1
24	9	9	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1
25	9	9	0	0	0	1	1	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	1	1	1	0	1

APPENDIX 2 *Continued*

	Outgrp		Lon	Platypezidae					Phoridae				Pipunc			Microdo		Syrphinae		Eristal		Schizo					
Character number	Rhagio	Systenus	Lonchoptera	Melanderomyia	Callomyia	Bolopus	Agathomyia	Platypeza	Triphelba	Aphiochaeta	Spingera	Megascelia	Chalarus	Nephrocerus	Verrallia	Microdon mut	Microdon egg	Pipizella	Platycheirus	Eumerus	Alipumilio	Lonchaea	Phaonia	Homalocephala	Scatophaga	Physocephala	Calliphora
26	9	9	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
27	9	9	0	1	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	1	1	0	1
28	9	9	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
29	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	9	9	9	9	9	1	9
30	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	2	2	2	2	2	2	0	2
31	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	2	2	9	9	9	9	9	9	0	9
32	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	2	3
33	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
34	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
35	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	2	2	2	2	1	2
36	9	9	9	9	0	9	9	9	0	0	0	0	9	9	9	9	9	9	9	0	0	1	1	1	1	1	1
37	9	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1
38	9	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
39	9	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	1	1	2	2	2	2	2	2	2	2
40	9	0	0	1	2	2	2	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
42	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
43	9	9	9	9	9	9	9	9	9	9	9	9	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
45	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	1	0
46	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
47	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1
48	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
49	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
50	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

51	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
53	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	1	1	2	2	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1
56	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	0	9	9	0	0	1	1	1	1	0	1
57	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	0	9	9	0	1	2	2	2	2	2	2
58	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
60	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	0	1	1	9	9	9	9	9	9
61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
62	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	0	0	0	0	0	0
63	0	0	1	1	1	1	1	1	2	2	2	2	0	0	0	2	2	2	2	1	2	2	2	2	2	2	2
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
65	0	0	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	0	0	1	1	1	0
66	0	0	0	2	2	2	2	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	2	3	2
67	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
68	9	9	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	9	9	9	9	9	9
69	0	0	0	1	1	1	1	2	1	1	1	1	0	1	0	2	2	2	2	2	2	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1
71	0	0	1	0	2	1	1	2	0	0	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0
72	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	9	2
73	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	2	2	2	2	2	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0
77	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	2	1
78	9	9	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	1	1	9	9	9	1	9	1
79	0	0	0	0	0	0	0	0	1	0	2	1	1	0	1	2	2	2	2	2	2	1	1	0	1	1	1
80	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	0
81	0	2	2	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2
82	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2	2	2
83	0	0	1	1	2	2	2	2	2	2	2	2	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1
86	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0

APPENDIX 3

List of apomorphies supporting numbered nodes in Figure 24.

Branch	Character	Steps	CI	Change
node_51 → *Rhagio*	2	1	1.000	1 ⇒ 0
	7	1	0.500	0 ⇒ 1
	32	1	0.750	1 ⇒ 0
	51	1	1.000	1 ⇒ 0
	80	1	0.667	1 ⇒ 0
	81	1	0.500	2 ⇒ 0
node_51 → *Systenus*	62	1	0.667	1 ⇒ 0
	82	1	0.500	0 ⇒ 1
node_51 → node_50	1	1	1.000	0 ⇒ 1
	3	1	1.000	0 ⇒ 1
	19	1	1.000	0 ⇒ 1
	33	1	1.000	0 ⇒ 1
	34	1	1.000	0 ⇒ 1
	49	1	1.000	0 ⇒ 1
	63	1	0.400	0 ⇒ 1
	65	1	0.333	0 ⇒ 1
	67	1	0.500	0 ⇒ 1
	71	1	0.286	0 → 1
	72	1	1.000	0 ⇒ 1
	77	1	0.667	0 ⇒ 1
	83	1	0.750	0 → 1
node_50 → Lonchoptera	21	1	0.200	0 → 1
	86	1	0.333	0 ⇒ 1
node_50 → node_49	4	1	1.000	0 ⇒ 2
	29	1	0.500	0 → 1
	32	1	0.750	1 ⇒ 2
	39	1	0.667	0 → 1
	48	1	1.000	0 ⇒ 1
	50	1	1.000	0 ⇒ 1
	51	1	1.000	1 ⇒ 2
	83	1	0.750	1 → 2
node_49 → node_35	12	1	1.000	0 → 1
	27	1	0.333	0 → 1
	28	1	1.000	1 ⇒ 0
	40	1	0.667	0 → 1
	54	1	0.500	0 ⇒ 1
	66	1	0.750	0 ⇒ 2
	69	1	0.500	0 ⇒ 1
	71	1	0.286	1 → 0
	81	1	0.500	2 ⇒ 1
node_35 → Melanderomyia	4	1	1.000	2 ⇒ 1
	29	1	0.500	1 → 0
	53	1	0.500	0 ⇒ 1
	78	1	0.333	1 ⇒ 0
	83	1	0.750	2 → 1
node_35 → node_34	23	1	0.333	0 ⇒ 1
	27	1	0.333	1 → 2
	35	1	0.400	0 → 1
	38	1	0.250	0 ⇒ 1
	40	1	0.667	1 → 2
node_34 → Callomyia	71	1	0.286	0 ⇒ 2
node_34 → node_33	8	1	1.000	0 ⇒ 1

APPENDIX 3 *Continued*

Branch	Character	Steps	CI	Change
	26	1	0.333	0 ⇒ 1
	31	1	1.000	0 ⇒ 1
	58	1	0.500	0 ⇒ 1
node_33 → node_29	25	1	0.400	0 → 1
	35	1	0.400	1 → 0
	53	1	0.500	0 ⇒ 1
	71	1	0.286	0 → 1
node_29 → node_28	11	1	0.333	0 ⇒ 1
	24	1	0.250	0 ⇒ 1
node_28 → Bolopus	65	1	0.333	1 ⇒ 2
node_28 → Platypeza	21	1	0.200	0 ⇒ 1
	25	1	0.400	1 → 0
	27	1	0.333	2 → 0
	69	1	0.500	1 ⇒ 2
	71	1	0.286	1 ⇒ 2
node_33 → node_32	10	1	1.000	0 ⇒ 1
	13	1	0.500	0 ⇒ 1
	27	1	0.333	2 → 0
	40	1	0.667	2 → 1
	63	1	0.400	1 ⇒ 2
	66	1	0.750	2 ⇒ 1
	73	1	1.000	0 ⇒ 1
	74	1	0.667	0 ⇒ 1
	79	1	0.286	0 → 1
	86	1	0.333	0 ⇒ 1
node_32 → node_31	38	1	0.250	1 ⇒ 0
node_31 → node_30	54	1	0.500	1 ⇒ 0
	79	1	0.286	1 → 0
node_30 → Aphiochaeta	22	1	0.200	0 ⇒ 1
node_30 → Spingera	24	1	0.250	0 ⇒ 1
	71	1	0.286	0 ⇒ 1
	79	1	0.286	0 → 2
node_32 → Megascelia	81	1	0.500	1 ⇒ 2
node_49 → node_48	2	1	1.000	1 ⇒ 2
	3	1	1.000	1 ⇒ 2
	7	1	0.500	0 ⇒ 1
	9	1	1.000	0 ⇒ 1
	22	1	0.200	0 → 1
	33	1	1.000	1 ⇒ 2
	39	1	0.667	1 → 2
	41	1	1.000	0 ⇒ 1
	46	1	1.000	0 ⇒ 1
	49	1	1.000	1 ⇒ 2
	55	1	0.333	0 → 1
	63	1	0.400	1 ⇒ 2
	72	1	1.000	1 ⇒ 2
	79	1	0.286	0 ⇒ 1
	82	1	0.500	0 → 2
node_48 → node_42	5	1	0.500	0 ⇒ 1
	6	1	0.500	0 → 1
	15	1	0.500	0 ⇒ 1
	25	1	0.400	0 → 2
	30	1	0.500	0 → 1
	43	1	0.500	0 → 1

APPENDIX 3 *Continued*

Branch	Character	Steps	CI	Change
	73	1	1.000	0 ⇒ 2
	74	1	0.667	0 → 1
	75	1	1.000	0 ⇒ 1
	85	1	0.500	0 ⇒ 1
	86	1	0.333	0 ⇒ 1
node_42 → node_36	13	1	0.500	0 ⇒ 1
	55	1	0.333	1 → 0
	63	1	0.400	2 ⇒ 0
	68	1	1.000	0 ⇒ 1
	78	1	0.333	1 ⇒ 0
	82	1	0.500	2 → 0
	83	1	0.750	2 ⇒ 3
node_36 → Nephrocerus	6	1	0.500	1 ⇒ 0
	69	1	0.500	0 ⇒ 1
	79	1	0.286	1 ⇒ 0
node_42 → node_41	59	1	1.000	0 ⇒ 1
	61	1	1.000	0 ⇒ 1
	62	1	0.667	1 ⇒ 2
	64	1	1.000	0 ⇒ 1
	69	1	0.500	0 ⇒ 2
	74	1	0.667	1 → 2
	79	1	0.286	1 ⇒ 2
	84	1	1.000	0 ⇒ 1
node_41 → node_37	54	1	0.500	0 ⇒ 1
	82	1	0.500	2 → 1
node_41 → node_40	20	1	0.500	0 ⇒ 1
	25	1	0.400	2 → 0
	26	1	0.333	0 ⇒ 1
	30	1	0.500	1 → 0
	31	1	1.000	0 → 2
	43	1	0.500	1 → 0
node_40 → node_38	39	1	0.667	2 ⇒ 1
	54	1	0.500	0 ⇒ 2
	55	1	0.333	1 → 0
	76	1	1.000	0 → 1
node_38 → Platycheirus	37	1	0.500	0 ⇒ 1
	76	1	1.000	1 → 2
	78	1	0.333	1 ⇒ 0
node_40 → node_39	11	1	0.333	0 ⇒ 1
	14	1	1.000	0 ⇒ 1
	16	1	1.000	0 ⇒ 1
	17	1	1.000	0 ⇒ 1
	22	1	0.200	1 ⇒ 0
	23	1	0.333	0 ⇒ 1
	27	1	0.333	0 ⇒ 2
	30	1	0.500	0 → 2
	32	1	0.750	2 ⇒ 3
	35	1	0.400	0 ⇒ 1
	38	1	0.250	0 ⇒ 1
	42	1	0.500	0 ⇒ 1
	44	1	0.500	0 ⇒ 1
	47	1	0.500	0 ⇒ 1
	58	1	0.500	0 ⇒ 1
	60	1	1.000	0 ⇒ 1

APPENDIX 3 *Continued*

Branch	Character	Steps	CI	Change
	65	1	0.333	1 ⇒ 2
	70	1	0.500	0 ⇒ 1
node_39 → Eumerus	24	1	0.250	0 ⇒ 1
	63	1	0.400	2 ⇒ 1
node_39 → Alipumilio	57	1	1.000	0 ⇒ 1
node_48 → node_47	11	1	0.333	0 ⇒ 1
	14	1	1.000	0 ⇒ 2
	18	1	0.500	0 ⇒ 1
	26	1	0.333	0 ⇒ 1
	35	1	0.400	0 → 1
	36	1	1.000	0 ⇒ 1
	37	1	0.500	0 ⇒ 1
	38	1	0.250	0 ⇒ 1
	42	1	0.500	0 → 1
	44	1	0.500	0 ⇒ 1
	57	1	1.000	0 → 2
	62	1	0.667	1 ⇒ 0
	67	1	0.500	1 ⇒ 0
	77	1	0.667	1 ⇒ 2
	80	1	0.667	1 ⇒ 2
node_47 → node_46	20	1	0.500	0 ⇒ 1
	21	1	0.200	0 → 1
	22	1	0.200	1 → 0
	23	1	0.333	0 ⇒ 1
	30	1	0.500	0 ⇒ 2
	32	1	0.400	1 → 2
	47	1	0.500	0 ⇒ 1
	56	1	1.000	0 ⇒ 1
	65	1	0.333	1 → 0
	70	1	0.500	0 ⇒ 1
	71	1	0.286	1 → 0
node_46 → node_45	25	1	0.400	0 ⇒ 1
node_45 → Phaonia	21	1	0.200	1 → 0
	52	1	0.500	0 ⇒ 1
node_45 → node_44	24	1	0.250	0 ⇒ 1
	27	1	0.333	0 ⇒ 1
	65	1	0.333	0 → 1
	66	1	0.750	0 ⇒ 2
node_44 → Homalocephala	79	1	0.286	1 ⇒ 0
node_44 → node_43	22	1	0.200	0 ⇒ 1
	77	1	0.667	2 ⇒ 1
	85	1	0.500	0 ⇒ 1
node_43 → Scatophaga	21	1	0.200	1 → 0
node_43 → Calliphora	5	1	0.500	0 ⇒ 1
	15	1	0.500	0 ⇒ 1
	18	1	0.500	1 ⇒ 0
	28	1	1.000	1 ⇒ 2
	52	1	0.500	0 ⇒ 1
	65	1	0.333	1 → 0
	80	1	0.667	2 ⇒ 0
node_47 → Physocephala	45	1	1.000	0 ⇒ 1
	66	1	0.750	0 ⇒ 3
	81	1	0.500	2 ⇒ 0