

# Final stage larvae and puparia of Platypezidae (Diptera)

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Platypezidae occupy an important basal position within the Muscomorpha. However, morphological analyses of larval Platypezidae are incomplete and early stage data is insufficient to inform phylogenetic analysis and recognition of groundplan characters and states within Muscomorpha. For example, knowledge is poor of the characters of respiratory organs, head, head skeleton, thorax and segmental sensilla. In this study we describe and compare these features of 16 species in 11 genera. The head appears as a distinct fleshy organ with atrium and antennae and maxillary organs separated on the dorsal surface. Head skeletons are characterised by an anteriorly projecting labrum and labium with laterally placed mandibles. The prothorax is frequently armoured with sclerotised regions and spicules. A repeated and uniform pattern of up to 11 pairs of sensilla circumvent each thoracic and abdominal segment. Respiratory organs vary little in size and arrangement of spiracular openings. Using a set of 43 larval and puparial characters and based on a Brachyceran outgroup, a sequence of genera is established which places *Melanderomyia* as the most basal. These results are compared with estimates of phylogeny based on adult characters.

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## Introduction

The Platypezidae comprise about 250 species worldwide of which 44 occur in Europe. They are small to medium-sized flies typical of forests and have male epigamic swarming and characteristic to-and-fro walking gaits reminiscent of adult Phoridae (Chandler 2001). About 30 species have been reared from fungi making the Platypezidae as far as is known, exclusively mycophagous (Chandler 2001). The morphology of platypezid larvae has been considered by several authors, reviewed by Chandler (2001). One of the most comprehensive accounts is that of Kessel et al. (1973) who described and keyed ten genera. Keys and descriptions were updated by Chandler and Shatalkin (1998) and Chandler (2001). Morphological features such as body size and shape, number and distribution of hair-like or fleshy, elongate processes on the dorsal surface are frequently described. Fortunately, these features are sufficient to enable the known genera to be recognised

(Chandler 2001). The larval stages of only two European genera are unknown, *Microsania* Zetterstedt and *Platypezina* Wahlgren.

Comparing previous descriptions with preserved larvae and puparia, we realised that their morphology has been poorly documented. Previous descriptions are generalised and incomplete. In particular we found little or no inclusion of the head skeleton, integumental armature of the head and thorax, lateral and ventral sensilla and the respiratory organs. Yet Platypezidae are an important taxon to understand because of their basal position in the phylogeny of the Muscomorpha, the most diverse and species-rich higher group within Diptera (McAlpine 1989; Wiegmann et al. 1993; Cumming et al. 1995). Given this basal position, understanding larval morphology in Platypezidae should provide insight into the evolution of characteristic muscomorphan features such as the reduced head and development of the cephalopharyngeal skeleton (Teskey 1981).

A start on such an understanding was made by Sinclair (1992) who corrected some previous errors concerning the identification of the mandible, showing that the most conspicuous sclerotised structure appearing at the front of the mouth is the labial hypopharyngeal sclerite (labium) and that the true mandible lies above or to the side of this structure. However Sinclair (1992) only figures and comments on the head skeletons of two platypezid species although 5 species in 4 genera were apparently studied. One important finding was the tapered and well developed labrum in the head skeleton of *Melanderomyia kahli* Kessel. Labrums of this type were considered by Hennig (1973) not to be a feature of final stage larval morphology in Cyclorrhapha (= Muscomorpha). Hennig (1952) refers to generic-level differences in head skeleton structure in Platypezidae but without giving further detail. In this study we describe and compare final stage larvae and/or puparia of 16 species in 11 genera, construct an exemplar phylogeny, consider morphological trends and, in comparison with larvae of Brachyceran and other Muscomorphan families attempt to diagnose and account for the morphology of the larval stages of Platypezidae.

### Materials and Methods

Larvae were collected in the field, details under each species, and preserved in 70% alcohol, or reared through to the adult stage. To examine thorax, head and head skeleton structure a number of approaches were taken. The external morphology of the thorax and head was studied using preserved larvae and a binocular microscope. Preserved larvae were either studied in alcohol in solid watch glasses or were examined dry. Where necessary, detail was confirmed using a temporary stain: larvae were removed from preservative, dried on tissue paper and a small amount of methylene blue in alcohol was applied with a pin. Within a few minutes the stain dried and larvae were ready for examination. After examination the stain was removed by placing larvae in 70% alcohol for several minutes.

To obtain further detail and examine functional relationships, the thoraces and heads of some preserved larvae were cleared in KOH. A cut was made across the first or second abdominal segments and the head and thorax placed in concentrated KOH for about 1 hour. This cleared the inter-

nal tissues which were then carefully removed with pins. The resulting preparation was sufficiently translucent to obtain clear views in situ, of the head skeleton, head and thorax which are attached to each other in that order. Functional relationships between the various parts were suggested by pushing down 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 folds present in the integument of the head and thorax. These folds are retained in preparations cleared in KOH and are places where the integument crumples and folds during movement (Rotheray and Gilbert 1999).

Finally, head skeletons were examined directly by dissecting them from preserved larvae or removing them from puparia after soaking in KOH for about 1 hour. When extracting head skeletons from puparia associated structures of the head which include oral ridges, maxillary palpi and antennae were attached. Care was taken to remove these structures with minimal damage.

The status of many larval characters is uncertain (Teskey 1981; Ferrar 1987; Chandler 2001) and it is not possible to apply a set of descriptive terms that reflect homology. For gross morphology we use the terms in Chandler (2001) with the substitution of "lappet" (Hartley 1961) for fleshy segmentally-arranged projections or processes that bear a sensillum. A pattern of segmentally arranged sensilla is present on all thoracic and abdominal segments but ventral and some lateral sensilla are not borne on lappets. The positions of individual lappets/sensilla are useful "markers" for determining positions on the body. Lappets are referred to by number, reading from the mid-dorsal (1) to the mid ventral position (10/11) on each segment (Fig. 1). For head skeleton characters we use terms found in Teskey (1981), Ferrar (1987) and Sinclair (1992).

To investigate relationships between our exemplar sample of platypezid species, a set of 43 characters were obtained from all over the body of the larva and/or puparium (Appendix 1) and scored on an outgroup consisting of 2 larval Brachyceran species (*Rhagio scolopaceus* (Linnaeus) (Rhagionidae) and *Systemus pallipes* (von Roser) (Dolichopodidae) and an ingroup of 16 platypezid species (Appendix 2). We used PAUP Version 4.0 to analyse these data. All characters were unordered and had equal weight. Four characters

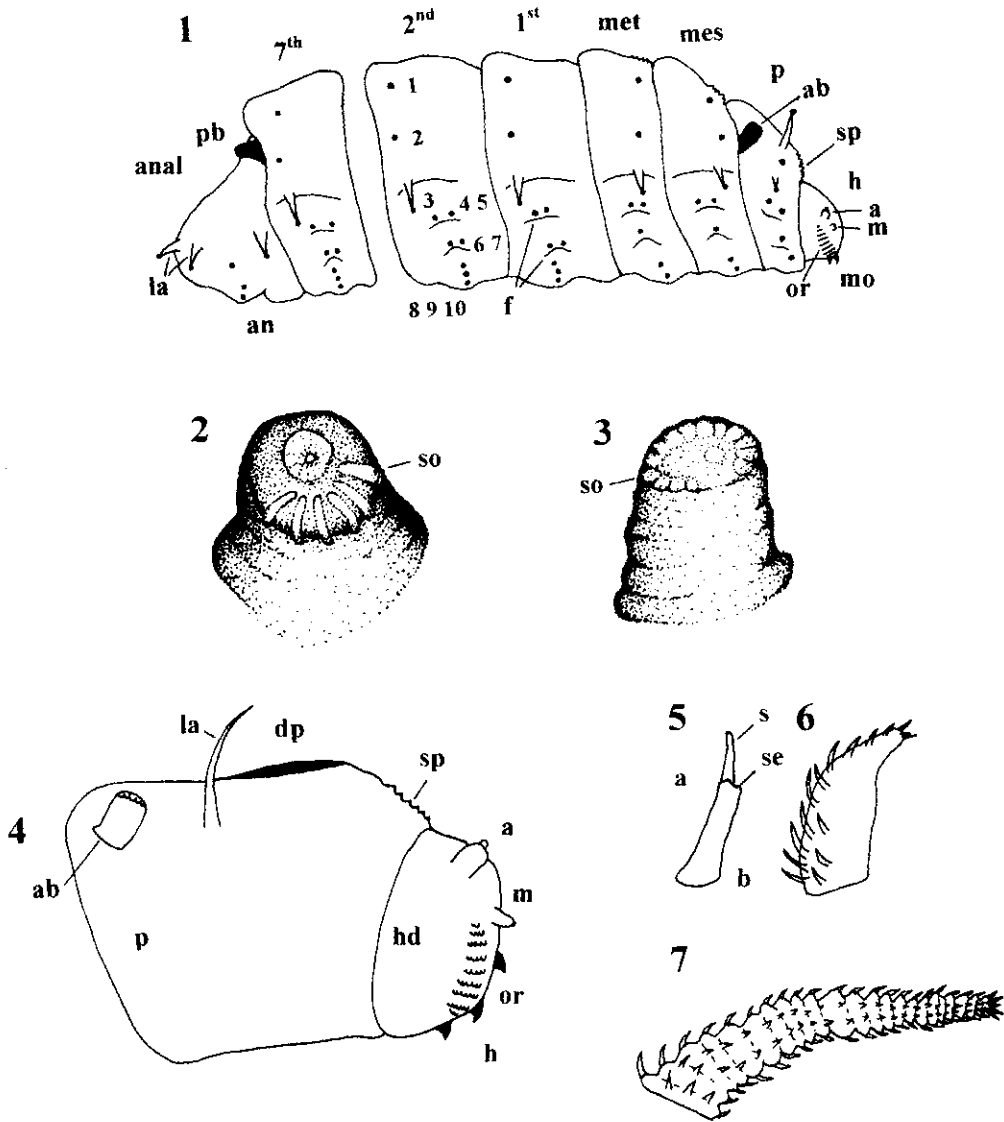


Figure 1. Morphological map of a third (=final) stage platypezid larva (Diptera, Platypezidae) showing main features and position and number of segmental sensilla, indicated as black dots, of one half of the body, dorsal side uppermost, head to the right; segments 3-6 not shown but similar to 2<sup>nd</sup> abdominal segment; a = antenna; ab = anterior breathing tube; an = anus; anal = anal segment; f = folds appearing as impressed lines or raised ridges on the integument; h = head; la = lappets; m = maxillary process; mes = mesothorax; met = metathorax; mo = mouth; or = oral ridges; p = prothorax; pb = posterior breathing tube; sp = spicule band on anterior fold; 1<sup>st</sup>, 2<sup>nd</sup>, 7<sup>th</sup> = abdominal segments; 1-10 = sensilla numbers.

Figures 2-3. *Platypeza consobrina*; 2, posterior breathing tube; so = spiracular openings; 3, anterior breathing tube; so = spiracular openings

Figure 4. *Bolopus furcatus*, head and prothorax, lateral view; a = antenna; ab = anterior breathing tube; dp = dorsal plate; h = labial hooks; hd = head; la = lappet; m = maxillary organ; or = oral ridges; p = prothorax; sp = spicule band on anterior fold.

Figures 5-7. third lappet on abdominal segment six, lateral view; 5, *Agathomyia falleni*; a = apex; b = base; s = accompanying seta; se = site of sensillum; 6, *Protoclythia modesta*; 7, *Platypeza consobrina*.

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 outgroup 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 (Con-level = 50, the default).

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

## Results

### *Diagnoses of outgroup taxa*

***Rhagio scolopaceus*** (Linnaeus) (Diptera, Rhagionidae)

**Size and shape:** larva white to pale brown, long and thin: length 15mm, width 1.5-2mm; in cross-section, subcylindrical (as wide as high); truncate posteriorly, tapering anteriorly; **head:** lacking atrium; maxillary palpi and antennae separated and on fleshy projections, those of antennae shorter than those of maxillary palpi; **head skeleton:** with sclerotised, brown, tapering mandibles projecting externally and downwards; mandibular brush present; head skeleton similar to *Rhagio* sp. illustrated by (James and Turner 1981); **anterior spiracles:** consisting of a pair of openings sited about halfway along the lateral margin of the prothorax; **thorax and abdomen:** anterior and posterior margins of each thoracic and abdominal segment, except compounded anal segment, with transverse rows of spicules circumventing the entire margin of each segment, otherwise integument smooth, lacking vestiture and lappets; spicules on ventral surface of abdominal segments 1-7 on slight projections (= locomotory projections); **anal segment:** smooth with apical margin bearing a pair of dorsal and a pair of ventral triangular-shaped lappets about as broad as long; dorsal lappets smaller than ventral lappets; apex of anal segment between the lappets curved with upper half bearing a pair of button-shaped flat spiracular plates; entire apical margin of spiracular plates comprising oval-shaped spiracular openings; anal opening parallel to longitudinal axis of the body.

**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 National Museums of Scotland, GE Rotheray.

**Previous descriptions:** – Roberts (1969).

***Systemus pallipes*** (von Roser) (Diptera, Dolichopodidae)

**Size and shape:** larva white, long and thin: length 8.0 mm, width 1.0mm; in cross-section, subcylindrical (as wide as high); truncate posteriorly, tapering anteriorly; **head:** lacking atrium; maxillary palpi and antennae separated; maxillary palpi approximated anteriorly and barely projecting; antennae and short (long as broad) fleshy projections; **head skeleton:** with sclerotised, brown, tapering mandibles projecting externally and downwards; mandibular brush absent; head skeleton similar to *Medetera* sp. illustrated by (Robinson and Vockeroth 1981); **anterior spiracles:** consisting of a pair of openings sited about halfway along the lateral margin of the prothorax; **thorax and abdomen:** anterior and posterior margins of each thoracic and abdominal segment, except anterior margin of prothorax and compounded anal segment, clearly marked with an indented region, width about 0.2 the length of a segment; integument within the indented region smooth lacking spicules; rest of integument smooth, lacking vestiture; antero-ventral surface of abdominal segments 2-7 on slight projections (= locomotory projections) coated in curved rows of spicules, locomotory projections on first abdominal segment elongate, about 3x as long as broad and tipped with crochet-like spicules; **anal segment:** smooth with apical margin bearing a pair of dorsal and a pair of ventral triangular-shaped lappets about as broad as long; dorsal lappets smaller than ventral lappets; apex of dorsal lappets with 3 groups of setae; one pair of setae at apex of ventral lappets; apex of anal segment between the lappets curved with a pair of inconspicuous spiracular openings at base of dorsal lappets; each side of the anal opening with a pair of button-shaped projections coated in 6 peg-like fleshy projections; anal opening parallel to longitudinal axis of the body.

**Material examined:** – one larva, Scotland, Perthshire, Dalguise nr Pithlochry; 26 April 1995, ex sap run on horse chesnut (*Aesculus hippocastanum* L.), identification confirmed by comparison with reared material in

collections of National Museums of Scotland, GE Rotheray.

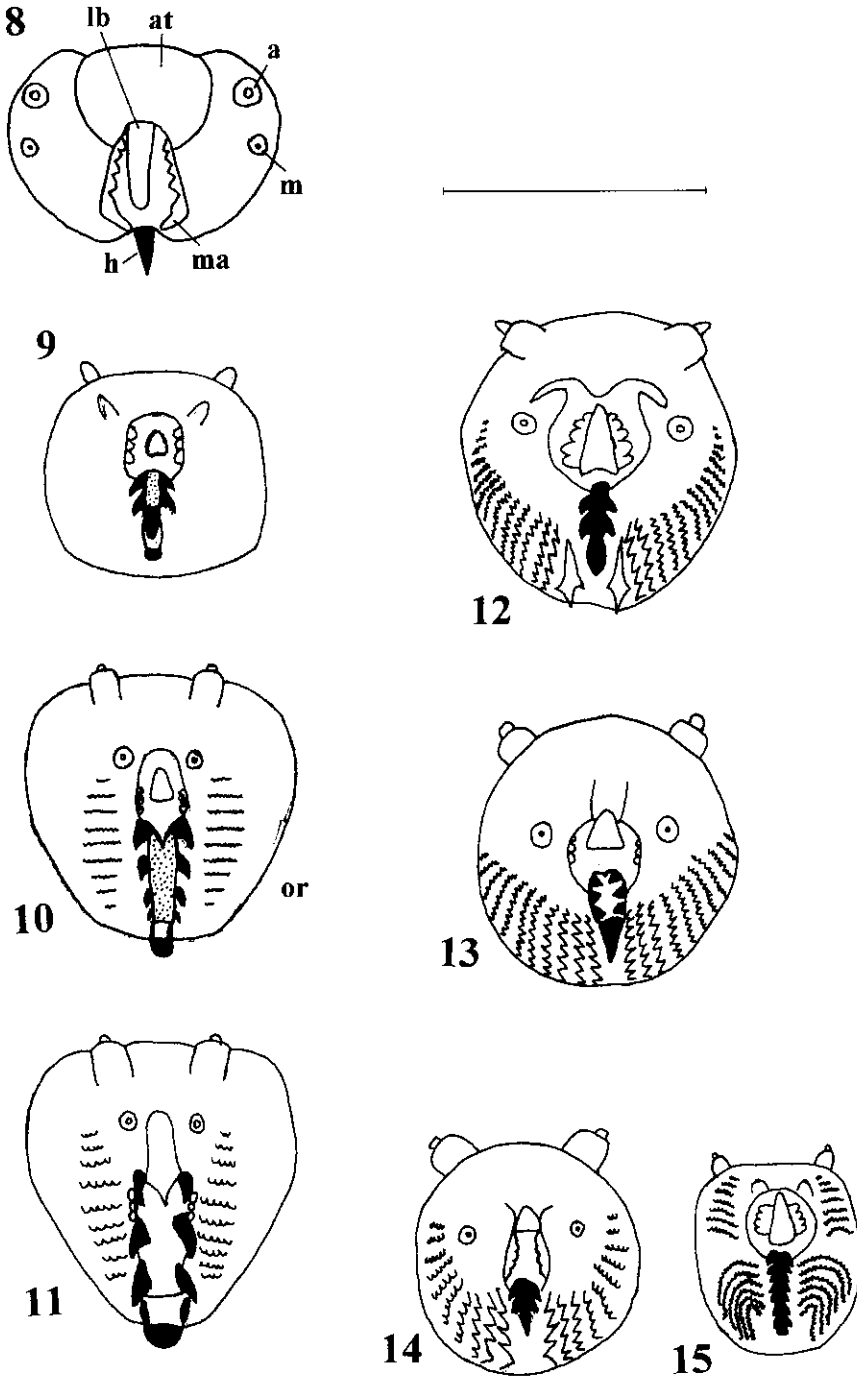
*Previous descriptions:* – Krivoscheina (1973).

### Diagnoses of ingroup taxa

#### *Diagnosis of platypezid final stage larva*

**Size and shape:** length 4-6mm, width 1.5-3mm; in cross-section, subcylindrical (as wide as high) to dorso-ventrally flattened (1-3x as wide as high); truncate posteriorly, tapering anteriorly; each thoracic and abdominal segment circumvented with sensilla: prothorax with 7-8 pairs of sensilla; mesothorax and metathorax with 8 pairs each; abdominal segments 1-7 with 10 pairs and anal segment with 6-7 pairs (Fig. 1); dorsal and some lateral sensilla mounted on processes or lappets i.e. each sensillum mounted apically on a fleshy projection of varying length and accompanied by one or more setae (Hartley 1963; Fig. 1); lappets smooth, sometimes with setae (Figs. 5-7); lateral sensilla mounted on short (wide as high) processes or processes absent; ventral sensilla without processes or accompanying setae and mounted mid-segmentally on slightly raised, elongate-oval locomotory pads delimited by an impressed line in the integument; a pair of anterior spiracles projecting from the postero-lateral margin of the prothorax; dorsal lappets towards the anterior margin of the thoracic segments and towards the posterior margin of abdominal segments (Fig. 1); anal segment with an inclined dorsal surface bearing up to 4 pairs of lappets on the apex and a pair of separated breathing tubes on the antero-dorsal margin (Fig. 1); breathing tubes usually partially concealed under a posterior fold of the 7<sup>th</sup> abdominal segment and sometimes further concealed on the posterior side by a fold in the integument of the compounded anal segment; anus transverse and posterior to the antero-ventral margin; **head:** distinguished from the prothorax by an integumental fold (impressed line); atrium present as a broad to narrow, fleshy section with separated antennae and maxillary organs on the dorso-lateral margin (Figs 1,4); antennae posterior to maxillary organs and lobes bearing one antenna and one maxillary organ not mounted on fleshy projections; oral ridges sometimes present surrounding lateral margins of the mouth (Figs 4, 10-15); ventral margin of head sometimes with sclerotised plates (Fig. 4); **head skeleton:** lightly to strongly sclerotised (Figs.

16,17); apex of labrum tapered and extending to mouth opening; labium also produced anteriorly and appearing at the opening of the mouth, apex with 1-8 pairs of hooks; labium often interrupted behind hooks (Fig. 20); mandibles very translucent and inconspicuous; square to rectangular-shaped with 1-5 rounded apical teeth; mandibles lying above and to the side of the apex of the labrum and labium at the opening of the mouth and posterior margins articulating either with a pair of bars extending narrowly from the anterior margin of the pharyngeal sclerite (Figs. 25, 27-29) or from a short, broad projection arising from the labium (Fig. 26); pharyngeal sclerite U-shaped sometimes with dorsal apodemes (Figs. 21-23, 27-29), ventral pharyngeal ridges (Fig. 17) and dorsal bridge (Fig. 21), usually translucent but sometimes with areas of sclerotisation, dorsal and ventral cornua rarely equally wide or long; **thorax:** tapering, sometimes abruptly in step-like fashion from metathorax to prothorax; mesothorax sometimes folded downwards and prothorax infolded ventrally so that the head projects ventrally and the anterior margin of the larva is the mesothorax; antero-dorsal margin of the prothorax forming an anterior fold i.e. usually folded downwards to meet the head and often coated in setae and spicules (spicules differ from setae in being broader than tall and lightly sclerotised); prothoracic mid-dorsal lappets sometimes longer than mid-dorsal lappets on other segments; antero-dorsum of mesothorax and metathorax also with setae and spicules; dorsal plates sometimes present on each segment i.e. integument bearing a rectangular-shaped, lightly sclerotised region; 2-4 pairs of lappets on the antero-dorsal margin of each segment; anterior spiracles usually flat-tipped with a horse-shoe-shaped arrangement of openings on the anterior and lateral margins (Fig. 3); **abdomen:** dorsum with 1-4 pairs of lappets and variably coated in setae, spicules and/or integument coriaceous with occasional dark blotches; first abdominal segment sometimes with a different pattern of setae and spicules to the remaining abdominal segments; locomotory organs little developed, appearing as pairs of oval-shaped pads on each abdominal segment bearing 2-3 pairs of sensilla; posterior breathing tubes tapering, variable in length with 1-6 radially-arranged oval-shaped spiracular openings extending over the sides of the apical rim (Fig. 2).



Figures 8-15. Platypezidae, heads of third stage larvae, apical view, scale line = 0.15mm; 8, *Melanderomyia kahli*, a = antenna; at = atrium; h = labial hook; lb = labrum; ma = mandible; 9, *Agathomyia unicolor*; 10, *Seri obscuripennis*, or = oral ridges; 11, *Bolopus furcatus*; 12, *Calotarsa insignis*; 13, *Platypeza consobrina*; 14, *Protoctylthia rufa*; 15, *Paraplatypeza atra*.

*Diagnosis of platypezid puparium*

Similar to the non-mobile or resting state of the final stage larva in gross morphology with prothorax folded ventrally and anal segment inclined dorsally. Puparia usually dorso-ventrally flattened. Pupal respiratory processes absent. To permit emergence of the adult, a section separates longitudinally below the long, upper lateral lappets and along transverse lines across the anterior margin of the mesothorax and posteriorly across the first or second abdominal segment. In *Callomyia* the anterior split is further forward and includes the prothorax. In *Paraplatypeza*, *Lindneromyia* and possibly other taxa, the posterior split may not occur so that complete separation of part of the puparium does not occur.

**Descriptions of platypezid final stage larvae***Melanderomyia kahli* (Kessel)

*Overall appearance:* – A subcylindrical larva with anterior and posterior breathing tubes on rounded fleshy projections and lappets short and inconspicuous. On the dorsal margin of each projection supporting the posterior breathing tubes is a sensillum. The dorsum of abdominal segments 1-7 bear two bands of setae.

*Diagnosis:* – **Shape and dimensions:** length 4-5mm; width 1.5-2mm; subcylindrical in cross-section, tapering anteriorly, truncate posteriorly; **head:** oral ridges absent; atrium broad and separating antennae and lobes bearing maxillary palpi (Fig. 8); **head skeleton:** very lightly sclerotised; apex of labium with a single downwardly directed hook; square-shaped mandibles with blunt-tipped teeth appearing on either side of the labrum and articulating with a sclerotised lateral extension of the labium, postero-apical margins of mandibles lightly sclerotised; labium uninterrupted, sclerotised at point of articulation with the mandibles and ventral margin thinly sclerotised; pharyngeal sclerite translucent, dorsal cornu narrower than ventral cornu and not diverging or particularly narrow; dorsal bridge and dorsal apodeme absent; ventral pharyngeal ridges present (Figs. 16-18); **thorax:** subcylindrical; dorsal plates absent; dorsum of each segment coated in a single band of setae; dorsum of prothorax with a pair of short projections (shorter than basally broad) and head and prothorax on the same level, separated by only

an indistinct fold; head about as wide as the anterior margin of the prothorax; prothorax not folded ventrally so that the mouth projects in an anterior direction; dorsum and lateral margins of each thoracic segment coated with setae; dorsum of mesothorax and metathorax with 3 pairs each of lappets on slightly broader and longer projections than surrounding setae; anterior breathing tubes: length 0.04mm, mounted on fleshy projections; apex with horseshoe-shaped arrangement of openings round anterior and lateral margins; **abdomen:** first two lappets on abdominal segments 1-7 reduced or absent, if present not longer than surrounding setae; 3<sup>rd</sup> lappet on upper dorsal margin about 0.09mm long on abdominal segment 7 and becoming shorter towards segment one (0.05mm); abdominal segments 1-7 each with two equally long bands of setae coating the dorsum, setae up to 0.04mm long; apex of anal segment with three pairs of lappets, middle lappet reduced; third pair of lappets i.e. those on the mid-line and most distant from the base of the segment each on a pair of fleshy projections; posterior breathing tubes: about twice as long as basally broad, length 0.09mm, basal width 0.04mm; parallel-sided with a sclerotised brown tip; each tube on a fleshy projection the dorsal margin of which bears a sensillum; 4 oval spiracular openings on the rim of the lateral and posterior margins.

*Material examined:* – 9 larvae, USA, Georgia, Tifton, 16 March 1969, from stinkhorn fungus (Phallaceae), JA Payne, CNC (Canadian National Collections), 2 larvae retained in NMS.

*Previous descriptions:* – puparium (Kessel et al. 1973); head skeleton (Sinclair 1982); whole larva figured in Kessel (1987).

*Callomyia amoena* Meigen

*Overall appearance:* – Dorso-ventrally flattened with a margin comprising flattened lappets and similar blind processes i.e. a projection similar to a lappet but lacking a sensillum at its apex. Prothorax and mesothorax narrow, about half as wide as metathorax. Mesothorax directed ventrally with posterior margin bearing dorsal lappets similar to marginal lappets appearing at the front of the puparium. Metathorax and first abdominal segment fused dorsally. Marginal lappets and processes with flattened setae along their sides. Lappets on the dorsum of prothorax, metathorax and abdomen consisting of smooth seta-like pro-

jections lacking a coating of micro-setae. Apical margin of the anal segment with 4 pairs of equally long lappets.

**Diagnosis:** – **Shape and dimensions:** length 5mm, width 3.5mm; dorso-ventrally flattened, truncate anteriorly and posteriorly, entire margin with lappets and blind processes i.e. a projection similar to a lappet but lacking a sensillum at its apex; except for mesothorax one pair of lappets and one pair of blind processes per segment; **head:** oral ridges apparently absent; **head skeleton:** strongly sclerotised; apex of labium not fused and with three pairs of similar sized hooks; labium interrupted and the two halves joined by two pairs of sclerotised connecting rods anterior and posterior to the point of interruption; labium posterior to interruption broad and heavily sclerotised; mandibles sclerotised, narrow and rectangular articulating with a projection from the labium anterior to the point of interruption; pharyngeal sclerite strongly sclerotised with dorsal bridge present; dorsal apodemes absent; ventral pharyngeal ridges not apparently present; dorsal cornu about the same length but wider than the ventral cornu (Figs. 19-20); **thorax:** dorso-ventrally flattened; dorsal plates absent; prothorax and mesothorax very narrow, about half as broad as metathorax and the first abdominal segment (0.92 v 1.84mm); metathorax and first abdominal segment fused dorsally as shown by the absence of a intersegmental transverse fold that separates the other abdominal segments; mesothorax modified and folded and hinged medially so that the anterior part articulates with the prothorax and the posterior part with the metathorax and the hinged midpoint bearing 4 pairs of lappets forms the anterior margin of the puparium, thus the entire margin of the puparium is coated in flattened lappets and processes; prothorax with 4 pairs of lappets and lacking a coating of setae; anterior spiracles triangular in shape about 0.16mm long; dorsum of mesothorax and metathorax smooth, lacking setae or spicules; first abdominal segment with a medial patch of upright, blunt-tipped spicules about as long as broad; **anterior breathing tubes:** length 0.18mm, triangular-shaped and strongly tapering to apex with horse-shoe-shaped arrangement of openings round anterior and lateral margins; **abdomen:** dorsum with 4 pairs of smooth seta-like lappets lacking a coating of micro-setae; mid-dorsally on each segment an inverted triangular-shaped patch of blunt-tipped

spicules; anal segment with 4 pairs of lappets; **posterior breathing tubes:** barely projecting from the segment, slightly broader than long (0.06 x 0.04mm) with 3-4 oval spiracular openings.

**Material examined:** – one puparium, England, Berkshire, Windsor Forest, 20 June 1968, ex decayed wood of beech stump (*Fagus*), female emerged August 1968, A.E. Stubbs.

**Previous descriptions:** – Lundbeck (1927); Brindle (1961); Chandler (2001); Kessel et al. (1973) described *Callomyia gilloglyorum* Kessel from the Nearctic region.

*Agathomyia falleni* (Zetterstedt),  
*Agathomyia unicolor* Oldenberg, *Agathomyia wankowiczii* (Schnabl)

**Overall appearance:** – Subcylindrical to slightly dorso-ventrally flattened larvae. Dorsum of mesothorax and metathorax with 4 pairs of lappets. Abdominal segment 7 with lappet pairs 1 and 2 approximated, lappet pair 1 slightly anterior to second pair. Anal segment with 4 pairs of lappets on the apical margin.

**Diagnosis:** – **Shape and dimensions:** length 3-5.5mm, width 1.5-3mm; subcylindrical (abdominal segment 6 about 2x as wide as body is high) to slightly dorso-ventrally flattened (abdominal segment 6 about 3x as wide as body is high); truncate posteriorly, tapering anteriorly; **head:** oral ridges absent; below the mouth is a U-shaped sclerotised plate (Fig. 9); **head skeleton:** (*wankowiczii* not examined) lightly sclerotised with labium and anterior part of the pharyngeal sclerite more heavily sclerotised; apex of labium fused and consisting of three pairs of hooks, upper two pairs separate from each other and smaller than the larger lower pair which are fused forming a single hook; lateral length of labial hooks longer than width of dorsal cornu; labium interrupted and not joined by sclerotised rods; mandibles very lightly sclerotised, translucent, articulating with a projection from the labium anterior to the point of interruption; pharyngeal sclerite with dorsal and ventral bridges present but not strongly sclerotised; dorsal apodeme absent; ventral pharyngeal ridges apparently not present, ventral cornu narrower and longer than dorsal cornu and not as strongly sclerotised; dorsal and ventral cornua not diverging (Fig. 24); **thorax:** dorsal plates absent; prothorax folded ventrally so that the dorsal rather than the



ventral margin projects further forward and mouth projects ventrally; anterior fold of prothorax coated with transverse rows of backwardly directed triangular-shaped spicules, these spicules extending to the lateral margins of the prothorax but ventral margin smooth, lacking spicules; antero-dorsal margin of mesothorax and metathorax with spicules reaching line of mid-segmental lappets on dorsum and lateral margins, spicules absent on ventral margin; prothorax with lappet 1 longer than lappet 2; dorsum of mesothorax and metathorax with 4 pairs of lappets; mesothorax with lappet pairs 1 and 4 longer than lappet pairs 2 and 3; metathorax with lappet 3 shorter than lappets 1, 2 and 4; **anterior breathing tubes:** length 0.04mm, basal width 0.02mm; mounted on fleshy projections; apex with horseshoe-shaped arrangement of openings round anterior and lateral margins; anterior spiracles in *falleni* and *unicolor* tapering and crenulate, in *wankowiczii* tapering and smooth sided, flattened tips with openings round the margin; **abdomen:** first abdominal segment with setulose anterior margin, setae absent on anterior margins of segments 2-7; lateral lappets and the 4 pairs lappets on dorsum of abdominal segments 1-7 tapering with a single apical seta accompanying sensilla and basal projection smooth, lacking micro-setae (Fig. 5); lateral lappets longer in *falleni* and *unicolor* than *wankowiczii* (eg on abdominal segment 6: 0.06-7 v 0.03mm); segment 7 with lappet pairs 1 and 2 approximated, lappet pair 1 slightly anterior to second pair; vestiture differing between *wankowiczii* and *falleni* + *unicolor*; in the latter two species dorsum of abdominal segments smooth between coating of upright spicules; in the former species the dorsum is coriaceous with some spicules and a narrow transverse line of setae just anterior to the lappets on abdominal segments 1-7; apex of anal segment with 4 pairs of lappets; in *falleni* and *unicolor* lappets with a few setae and equidistant from each other, in *wankowiczii* lappets smooth without setae and middle two pairs of lappets approximated; **posterior breathing tube:** longer than basally broad in all three species; *falleni* and *unicolor*: length 0.18-0.23mm, smooth-sided and tapering with 4 oval spiracular openings on the rim of the lateral and posterior margins; *wankowiczii* length 0.33mm, parallel-sided and rugulose with a rounded tip and 4 oval spiracular openings on the rim of the lateral and posterior margins.

*Distinguishing species:* – *Agathomyia wankowiczii* differs from *falleni* and *unicolor* in several ways but is most easily distinguished by the round tipped, not tapering posterior breathing tubes and having the middle two pairs of lappets on the margin of the anal segment close together rather than equidistant. *Agathomyia falleni* and *unicolor* are very similar but can be distinguished by the anterior breathing tubes. In *falleni* the anterior breathing tubes are crenulated, almost stepped whereas in *unicolor* the crenulations are inconspicuous.

*Material examined:* – *falleni*, 4 larvae, England, Kent, Chislehurst, Pond Wood, in *Bjerkandera adusta* (Willd.) P. Karst (Coriolaceae), 7.x.1971, PJC (Peter J. Chandler); *unicolor*, 2 larvae, England, Berkshire, Windsor Great Park, Paddock Wood, in *B. adusta*, 31.viii.1980, PJC; *wankowiczii*, one larva, Belgium, Nassogne, ex galls on *Ganoderma applanatum* (Pers) Pat. (Ganodermataceae) on a beech stump, 9.ix.1990, PJC

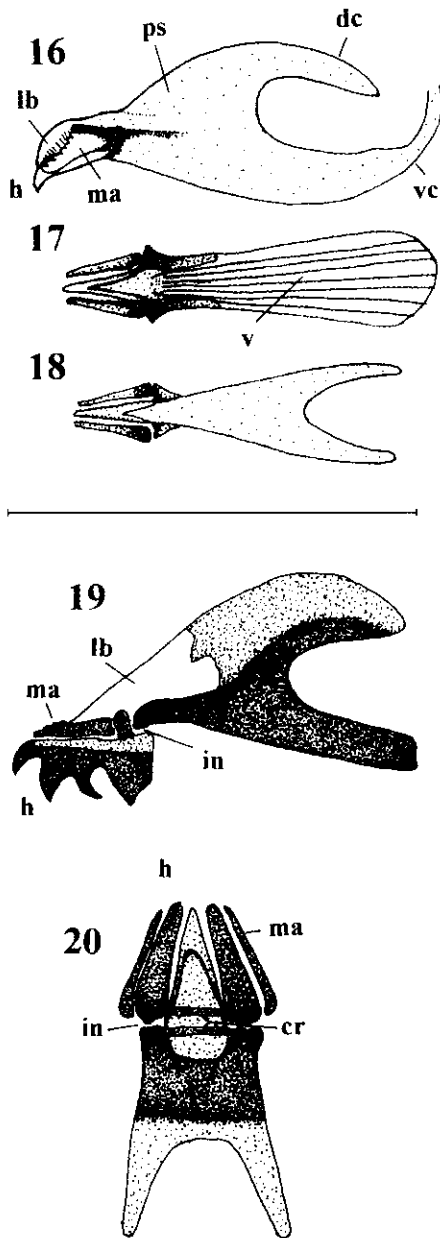
*Previous descriptions:* – *wankowiczii*, Weidner and Schremmer (1962), Chandler (2001); *falleni* and *unicolor*, Chandler (2001).

*Protoclythia modesta* (Zetterstedt),

*Protoclythia rufa* (Meigen)

*Overall appearance:* – Slightly dorso-ventrally flattened. Dorsum of mesothorax and metathorax with 3 pairs of lappets. Abdominal segment 7 with lappet pairs 1 and 2 approximated, lappet pair 1 slightly anterior to second pair. Anal segment with 3 pairs of lappets on the apical margin. Lappets on anal segment and lateral lappets coated in setae. Lappets on dorsum with smooth sides lacking setae but several setae accompanying sensilla at the apex. Dorsum of abdominal segments 1-7 behind lappets setolose, anterior part of dorsum coriaceous.

*Diagnosis:* – **Shape and dimensions:** slightly dorso-ventrally flattened (abdominal segment 6 about 3x as wide as body is high); length 5.8-6mm, width 2-3mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges prominent, extending from labium to either side of the maxillary palpi; ridge closest to the mouth with larger, more sclerotised serrations (Fig. 14); **head skeleton:** lightly sclerotised; apex of labium fused and consisting of three pairs of hooks which together in lateral view are shorter than width of dorsal cornu, upper 2 pairs separate from each other and smaller than the lower third pair which are larger and fused form-



Figures 16-20. Platyzepidae, head skeletons of third stage larvae, scale line = 0.7mm; 16-18, *Melanderomyia kahlī*, 16, lateral view, dc = dorsal cornu; h = labial hook; lb = labrum; ma = mandible; ps = pharyngeal sclerite; vc = ventral cornu; 17, ventral view, v = ventral pharyngeal ridges; 18, dorsal view; 19-20, *Callomyia amoena*, 19, lateral view, h = labial hook; in = interruption in labium; lb = labrum; ma = mandible; 20, ventral view, cr = rods connecting two halves of labium; h = labial hook; in = interruption in labium; ma = mandible.

ing a single hook; labium narrow in profile view and interrupted behind hooks; mandibles translucent and articulating with a thin rod extending from the pharyngeal sclerite; pharyngeal sclerite with dorsal bridge present; dorsal apodeme absent; ventral pharyngeal ridges present; dorsal and ventral cornua about equal in width but ventral cornu longer and both diverging from each other (Fig. 25); **thorax**: subcylindrical; dorsal plates on each thoracic segment slight; prothorax folded so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; prothorax narrow as shown by position of lappet pairs 2 and 3 being on the rounded lateral margins, not the dorsum; anterior and lateral margins of prothorax with backwardly directed triangular-shaped setae; dorsum of mesothorax and metathorax with rows of similar setae up to line of mid-segmental lappets, beyond this to rear of segments surface coriaceous; antero-ventral margin of each thoracic segment with transverse rows of micro-setae; prothorax with lappet pair 1 longer than lappet 1 of mesothorax and metathorax; dorsum of mesothorax and metathorax with 3 pairs of lappets; mesothorax with lappet 2 shorter than lappets 1 and 3; metathorax with lappets 1 and 2 shorter than lappet 3; **anterior breathing tubes**: 0.07mm long, smooth-sided slightly tapering towards flat apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen**: first abdominal segment with setulose anterior margin, setae absent on anterior margins of segments 2-7; dorsum of abdominal segments 1-7 with the 3 pairs of lappets tapering with a group of apical setae accompanying sensilla and basal projection smooth, lacking micro-setae; lateral lappets setulose (Fig. 6); abdominal segment 7 with lappet pairs 1 and 2 approximated, lappet pair 1 slightly anterior to second pair; dorsum of abdominal segments 2-7 coriaceous anterior to lappets and setulose posterior to them, these setae orientated towards the mid-line of the abdomen; anal segment with 3 pairs of lappets on the apical margin; second i.e. middle lappet approximated to first lappet at the base so that margin appears to have 3 approximated pairs of lappets, two at the base, one in the middle; lappets on anal segment and lateral lappets coated in setae; **posterior breathing tubes**: broader than long (0.12 x 0.09mm); tapering and slightly curved outwards with 2 pairs of openings on the outer lateral rim.

*Distinguishing species:* – *Protoctlythia modesta* appears to be more heavily setulose than *modesta* and has longer, thicker lappets. In particular, in *modesta* the lateral lappets on abdominal segment 7 are about as basally broad as the apex of the posterior breathing tubes and the mid-dorsal, third pair of lappets on the apex of the anal segment are about as long as they are separated from the second pair at the base of the segment. In *modesta* the lateral lappets on the 7<sup>th</sup> abdominal segment are thinner than the apex of the posterior breathing tube is wide and the 3<sup>rd</sup> pair of lappets on the anal segment are shorter than the distance separating them from the 2<sup>nd</sup> pair.

*Material examined:* – *Protoctlythia modesta*, 5 larvae, England, Cambridgeshire, Chippenham Fen, in *Armillaria mellea* (Wahl.) Kummer (Tricholomataceae) 20.x.1990, PJC; *Protoctlythia rufa*, 4 larvae, Hants, Wyck Place, in *A. mellea*, 12.x.1989, PJC.

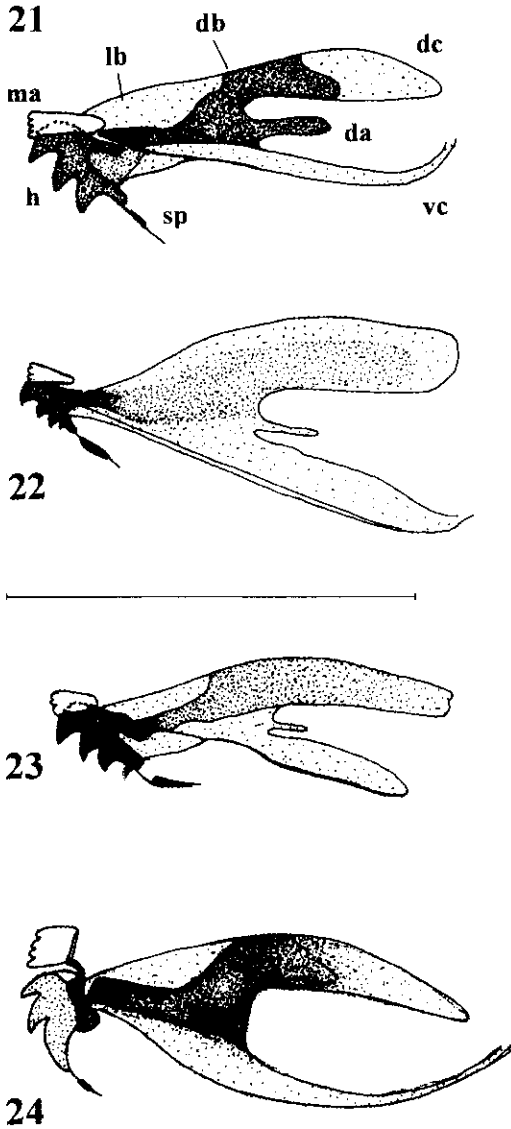
*Previous descriptions:* – Chandler (2001).

### *Calotarsa insignis* (Aldrich)

*Overall appearance:* – Slightly dorso-ventrally flattened. Dorsum of mesothorax and metathorax with 3 pairs of lappets. Abdominal segment 7 with lappet pairs 1 and 2 approximated, lappet pair 1 slightly anterior to second pair. Anal segment with 3 pairs of lappets on the apical margin. Lappets on anal segment and lateral lappets coated in setae. Lappets on dorsum with a few setae on the sides and 2-4 setae accompanying sensilla at the apex. Dorsum of abdominal segments 1-7 behind lappets setulose, anterior part of dorsum coriaceous. Very similar to *Protoctlythia* from which it differs in the development of the setae on the rear of the abdominal segments. In *Calotarsa* these setae are short and indistinct (up to 0.03mm long), whereas in *Protoctlythia* they are much longer and conspicuous (0.07mm long).

*Diagnosis:* – **Shape and dimensions:** slightly dorso-ventrally flattened (abdominal segment 6 about 3x as wide as body is high); length 4-6mm, width 2-3mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges present from labium to either side of the maxillary palpi; those closest to the mouth longer and serrated margins larger and more sclerotised; apices of mandibles and labrum projecting from the mouth (Fig. 12); **head skeleton:** lightly sclerotised; apex of labium fused and consisting of three pairs of hooks which together

in lateral view are shorter than width of dorsal cornu, upper 2 pairs separate from each other and smaller than the lower third pair which are larger and fused forming a single hook; labium narrow in profile view and interrupted behind hooks; mandibles translucent and articulating with a short projection from the labium; pharyngeal sclerite with dorsal bridge; dorsal apodeme absent; ventral pharyngeal ridges present; dorsal cornu wider and shorter than ventral cornu and both diverging from each other (Fig. 26); **thorax:** subcylindrical; dorsal plates on each thoracic segment slight; prothorax folded so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; prothorax narrow as shown by position of lappet pairs 2 and 3 being on the rounded lateral margins, not the dorsum; entire anterior margin of prothorax with 8+ transverse rows of backwardly directed setae; antero-dorsal margin of mesothorax with indistinct rows of setae up to line of mid-segmental sensilla on dorsum and setae absent on ventral margin; setae more evenly distributed on the metathorax; prothorax with lappet pair 1 longer than lappet 1 of mesothorax and metathorax; dorsum of mesothorax and metathorax with 3 pairs of lappets; mesothorax with lappet 2 shorter than lappets 1 and 3; metathorax with lappets 1 and 2 shorter than lappet 3; **anterior breathing tubes:** 0.07mm long, smooth-sided slightly tapering towards flat apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen:** first abdominal segment with setulose anterior margin, setae absent on anterior margins of segments 2-7; dorsum of abdominal segments 1-7 with 3 pairs of lappets tapering with a few setae on the margins and 2-4 apical setae accompanying sensilla; lateral lappets setulose; abdominal segment 7 with lappet pairs 1 and 2 approximated, lappet pair 1 slightly anterior to second pair; dorsum of abdominal segments 2-7 coriaceous anterior to lappets and setulose posterior to them, these setae orientated towards the mid-line of the abdomen; anal segment with 3 pairs of lappets on the apical margin; second i.e. middle lappet approximated to first lappet at the base so that margin appears to have 3 approximated pairs of lappets, two at the base, one in the middle; lappets on anal segment and lateral lappets coated in setae; **posterior breathing tubes:** broader than long (0.15 x 0.12mm); tapering and slightly curved outwards with 2 pairs of openings on the outer lateral rim.



Figures 21-24. Platypezidae, head skeletons of third stage larvae, scale line = 0.7mm; 21, *Bolopus furcatus*, lateral view, da = dorsal apodeme; db = location of dorsal bridge; dc = dorsal cornu; h = labial hook; lb = labrum; ma = mandible; sp = sclerotised plate; vc = ventral cornu; 22, *Seri obscuripennis*; 23, *Polyporivora ornata*; 24, *Agathomyia unicolor*.

*Material examined*: – 3 larvae, USA, det Kessel, ex *A. mellea*.

*Previous descriptions*: – Kessel et al. (1973).

### *Seri obscuripennis* (Oldenberg)

*Overall appearance*: – Slightly dorso-ventrally flattened. Dorsum of mesothorax and metathorax with 3 pairs of reduced and inconspicuous lappets. Abdominal segment 7 with lappet pairs equidistant. Anal segment with 3 pairs of lappets but lappet pairs 1 and 2 reduced, mid-dorsal pair approximated and on broader than long projections. Lappets on abdominal segments reduced and inconspicuous, tapering without additional setae. Dorsum of abdominal segments smooth with only an incomplete and inconspicuous medial transverse patch of spicules.

*Diagnosis*: – **Shape and dimensions**: slightly dorso-ventrally flattened (abdominal segment 6 about 3x as wide as body is high); length 4.8mm, width 2.6mm; truncate posteriorly, tapering anteriorly; **head**: oral ridges forming a narrow inconspicuous band from labium to either side of the maxillary palpi; below the mouth is a square-shaped sclerotised plate with lateral extensions reaching the oral ridges (Fig. 10); **head skeleton**: lightly sclerotised; apex of labium fused and consisting of four separate pairs of hooks which together in lateral view are about as wide as dorsal cornu, upper pair largest; labium interrupted and apparently short and not much sclerotised behind point of interruption; mandibles translucent and not articulating with any obvious projection; pharyngeal sclerite with lightly sclerotised dorsal bridge; dorsal apodeme present; ventral pharyngeal ridges apparently not present and ventral margin of pharyngeal sclerite sclerotised; dorsal cornu wider than but about as long as ventral cornu and slightly diverging (Fig. 22); **thorax**: subcylindrical; dorsal plates on prothorax and mesothorax; prothorax folded ventrally so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; anterior fold of prothorax coated with transverse rows of backwardly directed setae; antero-dorsal margin of mesothorax and metathorax with a narrow band of setae not reaching line of mid-segmental lappets on dorsum and setae absent on ventral margin; dorsum of mesothorax and metathorax with 3 pairs of lappets; **anterior breathing tubes**: 0.12mm long, smooth-sided, slightly tapering towards flat apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen**: antero-dorsal margin of first abdominal segment with a medial patch of setae; dorsum of abdominal

segments 2-7 smooth on antero-dorsal margin, with a transverse, medial patch of inconspicuous spicules; the 3 pairs of dorsal lappets reduced and inconspicuous, tapering without additional setae; lappets on abdominal segment 7 equidistant; anal segment with 3 pairs of lappets but first two pairs reduced, mid-dorsal pair approximated and on slightly broader than long, triangular-shaped projections (0.07 x 0.06mm); **posterior breathing tubes:** broader than long (0.15 x 0.07mm); tapering and flat-tipped with 4-5 oval-shaped, radially arranged spiracular openings.

*Material examined:* – one larva, two puparia, England, Surrey, Horsley, Sheep Leas, from an unidentified fungus, 26.ix.1971, A.E. Stubbs.

*Previous descriptions:* – Chandler (2001).

### *Bolopus furcatus* (Fallén)

*Overall appearance:* – Larva subcylindrical. Dorsum of mesothorax and metathorax with 3 pairs of conspicuous lappets. Abdominal segment 7 with lappet pairs equidistant. Anal segment with 3 pairs of lappets but lappet pairs 1 and 2 reduced, mid-dorsal pair approximated and on longer than broad projections. Lappets on abdominal segments long and conspicuous, tapering with one apical seta. Dorsum of abdominal segments smooth except for anterior margin which is coated in spicules.

*Diagnosis:* – **Shape and dimensions:** larva subcylindrical (abdominal segment 6 about 2x as wide as body is high); length 4.5-6mm, width 2.5mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges present from labium to either side of the maxillary palpi; oral ridges longest in the middle and not sclerotised; below the mouth is a broad U-shaped sclerotised plate and on each side, extending from the posterior end of the oral ridges are a pair of elongate sclerotised plates (Fig. 11); **head skeleton:** lightly sclerotised; apex of labium fused with three separate pairs of hooks which together in lateral view are wider than dorsal cornu, upper pair largest and behind them is a short sclerotised region which articulates with the interrupted labium and the mandibles; labium behind interruption heavily sclerotised and area of sclerotization continues on to the pharyngeal sclerite; pharyngeal sclerite with lightly sclerotised dorsal bridge; dorsal apodeme present; ventral pharyngeal ridges apparently not present and ven-

tral margin of pharyngeal sclerite sclerotised; dorsal cornu wider and about as long as ventral cornu and not diverging (Fig. 21); **thorax:** subcylindrical; dorsal plates on prothorax and mesothorax (dp, Fig. 4); prothorax folded ventrally so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; anterior fold of prothorax coated with transverse rows of backwardly directed triangular-shaped spicules (sp, Fig. 4); antero-dorsal margin of mesothorax and metathorax with narrow band of up to 3 rows of spicules not reaching line of mid-segmental lappets on dorsum and setae absent on ventral margin; mesothorax with lappet 1 on longer projections than lappets 2 and 3; metathorax with lappets 1-3 on about equally long projections; **anterior breathing tubes:** 0.04mm long, smooth-sided, slightly tapering towards flat apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen:** dorsum of abdominal segments smooth except for a transverse band of spicules on the anterior margin of segments 1-7; the 3 pairs of dorsal lappets long and conspicuous with a single apical seta; lappets equidistant on abdominal segment 7; anal segment with 3 pairs of lappets but first two pairs reduced, mid-dorsal pair approximated and on longer than broad, triangular-shaped, lightly sclerotised projections (0.15 x 0.06mm); **posterior breathing tubes:** as broad as long (0.07 x 0.07mm); tapering and flat-tipped with 4-5 oval-shaped, radially arranged spiracular openings.

*Material examined:* – 5 larvae England, Sussex, Rogate, in *Polyporus squamosus* Huds. (Polyporaceae), vi.1979, PJC; 15+ larvae England, Lancashire, Whalley, ex *P. squamosus*, 14.vii.1963, A. Brindle, NHM.

*Previous descriptions:* – Brindle (1961); Kessel et al. (1973) based their description on Brindle (1961); Chandler (2001).

### *Polyporivora ornata* (Meigen),

### *Polyporivora picta* (Meigen)

*Overall appearance:* – Larva subcylindrical. Dorsum of mesothorax and metathorax with 3 pairs of conspicuous lappets. Abdominal segment 7 with lappet pairs equidistant. Anal segment with 3 pairs of lappets but lappet pairs 1 and 2 reduced and mid-dorsal pair fused basally, forming a Y-shape. Dorsum of abdominal segments smooth except for anterior and posterior margins which are coated in spicules.

**Diagnosis:** – **Shape and dimensions:** larva subcylindrical (abdominal segment 6 about 1.5x as wide as body is high); length 4.5mm, width 2.5mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges present from labium to either side of the maxillary palpi; below the mouth is a broad square-shaped sclerotised plate with arms reaching the oral ridges; **head skeleton:** lightly sclerotised; apex of labium fused with four separate pairs of hooks which together in lateral view are wider than dorsal cornu, upper pair largest and behind them is a short sclerotised region which articulates with the interrupted labium and the mandibles; labium behind interruption heavily sclerotised at apex and area of less heavy sclerotization continues on to the pharyngeal sclerite; pharyngeal sclerite with lightly sclerotised dorsal bridge; dorsal apodeme present; ventral pharyngeal ridges apparently not present and ventral margin of pharyngeal sclerite sclerotised; dorsal cornu wider and about as long as ventral cornu and not diverging (Fig. 23); **thorax:** subcylindrical; dorsal plates weak on prothorax and mesothorax; prothorax folded ventrally so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; anterior fold of prothorax coated with transverse rows of backwardly directed triangular-shaped spicules; antero-dorsal margin of mesothorax and metathorax with narrow band of spicules not reaching line of mid-segmental sensilla on dorsum and setae absent on ventral margin; all thoracic segments with lappets 1-3 about equally long; anterior breathing tubes 0.38 mm long, smooth-sided slightly tapering towards inclined apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen:** dorsum of abdominal segments 1-7 smooth medially and with transverse bands of setae and spicules on the anterior and posterior margins; spicules longer in *picta* than *ornata* (0.03 v 0.01mm); the 3 pairs of dorsal lappets with a single apical seta; lappets long in *picta* (0.09mm), short and inconspicuous in *ornata* (0.03mm); lappets equidistant on abdominal segment 7; anal segment with 3 pairs of lappets but first two pairs reduced, mid-dorsal pair lightly sclerotised, Y-shaped (fused basally, divergent apically); **posterior breathing tubes:** set in a pocket of the integument which encloses the posterior margin; about as broad as long (0.1 x 0.09mm); tapering and flat-tipped with 4-5 oval-shaped, spiracular openings arranged on the posterior margin.

**Distinguishing species:** – lappets on the dorsum of the abdominal segments are long and conspicuous in *picta* but are short and inconspicuous in *ornata* (0.09 v 0.03mm).

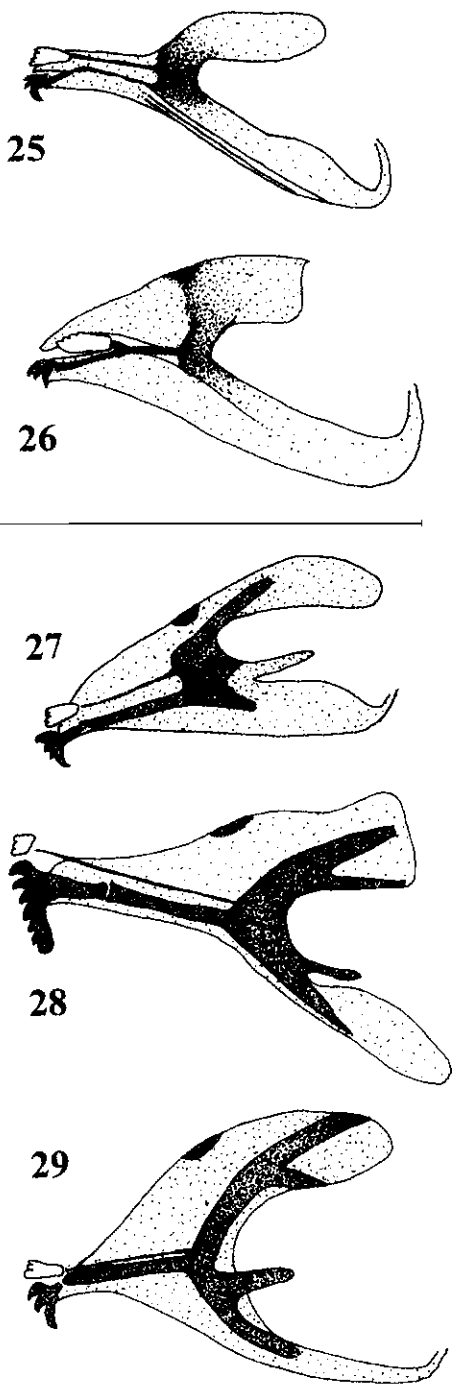
**Material examined:** – *ornata*, 2 puparia, England, Kent, Hosey Common, ex *Trametes versicolor* (L.) Pilát (Coriolaceae) England, Surrey, Gracious Pond, cocoon collected 18.iii.1978, PJC; *picta*, one larva, England, Surrey, Chobham Common, Gracious Pond, in *T. versicolor*, 28.x.1971, PJC.

**Previous descriptions:** – De Meijere (1911); Hennig (1952) (*ornata* head skeleton); Krivosheina and Mamaev (1967); Kessel et al. (1973); Santini and Raspi (1994); Chandler (2001).

***Platypeza consobrina* (Zetterstedt), *Platypeza* sp.**

**Overall appearance:** – Larva slightly dorso-ventrally flattened. Dorsum of mesothorax and metathorax with 2 and 3 pairs of conspicuous lappets respectively. Abdominal segment 7 with lappet pairs equidistant. Anal segment with 3 pairs of well developed approximately equidistant lappets. Lappets on all segments crenulated and setulose (Fig. 7), except setae absent on the mid-dorsal lappets of the prothorax. Dorsum of abdominal segments 2-7 with spicules from base to lappets and a band of setae behind lappets to rear of segment, on the lateral margins these setae directed upwards to the mid-line of the segment.

**Diagnosis:** – **Shape and dimensions:** larva slightly dorso-ventrally flattened (abdominal segment 6 about 3x as wide as body is high); length 5-6mm, width 2.5-3mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges prominent, extending from labium to either side of the maxillary palpi; those closest to the mouth longer and serrated margins larger and more sclerotised (Fig. 13); **head skeleton:** with regions of light and heavy sclerotisation; apex of labium fused and consisting of four pairs of hooks which are together in lateral view, about as long as dorsal cornu, upper 3 pairs separate from each other and smaller than the lower fourth pair which are larger and fused forming a single downwardly projecting hook; labium narrow and interrupted behind hooks; mandibles translucent and articulating with a thin rod extending from the pharyngeal sclerite; pharyngeal sclerite with dorsal bridge present; dorsal apodeme present; ventral pharyngeal ridges weakly indicated; dorsal and ventral cornua about equal in width and length and not diverging (Fig. 27); **thorax:**



Figures 25-29. Platypezidae, head skeletons of third stage larvae, scale line = 0.7mm; 25, *Protoclythia modesta*, lateral view, 26, *Calotarsa insignis*; 27, *Platypeza* sp.; 28, *Paraplatypeza atra*; 29, *Lindneromyia dorsalis*.

dorso-ventrally flattened; dorsal plates on each thoracic segment but that on prothorax smooth without spicules; prothorax folded so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; prothorax narrow as shown by position of lappet 2 being on the rounded lateral margins, not the dorsum; anterior and lateral margins of prothorax with transverse rows of backwardly directed setae; dorsum of mesothorax and metathorax with rows of setae up to line of mid-segmental lappets, beyond this to rear of segments setae longer; ventral surface of prothorax and mesothorax mostly bare of setae; setae evenly distributed on the ventral surface of the metathorax; prothorax with lappet 1 crenulated but without a coating of setae, this lappet longer than those supporting lappet 1 on mesothorax and metathorax; mesothorax with lappets 1 and 2 longer than the rest; metathorax with lappets 1 and 2 shorter than lappet 3; anterior breathing tubes 0.11mm long, smooth-sided slightly tapering towards flattened apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen:** posterior margins of abdominal segments 1-7 deeply folded ventrally; dorsum of abdominal segments 2-7 with spicules from base to lappets and a band of setae behind lappets to rear of segment, on the lateral margins these setae directed upwards to the mid-line of the segment; abdominal segment 1 similar but bands of setae present on the posterior and anterior margins; 3 pairs of dorsal lappets on each segment; lappets equidistant on abdominal segment 7; anal segment with 3 pairs of equidistant lappets, middle pair shortest; **posterior breathing tubes:** set in a slight pocket of the integument which encloses the posterior margin and covered by the posterior fold of the 7<sup>th</sup> abdominal segment; slightly broader than long (0.1 x 0.07mm); tapering and flat-tipped with 4-6 oval-shaped, spiracular openings arranged round the lateral and posterior margins.

*Distinguishing species:* – the larvae of both species are very similar but that of *consobrina* appears to have longer, denser vestiture.

*Material examined:* – *consobrina*, 2 larvae, England, Herts, Ashridge; 6 puparia, England, Kent, Knole Park, 1.x.1967, ex *A. mellea*, PJC; *Platypeza* sp., 2 larvae, Scotland, Sutherland, Migdale Wood ex *A. mellea*, 18.ix.1989, PJC.

*Previous descriptions:* – *consobrina*, Kessel et al. (1973); Chandler (2001).

*Paraplatypeza atra* (Meigen)

**Overall appearance:** – Larva slightly dorso-ventrally flattened. Mid-dorsal mesothoracic lappets same length as mid-dorsal prothoracic lappets. Dorsum of mesothorax and metathorax with 2 and 3 pairs of conspicuous lappets respectively. Abdominal segment 7 with lappet pairs equidistant. Anal segment with 3 pairs of well developed approximately equidistant lappets. Lappets on all segments crenulated and setulose, except setae absent on the mid-dorsal lappets of the prothorax. Dorsum of abdominal segments 2-7 entirely coated with spicules.

**Diagnosis:** – **Shape and dimensions:** larva slightly dorso-ventrally flattened (abdominal segment 6 about 3x as wide as body is high); length 4-5mm, width 2-2.5mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges forming a narrow band extending each side of the labium and then broadening to coat the lobe bearing the maxillary palpi (Fig. 15); **head skeleton:** with regions of light and heavy sclerotisation; apex of labium fused and consisting of six pairs of hooks which together in lateral view are about as long as width of dorsal cornu, hooks orientated in the same direction, no downwardly projecting lower hook; labium narrow and interrupted behind hooks; mandibles translucent and articulating with a thin rod extending from the pharyngeal sclerite; pharyngeal sclerite with dorsal bridge present; dorsal apodeme present; ventral pharyngeal ridges weakly indicated; dorsal cornu wider and shorter than ventral cornu and diverging (Fig. 28); **thorax:** dorso-ventrally flattened; dorsal plates on each thoracic segment absent or slight; prothorax folded so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; prothorax narrow as shown by position of lappet 2 being on the lateral margin and about half as wide as mesothorax; mesothorax elongate and also narrow; mid-dorsal mesothoracic lappets same length as mid-dorsal prothoracic lappets; anterior and lateral margins of prothorax with backwardly directed setae; dorsum of mesothorax and metathorax with rows of setae up to line of lappets, beyond this to rear of segments surface setae more dispersed; antero-ventral margin of each thoracic segment with transverse rows of micro-setae; metathorax with lappets 1 and 2 shorter than lappet 3; **anterior breathing tubes:** 0.07mm long, rugulose-sided, slightly tapering to-

wards flattened apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen:** posterior margins of abdominal segments 1-7 folded ventrally; abdominal segments 2-7 with spicules entirely coating the dorsum of each segment; abdominal segment 1 similar but narrow bands of setae present on the posterior and anterior margins; 3 pairs of lappets on each segment; lappets equidistant on abdominal segment 7; anal segment with 3 pairs of equidistant lappets, middle pair shortest; **posterior breathing tubes:** broader than long (0.12 x 0.07mm); tapering and flat-tipped with 4-6 oval-shaped, spiracular openings arranged round the lateral and posterior margins.

**Material examined:** – 2 larvae, 3 puparia, England, Berkshire, Wokefield Common, 1.x.1972, ex *Pluteus cervinus* (Schaeff.) Kummer (Pluteaceae), PJC.

**Previous descriptions:** – Kessel et al. (1973); Chandler (2001).

*Lindneromyia dorsalis* Meigen

**Overall appearance:** – Puparium dorso-ventrally flattened. Mid-dorsal mesothoracic lappets longer than mid-dorsal prothoracic lappets. Dorsum of mesothorax and metathorax with 2 and 3 pairs of conspicuous lappets respectively. Abdominal segment 7 with lappet pairs equidistant. Anal segment with 3 pairs of well developed approximately equidistant lappets. Abdominal segments 1-7 with second pair of lappets reduced and inconspicuous, about as broad as high. Remaining lappets crenulated without or only a few basal setae. Dorsum of abdominal segments 2-7 entirely coated with spicules.

**Diagnosis:** – **Shape and dimensions:** puparium, dorso-ventrally flattened; length 5-6mm, width 3-4mm; truncate posteriorly, tapering anteriorly; **head:** oral ridges forming a narrow band extending each side of the labium and then broadening to coat the lobe bearing the maxillary palpi; **head skeleton:** with regions of light and heavy sclerotisation; apex of labium fused and consisting of three pairs of hooks which together in lateral view are about as long as dorsal cornu, upper 2 pairs separate from each other and smaller than the lower third pair which are larger and fused forming a single downwardly projecting hook; labium narrow and interrupted behind hooks; mandibles translucent and articulating with a thin rod extend-



ing from the pharyngeal sclerite; pharyngeal sclerite with dorsal bridge present; dorsal apodeme present; ventral pharyngeal ridges weakly indicated; dorsal cornu wider and shorter than ventral cornu and not diverging (Fig. 29); **thorax**: dorso-ventrally flattened; dorsal plates on each thoracic segment absent or slight; prothorax folded so that the dorsal rather than the ventral margin projects further forward and mouth projects ventrally; prothorax narrow as shown by position of lappet 2 being on the rounded lateral margins and about half as wide as mesothorax; mid-dorsal mesothoracic lappets longer than mid-dorsal prothoracic lappets; dorsum of mesothorax and metathorax with 2 and 3 pairs of conspicuous lappets respectively; anterior and lateral margins of prothorax with backwardly directed setae; dorsum of mesothorax and metathorax with rows of setae up to lappets, beyond this to rear of segments surface setae more dispersed; antero-ventral margin of each thoracic segment with transverse rows of micro-setae; mesothorax with lappets 1 and 2 on long projections; metathorax with lappets 1 and 3 on long projections, lappet 2 reduced; **anterior breathing tubes**: 0.07mm long, rugulose-sided, slightly tapering towards flattened apex; apex with horseshoe-shaped arrangement of openings round anterior and lateral margin; **abdomen**: posterior margins of abdominal segments 1-7 folded ventrally; abdominal segments 2-7 with spicules entirely coating the dorsum of each segment and lappet 2 reduced, about as broad as high; abdominal segment 1 similar but narrow bands of setae present on the posterior and anterior margins; 3 pairs of dorsal lappets per segment; lappets equidistant on abdominal segment 7; anal segment with 3 pairs of equidistant lappets, middle pair shortest; **posterior breathing tubes**: broader than long (0.12 x 0.07mm); tapering and flat-tipped with 4-6 oval-shaped, spiracular openings arranged round the lateral and posterior margins.

*Material examined*: - 3 puparia, England, Somerset, found in the unnatural situation of a towel used to dry a dog, no further details, NHM (Natural History Museum, London); 5 puparia, no further data, PJC.

*Previous descriptions*: - Dufour (1840); Bergengstamm (1870); Krivosheina and Mamaev (1967); Chandler (2001).

### Cladistic analysis

Based on a set of 43 characters (Appendices 1 and 2) the analysis revealed 12 trees summarised in a strict consensus tree (Fig. 30). The stability of the characters in the character matrix are shown by a bootstrap analysis which shows obtained group frequencies in 50% and above of 100 replicates (Fig. 31). The results show that *Melanderomyia* was basal within the taxa tested. All genera in which more than one species was included were supported as monophyletic. Groups of genera revealed by the analysis include: *Seri* + *Bolopus* + *Polyporivora* and *Platypeza* + *Paraplatypeza* + *Lindneromyia*.

### Discussion

One of the outstanding morphological changes across the Diptera is the reduction of the larval head and the development of the cephalopharyngeal (=head) skeleton (Teskey 1981). Such a set of changes are particularly clear when comparing basal with derived taxa such as many Nematocera versus Schizophora. However tracing the homology of individual characters across these changes is problematic because of the apparent lack of intermediates (Teskey 1981). A search for intermediates might be fruitful within Platypezidae given the apparent basal position of the family within the Muscomorpha (McAlpine 1989; Wiegmann et al. 1993; Cumming et al. 1995).

According to Teskey (1981) the muscomorphan larval head is reduced to an outer, membranous cephalic or pseudocephalic segment bearing dorsally, antennae and maxillary papillae and ventrally, normally bearing oral ridges which radiate from the mouth and within which are additional sensory papillae. In shape, the head is bilobed anteriorly with an antenna and a maxillary papilla approximated at the apex of each lobe. It is separated from the thorax by a fold but this fold is only clearly visible on the ventral aspect. The head skeleton consists of three main parts which usually articulate with each other, from posterior to anterior: a U-shaped pharyngeal sclerite; a H-shaped intermediate sclerite and a pair of hook-like mandibles (Teskey 1981).

This description may apply to many Schizophora but it is inaccurate for Platypezidae. In Platypezidae the cephalic segment is relatively large, being more than just sensory organs and the integument connecting them. It is membranous

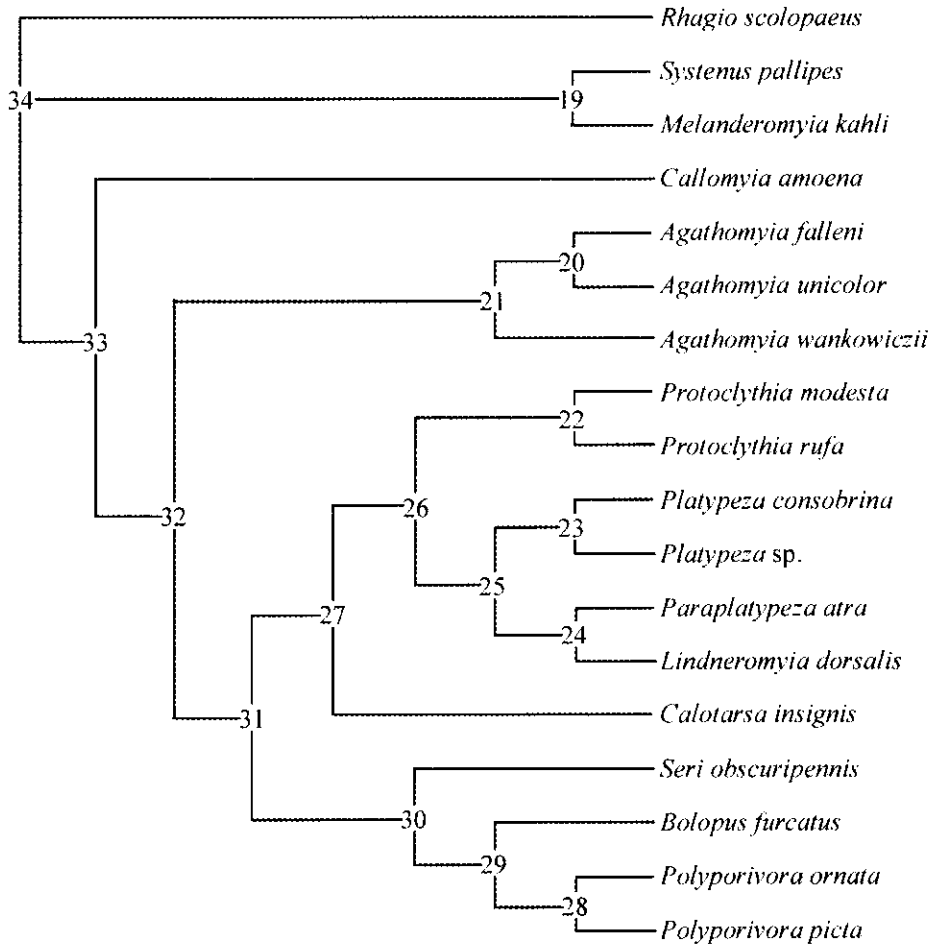


Figure 30. The strict consensus of 12 trees revealed by parsimony analysis using PAUP version 4.0 (details in text) of platypezid larvae and puparia based on a set of 43 characters (Appendix 1) scored on a Brachyceran outgroup (Appendix 2) (length = 102; consistency index (CI) = 0.61; retention index (RI) = 0.79). Apomorphies supporting each numbered node point are listed in Appendix 3.

and distinct, being delimited posteriorly by an impressed fold marking an external boundary between it and the prothorax round its entire circumference. Anteriorly the head is not bi-lobed. On each dorso-lateral margin of the head, separated from each other, is a maxillary papilla and behind it an antenna. Between these margins is a clearly defined, dorsal atrium which infolds anteriorly to connect with the labrum. The apex of the labrum is tapered, translucent and can protrude from the mouth. Ventrally the head connects with a hooked labium which also protrudes from the mouth. The opening to the mouth is between the

labium and the labrum on either side of which lie the mandibles. The mandibles barely protrude from the mouth and are usually translucent and very inconspicuous. The intermediate sclerite is not well defined and is not separated from the pharyngeal sclerite. Oral ridges do not radiate from the mouth but if present, lie on the lateral and ventral margins of the head outside of the mouth. Within the platypezid taxa studied, oral ridges vary in size, shape and distribution (Figs. 10-15).

In Platypezidae, the relatively large cephalic segment bearing a distinct atrium with antennae and maxillary papillae not approximated and not

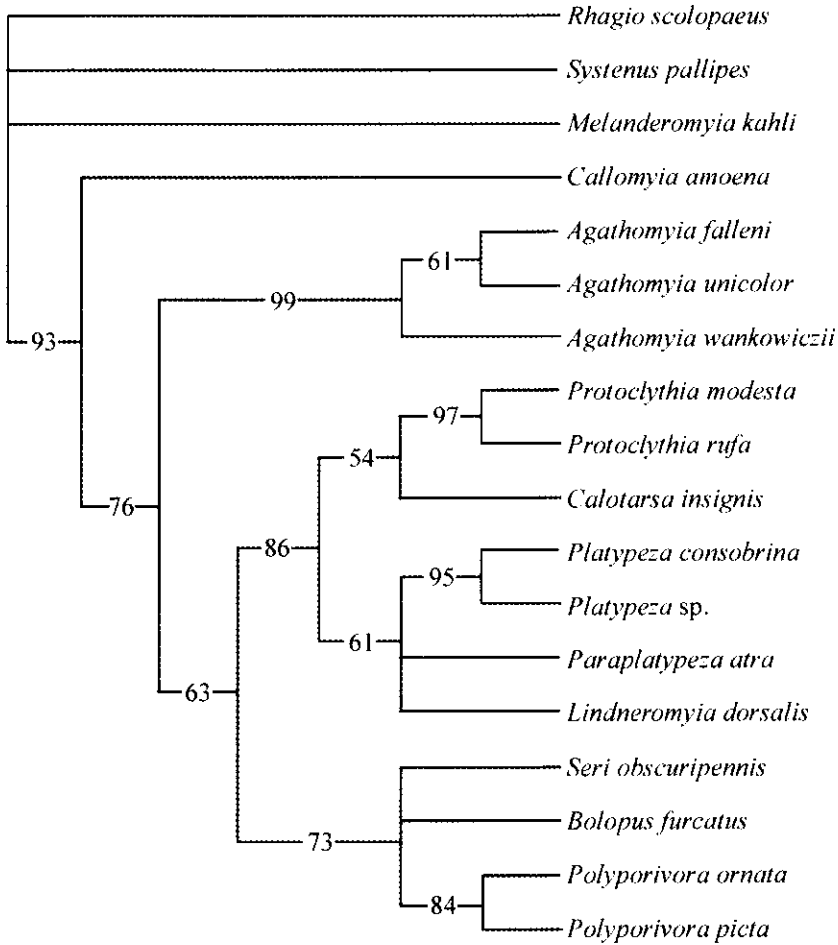


Figure 31. Bootstrap 50% majority-rule consensus tree generated from 100 replicate searches. Numbers refer to branches appearing in more than 50% of bootstrap replicates.

on apical lobes, oral ridges separate from the mouth, pointed labrum above the mouth, hooked labium below it, inconspicuous mandibles either side of the mouth and poorly defined intermediate sclerite may represent intermediate states in the development from a brachyceran ancestor of the schizophoran head as described by Teskey (1981). For example, the platypezid atrium is easily derived if the fleshy lobes bearing the maxillary palpi characteristic of Brachyceran larvae like *Rhagio scolopaceus*, became fused along their inner lateral margins. It is then a small step for the characteristic schizophoran head to be produced in

which the atrium reduces and narrows. This brings the antennae and maxillary palpi into approximated positions and the oral lobes more closely associated with the mouth. The main changes to the labrum and labium from a brachyceran state like that of *Systemenus pallipes* to the one found in platypezids, is a simple anterior extension in the case of the labrum and the acquisition of apical hooks in the labium. The change from a brachyceran mandibular state of 3-4 separate sclerites (Sinclair 1992) to one characteristic of platypezids in which it is a single, broad, flat structure with a serrated apical margin is also simply envisaged as a fusion

product. From the platypezid labrum, labium and mandible to those characteristic of Schizophora, the main changes appear to be a reduction of the labrum and labium and their replacement by enlarged mandibles articulating with a well developed intermediate sclerite. Although our studies of larvae in related aschizan and schizophoran families are incomplete, additional intermediate states appear to be present in Lonchopteridae and Phoridae.

Unlike many Schizophora where the main food gathering structures are a pair of hook-like mandibles which protrude from the mouth, in platypezids food gathering is probably done by the tapered labrum and hooked labium with the mandibles playing a relatively minor role, possibly little more than guiding food into the mouth.

A basal position within Platypezidae for Melanderomyiinae + Microsaniinae was found by Chandler (2001) based on an analysis of mostly adult but also including some early stage characters. We found a basal position for *Melanderomyia* on larval characters alone (Fig. 30). On adult characters Platypezidae is a well-supported monophyletic taxon which suggests that the common ancestor shared with the rest of the Aschiza is likely to be more similar to Melanderomyiinae + Microsaniinae than any of the other platypezid taxa studied here. It is unfortunate that the only larva known within Melanderomyiinae + Microsaniinae is that of *M. kahli* and also, that no larva is known within the possibly even more basal taxon, Opetiidae (Chandler 2001). The larva of *M. kahli* has numerous features that characterise it from other species studied here and some of these appear highly derived. This indicates that it may be derived within Melanderomyiinae + Microsaniinae. However without other melanderomyine, microsaniine and opetiid larvae to study, the status of these features cannot be further assessed. These features include: lappets on most segments undeveloped and not longer than the surrounding vestiture; very broad atrium; anterior and posterior breathing tubes mounted on fleshy lobes with, on the anal segment, the dorsal margin of these lobes bearing a sensillum; dorsum of abdominal segments 1-7 each with a pair of equally wide bands of vestiture; apex of the anal segment with 3 pairs of equidistant lappets, middle pair inconspicuous and short, not longer than the surrounding vestiture; head skeleton barely sclerotised and lacking many features seen in other platypezids such as dorsal

bridge, apodemes, interrupted labium and more than one hook at the apex of the labium and relatively large and sub-rectangular mandibles; head apparently lacking oral ridges.

The apparent absence of oral ridges was determined using light microscopy and even when the head was stained no oral ridges were revealed. In other platypezid larvae oral ridges are clearly visible using light microscopy. If they are present in *M. kahli* they must be very small and little developed. Electron microscopy would probably settle whether they are present or not. Even if present, their lack of size in relation to those of other platypezids is a notable difference.

Sinclair (1992) suggests that the presence of a tapered labrum in the final stage larva of *M. kahli* lends support to a basal position of Platypezidae over the Lonchopteridae on the grounds of the assertion by Hennig (1973) that a developed labrum is a feature only of first stage cyclorhaphan larvae. A tapered labrum is, however, present in final stage lonchopterid larvae and was figured but unrecognised as such by de Meijere (1900) (figure reproduced in Ferrar 1987). Furthermore, we found that a relatively well developed, tapered labrum is a characteristic feature of all platypezid larvae we studied.

Head skeleton morphology is diverse in platypezids (Figs. 16-29). Some of these differences may be explained by the type of fungus exploited for food. Larvae of *Agathomyia*, *Bolopus*, *Polyporivora* and *Seri* feed within polypore fungi. A broad, sclerotised labium supporting large hooks characterises these larvae. This is presumably an adaptation for scraping the relatively firm tissues of their fungal food. Also, these taxa possess sclerotised plates on the head just below the mouth which may reduce wear and tear. The pharyngeal sclerites are relatively narrow and elongate which may enhance the amount of muscle able to be attached. In *Bolopus*, *Polyporivora* and *Seri* a further point of muscle attachment is provided by a dorsal apodeme. However this feature is also present in platypezid larvae feeding on other types of fungi. Body shape also appears to be involved. The larvae of these genera tend to be subcylindrical or slightly flattened with lappets and vestiture short or absent giving them a smooth, tube-like appearance. Such a shape may facilitate tunnelling through polypore fungi.

In *Calotarsa*, *Platypeza*, *Paraplatypeza*, *Protoclythia* that feed in lignicolous gill fungi and

*Lindneromyia* which feeds in terrestrial gill fungi, there are also shared states in the head skeleton. In contrast to the polypore feeders, the labial hooks are smaller (uniquely more numerous in *Paraplatypeza*), the labium is longer and narrower, the pharyngeal sclerite is broader and the ventral cornua often more elongate than the dorsal cornua and a dorsal bridge is present. These features suggest adaptation to feeding on softer fungal tissues. These larvae are often dorso-ventrally flattened which shape enables movement between the gills of their host fungi.

The tree (Fig. 30) suggests close relationships between such groups of taxa. This could either be due to diversification following colonisation of these different types of fungi or it may be due to more than one group colonising such fungi with subsequent convergence. Adult characters confirm these groupings of genera (Chandler 2001) which suggests the former explanation is more likely. Fig. 30 is, however, of limited value in interpreting relationships due to the small number of included taxa. The characters and their scores used to construct it (Appendices 1 and 2), nonetheless, provide a foundation on which to build. A particular point of difference between Fig. 30 and relationships derived by Chandler (2001) based on adult and some larval characters is the position of *Agathomyia*. On adult characters it is part of the Callomyiinae but is in a more derived position in Fig. 30. Such a position could be explained by *Agathomyia* sharing characters with *Calotarsa* and *Protoclythia* because the latter are basal within the Platypezinae and many characters exhibit altered states in the highly derived larva of *Callomyia*. A combined analysis involving both adult and early stage sets of characters may help resolve this and other points of difference between Fig. 30 and the conclusions reached by Chandler (2001).

Platypezid larvae closely resemble those of Phoridae. Like platypezids, phorid larvae possess a labium bearing sclerotised hooks. However the fleshy head is smaller in phorid larvae such that the dorso-lateral margins bearing antennae and maxillary organs are approximated, being closer together than the length of the antennae and are sited immediately above, rather than to the lateral margins of the mouth. Also phorid larvae are generally smaller and possess transverse impressed lines on the dorsal surface of the abdominal segments. These lines are where the integument collapses and folds during locomotion.

They also resemble Lonchopteridae. Of platypezid larvae studied, that of *Callomyia* most closely resembles the larva of Lonchopteridae. Larvae of both taxa are dorso-ventrally flattened with the upper-lateral margin well defined by integumental features and bearing a pair of segmental processes. In both taxa the metathorax and first abdominal segments are fused dorsally and the mesothorax and prothorax are much narrowed, to about half or less the width of the metathorax. However larvae of the two taxa are easily separated by numerous characters such as the fleshy projections on either side of the mouth and the possession of a pair of processes on the 7<sup>th</sup> abdominal segment which exceed the combined length of the 6<sup>th</sup> and 7<sup>th</sup> abdominal segments in lonchopterid larvae. The labium of *Callomyia* larvae bears three heavily sclerotised teeth but such teeth are lacking in the labium of lonchopterid larvae. The similarities in gross morphology between the two taxa may be convergence due to similar feeding habits. They both gather food from the surface of substrates (Kessel et al. 1973; Ferrar 1987). However their head skeletons are very different. The head skeleton of *Callomyia* is the most heavily sclerotised of those platypezids studied. In dorsal view it is broad apically with sclerotised rods connecting the two halves of the labium just behind and in front of the break (Fig. 20). The labial hooks are large, broad and heavily sclerotised. These features suggest a strengthening of the head skeleton. This correlates to the scraping of firm encrusting fungal tissue which is the food of *Callomyia* larvae. In contrast, the head skeleton of lonchopterid larvae is small, poorly sclerotised with unique fleshy projections and lacking labial teeth. Such an arrangement may be better suited to gathering food particles suspended in a film of liquid which is the typical feeding mode of lonchopterid larvae (Ferrar, 1987).

Platypezid larvae can be distinguished from all other Diptera larvae by the following combination of characters: head fleshy with antennae and maxillary organs not approximated on lobes; tapered labrum and apex of labium protruding from the mouth; apex of labium bearing 1-8 sclerotised hooks; mandibles with blunt rounded apical teeth and usually translucent, barely sclerotised; anterior spiracles flat-tipped bearing a horseshoe-shape arrangement of 10+ openings; dorsum of thorax and/or abdomen with at least some sensilla borne on fleshy projections or lappets and lacking transverse impressed lines or folds. Puparia can simi-

larly be recognised by these features but the head characters are difficult to see. Platypezid puparia lack pupal spiracles.

### Acknowledgements

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### References

- Brindle, A. (1961) Taxonomic notes on the larvae of British Diptera. 5. The Clythiidae (Platypezidae). *The Entomologist*. 94: 274-278.
- Chandler, P.J. (2001) The Flat-footed Flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomologica Scandinavica*. 36: 1-276.
- Chandler, P.J. and Shatalkin, A.I. (1998) Family Platypezidae. Pp. 27-49 in Papp, L. and Darvas, B. (Eds.): *Contributions to a Manual of Palaearctic Diptera*. 3: 1-880. Science Herald, Budapest.
- Cumming, J.M., Sinclair, B.J. and Wood, D.M. (1995) Homology and phylogenetic implications of male genitalia in Diptera – Eremoneura. *Insect Systematics & Evolution*. 26: 121-151.
- de Meijere, J.C.H. (1900) Ueber die Larve von Lonchoptera. Ein Beitrag zur Kenntnis der cyclorraphen Dipterenlarven. *Zoologische Jahrbücher (Abteilungen Systematik.)* 14: 87-132.
- de Meijere, J.C.H. (1911) Zur Kenntnis der Metamorphose von *Platypeza* und der verwandtschaftlichen Beziehungen der Platypezinen. *Tijdschrift voor Entomologie*. 54: 241-254.
- Dufour, L. (1840) Séconde mémoire sur les métamorphoses de plusieurs larves fongivores appartenant à des Diptères. *Annales des sciences naturelles*. 13: 148-163.
- Ferrar, P. (1987) A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrapha. *Entomograph*. 8, 2 vols. E.J. Brill, Leiden.
- Hennig, W. (1952) *Die Larvenformen der Dipteren*. Vol. 3, 1-628. Berlin.
- Hennig, W. (1973) Ordnung Diptera (Zweiflügler). *Handbuch der Zoologie*. 4: 1-337.
- James, M.T. and Turner, W.J. (1981) Rhagionidae. Pp. 483-488 in McAlpine, J.F. et al. (Eds.), *Manual of Nearctic Diptera*. Vol. 1. Agriculture Canada, Monograph No. 27.
- Kessel, E.L., Buegler, Marion E. and Keyes, P.M. (1973) A survey of the known larvae and puparia of Platypezidae, with a key to ten genera based on immature stages (Diptera). *Wasmann journal of Biology*. 31: 233-261.
- Kessel, E.L. (1987) 50. Family Platypezidae. Pp. 681-688 in McAlpine, J.F. et al. (Eds.), *Manual of Nearctic Dipt.* Vol. 2. Agriculture Canada, Monograph No. 27.
- Krivosheina, N.P. 1973. Larvae of the genus *Systemus* (Diptera, Dolichopodidae). *Zoologicheskī Zhurnal*. 52: 1095-1097.
- Krivosheina, N.P. and Mamaev, B.M. (1967) *Classification key to larvae of arboricolous Dipteran Insects*. Nauk. S.S.S.R. "Nauki" 366 pp.
- Lundbeck, W. (1927) *Diptera Danica*. Vol. 7, Platypezidae and Tachinidae. 571pp. Copenhagen.
- McAlpine, J.F. (1989) 116. Phylogeny and classification of the Muscomorpha. Pp. 1397-1515 in McAlpine, J.F. et al. (Eds.), *Manual of Nearctic Diptera*. Vol. 3. Agriculture Canada, Monograph No. 32.
- Roberts, M.J. (1969) Structure of the mouthparts of the larvae of the flies *Rhagio* and *Sargus* in relations to feeding habits. *Journal of Zoology, London* 159: 381-398.
- Robinson, H. and Vockeroth, J.R. 1981. Dolichopodidae. Pp. 625-639 in McAlpine, J.F. et al. (Eds.), *Manual of Nearctic Diptera*. Vol. 1. Agriculture Canada, Monograph No. 27.
- Santini, L. and Raspi, A. (1994) Note biologiche sul dittero micofilo platipezide *Polyporivora infumata* (Haliday) (Platypezidae). *Atti XVII Congresso nazionale italiano di Entomologia Udine 13-18 giugno 1994*: 431-434.
- Sinclair, B.J. (1992) A phylogenetic interpretation of the Brachycera (Diptera) based on the larval mandible and associated mouthpart structures. *Systematic Entomology*. 17: 233-252.
- Teskey, H.J. (1981) Morphology and terminology, larvae. Pp. 65-88 in McAlpine, J.F. et al. (Eds.), *Manual of Nearctic Diptera*. Vol. 1. Agriculture Canada, Monograph No. 27.
- Weidner, H. and Schremmer, F. (1962) Zur Erforschungsgeschichte zur Morphologie und Biologie der Larve von *Agathomyia wankowiczī* Schnabl, einer an Baumpilzen gallenerzeugenden Dipterenlarve. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*. 2: 355-366.
- Wiegmann, B.M., Mitter, C. and Thompson, F.C. (1993) Evolutionary origin of the Muscomorpha (Diptera): tests of alternative morphological hypotheses. *Cladistics*. 9: 41-81.

**Appendix 1. Characters used for scoring and phylogenetic analysis**

Numbers in parentheses after character states show polarity based on outgroup comparison, (0) = primitive; (1), (2), (3) = derived; 9 = unscorable.

**Head**

- 1) Size of atrium.  
Broad sections bearing antennae and maxillary organs on either side of a mid-section covering the head skeleton (0); narrow, one section visible (1).
- 2) Presence of oral ridges.  
A series of close-set serrated ridges may appear on the head. They are usually on each side of the lower part of the mouth (1); or they may be absent (0).
- 3) Distribution of oral ridges.  
Oral ridges are usually confined to the lower margin of the mouth (0); or they extend up behind the maxillary palpi (1).
- 4) Position of largest oral ridge.  
Oral ridges are unequal in length and degree of sclerotization. The longest most sclerotised oral ridge is usually the most anterior (1), but the middle ridge may be largest (0).
- 5) Interrupted labial hypopharyngeal sclerite.  
The labial hypopharyngeal sclerite may be interrupted by a break, usually this occurs just behind the hooks at the apex (1), or the labial hypopharyngeal sclerite may be complete and unbroken (0).
- 6) Shape of mandibles.  
The mandibles may be tapering (0), subrectangular (1), or they may be rod-like (2).
- 7) Articulation of the mandibles.  
The mandibles may articulate with the labial hypopharyngeal sclerite (0), or they may articulate with the pharyngeal sclerite (1).
- 8) Position of mandibular articulation point.  
Where articulation is with the labial hypopharyngeal sclerite, it may be with a lateral extension (0), a dorsal extension anterior to the break (1), or with a dorsal extension posterior to the break (2).
- 9) Number of hooks at the apex of the labium.  
The labium is usually fused at its apex and projects from the mouth. It bears a number of hooks: one hook (0); 3 hooks (1); more than 3 hooks (2).
- 10) Fusion of the hooks at the apex of the labium.  
The lower pair of hooks are often fused (0), but they may also be separate (1).
- 11) Size of hooks.  
In relation to the width of the dorsal cornu of the pharyngeal sclerite, the labial hooks may be large (0), or small (1).
- 12) Sclerotization of lower margin of mouth.  
Round the lower margin of the mouth and often connecting to the oral ridges, are one or more rectangular sclerotised plates (1) or, such plates may be absent (0).
- 13) Presence of dorsal bridge in the head skeleton.  
The two halves of the U-shaped part of the pharyngeal sclerite may be joined anteriorly by a sclerotised region, the dorsal bridge (1) or, this bridge may be absent (0).
- 14) Presence of dorsal apodeme in the head skeleton.  
Between the dorsal and ventral cornua of each half of the pharyngeal sclerite a sclerotised projection may occur (1) or, this apodeme may be absent (0).
- 15) Presence of ventral pharyngeal ridges in the head skeleton.  
The ventral floor of the pharyngeal sclerite may have a series of longitudinal ridges or, they may be absent (0).
- 16) Shape of the pharyngeal sclerite.  
The pharyngeal sclerite may be U-shaped (0), or it may be narrow with the dorsal and ventral cornua approximated (1), or it may be diverging with dorsal and ventral cornua widened (2).

**Thorax**

- 17) Infolded shape of the prothorax.  
The ventral surface of the prothorax may be infolded at the junction of the mesothorax so that, in profile, the prothorax appears longer dorsally than ventrally. The effect of this infolding is to project the head downwards (1) or, infolding may be absent and the head projects in a plane more parallel to the abdomen (0).
- 18) Number of lappets on the prothorax.  
Segmentally arranged pairs of sensilla are often borne on fleshy projections of varying width and length. The first three sensilla may be on fleshy projections (0) or, the first two (1) or, only the first mid-dorsal pair (2).
- 19) Relative length of lappets on the mesothorax.  
Those sensilla borne on lappets may be equal in length (0) or, the middle lappets may be reduced (1) or, the mid-dorsal pair may be longest (2), finally the most lateral pair of processes may be longest (3).
- 20) Presence of dorsal plates on the prothorax.  
The dorsum of the prothorax may be lightly sclerotised (1) or, sclerotization may be absent (0).

- 21) Number of lappets on dorsum of mesothorax.  
The number of lappets may be 3 (0) or, 4 (1) or, 2 (2).
- 22) Number of lappets on dorsum of metathorax.  
The number of lappets may be either 3 (0) or 4 (1).

### Abdomen

- 23) Shape of the posterior breathing tubes.  
These may be parallel-sided (0) or, tapering (1).
- 24) Length of posterior breathing tubes.  
The tubes may be as long as basally broad (0) or, longer than basally broad (1) or, broader than long (2).
- 25) Vestiture of lappets on dorsum of abdominal segments 2-7.  
Vestiture may be absent so that the lappets are smooth (0) or, several setae may be at the apex (1) or, they have bands of setae round them (2).
- 26) Vestiture and folding pattern of first abdominal segment compared with abdominal segments 2-7.  
The vestiture and folding may be the same (0) or, it may differ (1).
- 27) Relative length of lappet 1 on prothorax.  
This lappet may be longer than lappet 1 on other body segments (1) or, it may be as long or shorter (0).
- 28) Distribution of vestiture on the dorsum of abdominal segments 2-7.  
Vestiture defined as microsetae clothing the integument, may be in two equally broad bands across the dorsum of abdominal segments 2-7 (0) or, it may be in two unequal bands (1) or, it may be largely confined mid-dorsally with clear areas each side (2) finally, it may be evenly distributed across the dorsum (3).
- 29) Length of vestiture on the dorsum of abdominal segments 2-7.  
It may be equal in length (0) or, unequal (1) or, absent/reduced (2).
- 30) Relative length of lateral versus mid-dorsal lappets on abdominal segments 2-7.  
These lappets may be equal in length (0) or, the lateral lappet may be longer (1).
- 31) Proximity of lappet pairs 1 and 2 on abdominal segment 7.  
These lappets may be separated (0) or, they may be approximated (1).
- 32) Sclerotization of dorsum of abdominal segments 1-7.  
These segments may not be sclerotized (0) or, they may be lightly sclerotised (1).
- 33) Vestiture of lateral lappets 3 or 4.  
These are the upper lateral lappets and may be bare of vestiture (0) or, they may have an apparently random arrangement of micro-setae (1) or, the micro-setae may be arranged in rings (2).
- 34) Direction of vestiture on posterior margins of abdominal segments 2-7.  
These setae may be upright (0) or, they may be inclined towards the mid-dorsal line (1) or, they may be absent (2).
- 35) Sculpture of integument on the dorsum of the abdomen.  
The surface of the integument may be smooth (0) or it may be coriaceous (1).
- 36) Shape of the posterior margins of abdominal segments 2-7.  
The posterior margin of the abdominal segments may be infolded to varying degrees. No fold may be present (0) or, a slight fold may be present (1) or, a large fold is present (2).
- 37) Number of lappets on the apical margin of the anal segment.  
One to three pairs (0); 4 pairs (1).
- 38) Relative length of lappets on the apical margin of the anal segment.  
Equal (0); middle pair longest (1); first (anterior) pair longest (2); middle pair reduced (3).
- 39) Relative distance between lappets on the apical margin of the anal segment.  
Equally spaced (0); lappets 2 and 3 approximated (1); lappets 1 and 2 approximated (2); lappets 3 fused at base (3).
- 40) Base of posterior breathing tubes.  
Borne on fleshy lobes (0); fleshy lobes absent (1).
- 41) Width of lappets on the apical margin of the anal segment.  
Some of these lappets may be thicker and wider than others. Lappets equal in basal width (0); lappets not equal in basal width, usually the middle pair wider (1).
- 42) Shape of abdomen in cross-section.  
Subcylindrical, as wide as high (0); slightly dorso-ventrally flattened, 1-2x wider than high (1); dorso-ventrally flattened, >2x wider than high (2).
- 43) Enclosed posterior breathing tubes.  
The posterior breathing tubes may not be partially covered posteriorly by a fold in the integument of the anal segment (0) or, they may be so covered (1).



**Appendix 2.** Character states of Platypezidae and Brachyceran outgroup

Brachyceran outgroup: Rs = *Rhagio scolopaceus* (Rhagionidae); Sp = *Systemus pallipes* (Dolichopodidae); Platypezidae: Mk = *Melanderomyia kahli*; Ca = *Callomyia amoena*; Af = *Agathomyia falleni*; Au = *Agathomyia unicolor*; Aw = *Agathomyia wankowiczii*; Pr m = *Protoctlythia modesta*; Pr r = *Protoctlythia rufa*; C in = *Calotarsa insignis*; So = *Seri obscuripennis*; Bf = *Bolophus furcatus*; Po = *Polyporivora ornata*; Pp = *Polyporivora picta*; Pl c = *Platypeza consobrina*; Pl = *Platypeza* sp.; Pa a = *Paraplatypeza atra*; Ld = *Lindneromyia dorsalis*.

Character	Rs	Sp	M. k	C. a	A. f	A. u	A. w	Pr m	Pr r	C in	So	Bf	Po	Pp	Pl c	Pl	Pa a	Ld
1	9	9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
3	9	9	9	9	9	9	9	0	0	0	0	0	0	0	0	0	1	0
4	9	9	9	9	9	9	9	1	1	1	0	0	0	0	1	1	0	0
5	9	9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6	0	0	1	2	1	1	1	2	2	2	2	2	2	2	2	2	2	2
7	9	9	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1
8	9	9	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
9	9	9	0	0	2	1	1	1	1	1	1	1	1	1	2	2	2	1
10	9	9	9	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0
11	9	9	9	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0
12	0	0	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0
13	9	9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
14	9	9	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	1
15	9	9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
16	9	9	0	0	0	0	0	2	2	2	1	1	1	1	1	1	2	2
17	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	9	9	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
19	9	9	0	0	1	1	1	1	1	1	0	2	0	0	3	3	3	0
20	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
21	9	9	9	1	1	1	1	0	0	0	0	0	0	0	2	2	2	2
22	9	9	9	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0
24	9	9	0	0	1	1	1	0	0	0	2	0	2	2	0	0	0	0
25	9	9	9	0	0	0	0	1	1	1	0	0	0	0	2	2	2	2
26	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0
27	9	9	0	0	0	0	0	1	1	1	0	1	0	0	1	1	1	0
28	9	9	0	2	2	2	2	2	2	3	2	1	1	1	3	3	3	3
29	9	9	0	2	2	2	2	1	1	1	2	1	0	0	1	1	1	1
30	9	9	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1
31	9	9	0	0	1	1	1	1	1	1	0	0	0	0	0	0	9	
32	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1	1
33	9	9	0	0	0	0	0	1	1	2	0	0	0	0	2	2	2	2
34	9	9	0	3	0	0	0	1	1	3	2	0	0	0	1	1	1	0
35	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0
36	0	0	0	0	1	1	1	2	2	1	2	1	1	1	2	2	2	2
37	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	2	2	2	2	2	3	1	0	1	1	0	0	2	2
39	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0
40	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	1	1	1	1	0	0	0	0
42	0	0	0	2	1	1	1	1	1	1	1	0	0	0	1	1	1	2
43	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1

**Appendix 3.** List of apomorphies supporting numbered nodes in Fig. 30.

Branch	Character	Steps	CI	Change
node_19 → Mk	6 (Character 6)	1	0.667	0 ==> 1
node_34 → node_33	1 (Character 1)	1	1.000	0 → 1
	5 (Character 5)	1	1.000	0 → 1
	6 (Character 6)	1	0.667	0 ==> 2
	8 (Character 8)	1	1.000	0 → 1
	13 (Character 13)	1	1.000	0 → 1
	15 (Character 15)	1	0.500	0 → 1
	17 (Character 17)	1	1.000	0 ==> 1
	18 (Character 18)	1	1.000	0 → 1
	28 (Character 28)	1	0.750	0 → 2
	29 (Character 29)	1	0.500	0 → 2
	30 (Character 30)	1	0.500	0 → 1
	37 (Character 37)	1	0.500	0 → 1
	40 (Character 40)	1	1.000	1 ==> 0
	42 (Character 42)	1	0.500	0 → 1
node_33 → Ca	10 (Character 10)	1	0.500	0 → 1
	34 (Character 34)	1	0.600	0 ==> 3
	42 (Character 42)	1	0.500	1 → 2
node_33 → node_32	9 (Character 9)	1	0.500	0 ==> 1
	12 (Character 12)	1	0.500	0 → 1
	19 (Character 19)	1	0.600	0 → 1
	20 (Character 20)	1	0.500	0 ==> 1
	26 (Character 26)	1	0.333	0 ==> 1
	31 (Character 31)	1	0.333	0 → 1
	32 (Character 32)	1	0.500	0 → 1
	36 (Character 36)	1	0.667	0 ==> 1
	38 (Character 38)	1	0.600	0 ==> 2
node_32 → node_21	6 (Character 6)	1	0.667	2 ==> 1
	24 (Character 24)	1	0.667	0 ==> 1
	35 (Character 35)	1	0.333	0 ==> 1
node_21 → node_20	23 (Character 23)	1	0.333	0 ==> 1
node_20 → Af	9 (Character 9)	1	0.500	1 ==> 2
node_32 → node_31	2 (Character 2)	1	1.000	0 ==> 1
	8 (Character 8)	1	1.000	1 ==> 2
	14 (Character 14)	1	0.333	0 → 1
	16 (Character 16)	1	0.667	0 → 1
	18 (Character 18)	1	1.000	1 ==> 2
	21 (Character 21)	1	1.000	1 ==> 0
	22 (Character 22)	1	1.000	1 ==> 0
	29 (Character 29)	1	0.500	2 → 1
	37 (Character 37)	1	0.500	1 → 0
	39 (Character 39)	1	0.500	0 ==> 1
node_31 → node_27	4 (Character 4)	1	0.500	0 → 1
	11 (Character 11)	1	1.000	1 ==> 0
	12 (Character 12)	1	0.500	1 → 0
	16 (Character 16)	1	0.667	1 → 2
	25 (Character 25)	1	1.000	0 ==> 1
	27 (Character 27)	1	0.333	0 ==> 1
	28 (Character 28)	1	0.750	2 → 3
	33 (Character 33)	1	1.000	0 ==> 2
	34 (Character 34)	1	0.600	0 → 1
node_27 → node_26	7 (Character 7)	1	1.000	0 ==> 1
	36 (Character 36)	1	0.667	1 ==> 2
node_26 → node_22	23 (Character 23)	1	0.333	0 ==> 1
	28 (Character 28)	1	0.750	3 → 2
	33 (Character 33)	1	1.000	2 ==> 1
	35 (Character 35)	1	0.333	0 ==> 1
node_26 → node_25	9 (Character 9)	1	0.500	1 → 2
	19 (Character 19)	1	0.600	1 ==> 3
	21 (Character 21)	1	1.000	0 ==> 2
	25 (Character 25)	1	1.000	1 ==> 2

	26 (Character 26)	1	0.333	1 ==> 0
	31 (Character 31)	1	0.333	1 -> 0
	39 (Character 39)	1	0.500	1 ==> 0
	43 (Character 43)	1	0.500	0 ==> 1
node_25 -> node_23	16 (Character 16)	1	0.667	2 ==> 1
	38 (Character 38)	1	0.600	2 ==> 0
node_25 -> node_24	4 (Character 4)	1	0.500	1 ==> 0
	15 (Character 15)	1	0.500	1 ==> 0
node_24 -> Paa	3 (Character 3)	1	1.000	0 ==> 1
	14 (Character 14)	1	0.333	1 ==> 0
node_24 -> Ld	9 (Character 9)	1	0.500	2 -> 1
	19 (Character 19)	1	0.600	3 ==> 0
	20 (Character 20)	1	0.500	1 ==> 0
	27 (Character 27)	1	0.333	1 ==> 0
	34 (Character 34)	1	0.600	1 ==> 0
	42 (Character 42)	1	0.500	1 ==> 2
node_27 -> Cin	14 (Character 14)	1	0.333	1 -> 0
	34 (Character 34)	1	0.600	1 -> 3
	38 (Character 38)	1	0.600	2 ==> 3
node_31 -> node_30	10 (Character 10)	1	0.500	0 -> 1
	19 (Character 19)	1	0.600	1 -> 0
	24 (Character 24)	1	0.667	0 -> 2
	30 (Character 30)	1	0.500	1 ==> 0
	31 (Character 31)	1	0.333	1 -> 0
	32 (Character 32)	1	0.500	1 -> 0
	38 (Character 38)	1	0.600	2 ==> 1
	41 (Character 41)	1	1.000	0 ==> 1
node_30 -> So	23 (Character 23)	1	0.333	0 ==> 1
	29 (Character 29)	1	0.500	1 -> 2
	34 (Character 34)	1	0.600	0 ==> 2
	36 (Character 36)	1	0.667	1 ==> 2
node_30 -> node_29	26 (Character 26)	1	0.333	1 ==> 0
	28 (Character 28)	1	0.750	2 ==> 1
	42 (Character 42)	1	0.500	1 ==> 0
node_29 -> Bf	19 (Character 19)	1	0.600	0 ==> 2
	24 (Character 24)	1	0.667	2 -> 0
	27 (Character 27)	1	0.333	0 ==> 1
	35 (Character 35)	1	0.333	0 ==> 1
	38 (Character 38)	1	0.600	1 ==> 0
node_29 -> node_28	29 (Character 29)	1	0.500	1 -> 0
	43 (Character 43)	1	0.500	0 ==> 1

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