A new family and genus of acalypterate flies from the Neotropical region, with a phylogenetic analysis of Carnoidea family relationships (Diptera, Schizophora)

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Abstract. The acalypterate family Inbiomyiidae **fam.n.** (Diptera, Carnoidea) is described for the newly discovered Neotropical genus *Inbiomyia* **gen.n.** with its type species *I. mcalpineorum* **sp.n.** from Costa Rica. The genus ranges from Guatemala south to French Guiana and Bolivia and includes a total of fourteen undescribed species, ten of which will be described formally in a separate paper. *Inbiomyia* is distinctive, with characteristic, extremely shortened head with nonfunctional ptilinum and reduced chaetotaxy, shortened first flagellomere with very elongate, dorsoapically inserted arista, proboscis with largely separate labellar lobes that point in different directions, mid tibia lacking apicoventral bristle, unusual fusion of male sternites 5–7, reduced male sternite 8, elongate surstyluslike ventral epandrial lobes, cerci absent in both sexes, extremely truncate female genitalia, and large, extremely flattened eggs. The larva of *Inbiomyia* and its biology are unknown. *Inbiomyia* occurs mostly in primary lowland rain forest and often is associated with the decaying foliage of fallen trees. Inbiomyiidae belong in the superfamily Carnoidea. The previously doubtful monophyly of the Carnoidea is accepted tentatively on the basis of newly established synapomorphies of the male genitalia. Family level relationships of the Carnoidea are analysed quantitatively for the first time based on a matrix of fifty-eight morphological characters. The putative sister group relationship of Inbiomyiidae to the monotypic Australasian family Australimyzidae is supported by several synapomorphies, mostly from the male and female postabdomen. Family status for the Australimyzidae is confirmed, rejecting previous claims of a sister group relationship (or synonymy) with the Carnidae. The analysis also leads to revised hypotheses of the relationships of Cryptochetidae and Acartophthalmidae, and the paraphyly of 'Tethinidae' with regard to Canacidae, suspected by previous authors, is confirmed.

Introduction

Inbiomyiidae is the first family of Cyclorrhapha to be described from the New World based on a newly discovered genus of flies. Only three Cyclorrhapha families have been newly discovered in the past 50 years: Xenasteiidae Hardy, 1980 (Hardy, 1980) and Neminidae D.K. McAlpine, 1983 (D.K. McAlpine, 1983) (originally as a subfamily of

Aulacigastridae) from the Australasian region, and Marginidae D.K. McAlpine, 1991 (D.K. McAlpine, 1991a) from the Afrotropical region. However, two new families of lower Brachycera, the Neotropical Ocoidae (Asiloidea) and the Nearctic Oreoleptidae (Tabanomorpha), were described recently based on newly discovered genera (Yeates *et al.*, 2003; Zloty *et al.*, 2005). The aims of the present paper are as follows: (i) to describe the genus *Inbiomyia* **gen.n.** with its type species *I. mcalpineorum* **sp.n.**; (ii) to provide a phylogenetic analysis of its relationships with other families; and (iii) thereby to justify the erection of a separate family. Formal

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descriptions of ten additional species of *Inbiomyia* from Central and South America, including a discussion of their species-level phylogenetic relationships, will be published elsewhere (Buck, in press). Supplementary notes on the morphology of its sister group, the poorly known family Australimyzidae, are provided. In the context of the phylogenetic analysis, the monophyly of related families is reviewed, including a new hypothesis on relationships within the canacid–tethinid complex.

History of discovery

The first specimen of *Inbiomyia* (a female of the type species) was collected in 1980 in Monteverde, Costa Rica by W.R.M. Mason of the Canadian National Collection of Insects (Ottawa). The specimen, examined initially by J.F. McAlpine, is labelled 'Aulacigastridae n. gen. det. J.F. McAlpine 1980', and keys to either Aulacigastridae (e.g. J.F. McAlpine, 1981b) or does not key properly (e.g. Hennig, 1973). The superficial similarity to Aulacigastridae is based on a few shared diagnostic characters commonly used in keys (absence of ocellar bristles, presence of vibrissae, two costal breaks, developed anal cell). The affinities of the 'Monteverde fly' remained puzzling and D.K. McAlpine (Australian Museum, Sydney) first suggested that it could represent an undescribed family, but no definitive conclusion could be reached in the absence of a male. Head and wing drawings were prepared (K.C. Khoo, Australian Museum, Sydney, unpublished, 1981; see also Fig. 3A), but later the specimen went missing. In 1999, the author discovered, in the University of Guelph collection, four more specimens of different species of *Inbiomyia* from Peru and Guatemala. It was only in the following year when Khoo's drawings were circulated that the Guelph specimens were recognized as belonging to the same, presumably new, family of flies. *Inbiomyia* was then rediscovered at the original locality (Monteverde) and at a second Costa Rican locality, where thirty-four specimens of both sexes were collected by the author. The later rediscovered original specimen (at the United States National Museum) is conspecific with the new Costa Rican material. Significant new material belonging to fourteen species from eight Central and South American countries has been discovered since then. A phylogenetic study based on fifty-eight morphological characters confirms D.K. McAlpine's initial assumption that the taxon indeed represents an undescribed family of Schizophora.

Inbiomyia is distinctive, rich in apomorphic characters and bears no close resemblance to any described acalypterate Schizophora. The relationships of *Inbiomyia* are difficult to ascertain because the genus does not belong in any well-defined Schizophora superfamily. Its affinities lie within three poorly defined superfamilies: Carnoidea, Opomyzoidea and Sphaeroceroidea. None of these superfamilies is satisfactorily characterized by apomorphic characters. The search for the sister group of *Inbiomyia* therefore had to focus on a large group of families, and analysis required a broader character set than previously (e.g. J.F. McAlpine, 1989). Exploration of new characters focused primarily on head morphology (including its appendages) and the male genitalia, yielding several new promising characters of phylogenetic relevance. The extensive taxon base allowed an evaluation of the distribution and frequency of newly discovered characters in a larger context. Exemplars from most Schizophora families (including almost all 'Acalyptratae' families) were examined (see Supplementary material). In families that are potentially closely related to *Inbiomyia*, exemplars from every subfamily or even genus were examined, except those thoroughly studied by previous authors (i.e. Chloropidae, Andersson, 1977; Milichiidae, Brake, 2000).

Although many synapomorphies support the monotypic Australasian family Australimyzidae as the sister group of *Inbiomyia*, the taxa are very dissimilar and their external appearance does not hint at a close relationship. Except for Griffiths (1972), who considered Australimyzidae of uncertain relationships, all previous authors placed *Australimyza* in the superfamily Carnoidea or one of its component families (Harrison, 1953, 1959; Colless & McAlpine, 1970, 1975, 1991; J.F. McAlpine, 1989; Grimaldi, 1997). The phylogenetic analysis of *Inbiomyia* family relationships therefore included the families that are assigned currently to the Carnoidea. Here, the Carnoidea is tentatively accepted as a monophyletic group based on new genitalic evidence that lends further support for the monophyly of this otherwise poorly defined superfamily.

Materials and methods

Morphology and terminology

Morphological terminology follows J.F. McAlpine (1981a) with few exceptions. Male and female terminalia, head capsule, antenna, proboscis and legs (tibial organ of Chloropidae and Cryptochetidae) were examined on specimens cleared in hot 10% KOH and neutralized subsequently in glacial acetic acid. All dissected parts were kept in glycerine in a microvial with the specimen. A list of the taxa examined for the morphological study of the genitalia and head structure is provided as Supplementary material.

Phylogenetic analysis

Parsimony analysis of the matrix was performed with PAUP* 4.0b10 for Windows (Swofford, 2001) using the 'branch and bound' algorithm. Characters were unweighted. Step matrices were defined for three characters. Branch support for each resolved node in the strict consensus trees was calculated with PAUP* according to Bremer (1994).

Abbreviations

Cs, costal sector: Cs2 is measured between the apices of R_1 and R_{2+3}, Cs3 between the apices of R_{2+3} and R_{4+5}, and Cs4 between the apices of R_{4+5} and M.

Acronyms of depositories

CNCI, Canadian National Collection of Insects, Ottawa, Ontario, Canada; DEBU, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada; INBC, Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Family Inbiomyiidae fam.n.

Type and only included genus: Inbiomyia **gen.n.**

Diagnosis. Inbiomyiidae are recognized easily by the following combination of characters. Small (body length 1.3–1.6 mm), acalypterate flies with: (1) extremely shortened head (frons) and protruding eyes; (2) one pair of inclinate orbital bristles only; (3) vibrissae present; (4) ocellar and postvertical bristles absent; (5) arista very long and dorsoapically inserted; (6) labella divergent and pointing in opposite directions; (7) posterior bristle of notopleuron inserted distinctly higher than anterior bristle; (8) anepisternum bare; (9) costa with both humeral and subcostal breaks; (10) subcosta fading away in apical half and not reaching costa; (11) tibiae completely without bristles (including preapical and apical ones). In J.F. McAlpine's key to Nearctic families (J.F. McAlpine, 1981b), Inbiomyiidae runs to couplet 118: Aulacigastridae. From this family Inbiomyiidae is distinguished by characters (1), (2), (5)–(8) and (11) (apical bristles absent). In Hennig (1973), Inbiomyiidae does not key beyond couplet 138, where it conflicts with both alternatives (leading to Carnidae on the one hand and Neottiophilidae [= Piophilidae], Cypselosomatidae, Odiniidae, Agromyzidae on the other). None of these families possesses characters (1), (2), (4) (postverticals absent in the genus *Carnus* only), (6), (7) or (11). Inbiomyiidae can be identified also using the key to Neotropical Diptera families by Buck *et al.* (in press).

Inbiomyia **gen.n.**

Type species: Inbiomyia mcalpineorum **sp.n.**

Description. Adult (Figs 1, 2). Small, mostly dark, subshining flies of stocky, humpbacked build. Body length 1.30–1.65 mm, wing length 1.26–2.02 mm; female slightly larger than male.

Head (Figs 3A; 9C). Broad and short, its maximum width *c*. 1.1× width of thorax. Eyes strongly convex and protruding, posteroventrally distinctly emarginate. Surface of eye covered in dense ommatrichia except around the margins. Eye colour reddish brown. Frons very short, approximately half head width, distance between front ocellus and ptilinal fissure 1.0–2.5× distance between posterior ocelli. Ocellar plate very broad, occupying virtually whole frons between orbital plates, subshining to very shining, with or without microtomentum. One pair of microscopic interfrontal hairs at anterior margin of frons (usually visible only in cleared specimens). Ocellar hairs minute (sometimes visible only in cleared specimens) or absent. Orbital plates shining to subshining, narrowly and indistinctly separated from ocellar plate by area of less reflective surface texture. Each orbital plate with one long inclinate bristle, one tiny inclinate to reclinate hair immediately anterolaterally to it, and 1–2 tiny reclinate to exclinate hairs posterolaterally to it (anterior one sometimes almost on same level as long inclinate bristle). Vertex concave in dorsal view. Inner and outer vertical bristles well developed but shorter than orbital bristle, with short occipital hair between. Postvertical and inner occipital bristles absent. Minute postocellar hairs present in two species only. Ptilinal fissure horizontal and completely straight, its ventrolateral portions secondarily closed. Ptilinum broad but very short, apparently nonfunctional, when fully inflated its length in cross-section not greater than *c*. 0.75× diameter of first flagellomere. Surface of ptilinum bare, without usual armature of small scales or scattered setulae, its integument very thin and membranous. Face bare and flat, with low and rounded median carina. Subcranial cavity anteriorly extending about halfway up towards ptilinal fissure, lower margin of face forming semicircle in anterior view. Vibrissal angle evenly rounded, not produced. Vibrissa long, subequal in size to orbital bristle, no enlarged peristomal or subvibrissal hairs. Gena narrow, receding towards subcranial cavity, its height *c*. 0.2× eye height; surface setulose with one enlarged but inconspicuous genal bristle near middle. Median occipital sclerite with 3–5 pairs of supracervical setae. Postgena laterally encroaching on strongly concave posteroventral eye margin. Postocular row of hairs present. Laterally visible ventral portion of postgena setulose, hairs near lower margin enlarged. Hypostomal bridge (Fig. 9C: hb) narrow, linear, not widened laterally. Posterior tentorial pit divided (Fig. 9C), i.e. tentorial process and anterior tentorial arm arising from separate pits. Anterior tentorial arm slender but well sclerotized. Antennae porrect and of moderate size, broadly separated. Scape very reduced, obscured by pedicel, medial surface with *c*. three tiny hairs, dorsolaterally with a long, basal apodeme extending into head capsule (Fig. 3B). Pedicel of moderate size, roughly hemispherical, its distal margin almost straight, not notched, dorsomedially with one distinctly enlarged, bristlelike hair, otherwise with a fringe of subequal hairs. First flagellomere roughly hemispherical, small, *c*. 1.6–2.0× as large as pedicel, with usual ventrolateral sensory pore. Arista inserted dorsoapically, two-segmented, very long, its length greater than combined length of head and thorax, long-pubescent, longest trichia *c*. 2× as long as greatest diameter of second aristomere. Clypeus of
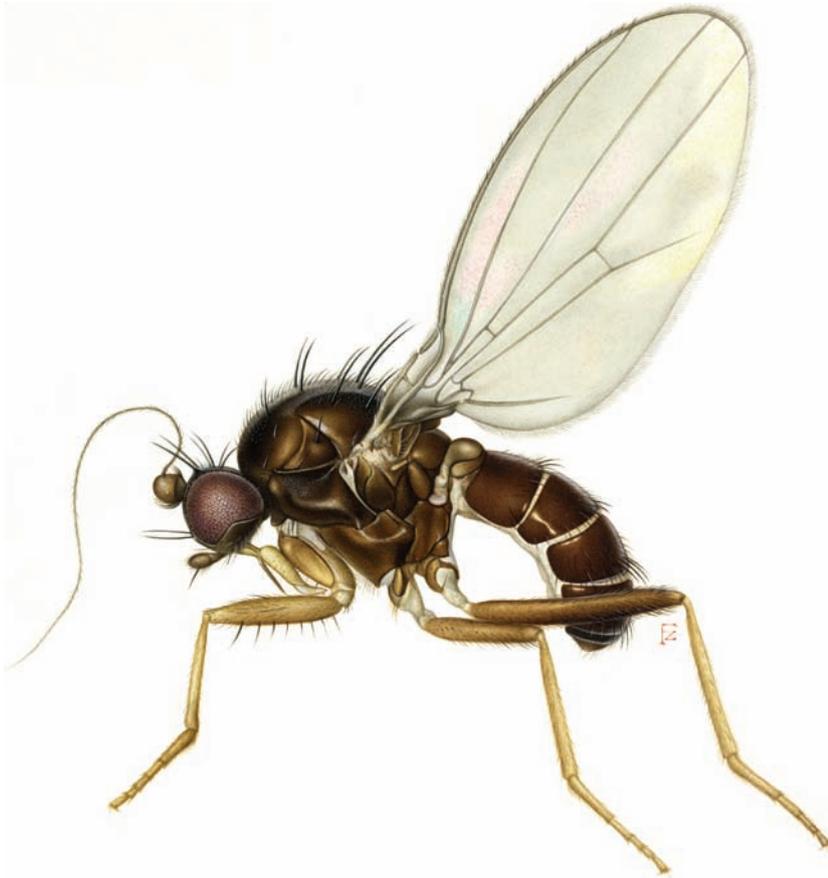
Fig. 1. *Inbiomyia mcalpineorum*. Female habitus (drawing by F. Zeledón).

moderate size, its height slightly less than diameter of palpus. Fulcrum (Fig. 11G) without internal filter apparatus (*sensu* Frey, 1921). Proboscis (Fig. 3C) of peculiar shape, when extended *c.* 2× height of head; prementum long, but

labella short. Maxillary palpus of moderate size, widest near apex and slightly tapered toward base, with short pubescence and one long conspicuous preapical ventral bristle. Stipes elongate, without ventral appendage; lacinia

Fig. 2. *Inbiomyia* sp. Adult perching on green leaf litter under a fallen tree (Costa Rica: Heredia, Rara Avis Nature Reserve, 700 m, February 2005; photograph by S.A. Marshall).
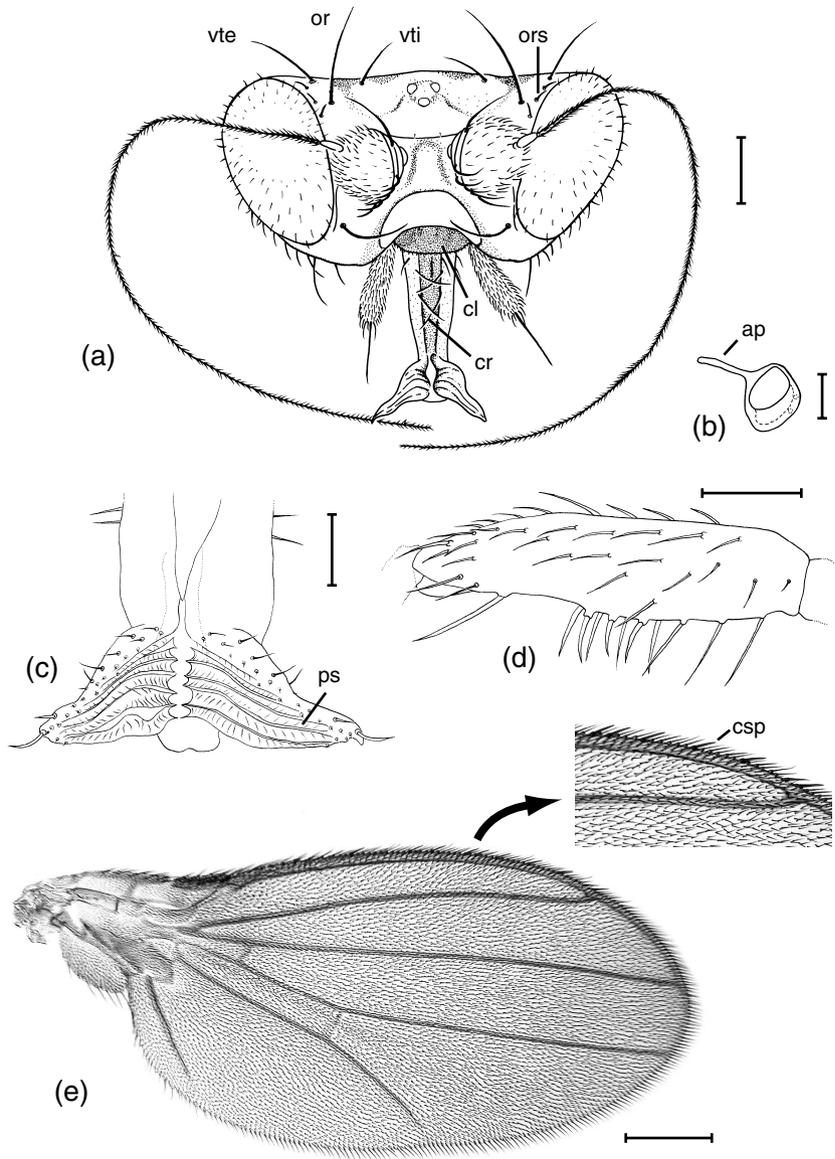
Fig. 3. *Inbiomyia mcalpineorum*. A, head, frontal (redrawn and modified from unpublished figure by K.C. Khoo, 1981); B, left scape, posterior (inner) view; C, proboscis, anterior; D, male left fore femur, outer surface; E, wing. Scale: 0.2 mm (E), 0.1 mm (A, D), 0.05 mm (B, C). ap, apodeme; cl, clypeus; cr, dorsally cruciate bristles; csp, costal spinules; or, orbital bristle; ors, orbital setulae; ps, pseudotracheae; vte, outer vertical bristle; vti, inner vertical bristle.

extremely reduced and knoblike (Fig. 10G). Prementum slightly over 2× as long as broad, its lateral margins strongly upcurved in basal half, with 2 pairs of cruciate bristles that cross over dorsally above the labrum (Fig. 3A: cr). Labrum narrow, almost parallel-sided, with tapered apex. Hypopharynx very short (*c.* one-sixth length of labrum), triangular with truncate apex, almost transparent. Labellum short, triangular, with conspicuously pointed apex. Labella (Fig. 3C) separate posteriorly along midline, their tips pointing in nearly opposite directions when expanded, each with six pairs of pseudotracheae (basal pair reduced and probably nonfunctional); prestomal teeth not developed.

Thorax (Fig. 1). About as high as long; mesoscutum as long as broad, strongly and evenly convex. Transverse suture strong but incomplete, extending medially to dorsocentral lines. One presutural and two postsutural pairs of dorsocentral bristles, decreasing in length from posterior to anterior pair. In some species, dorsocentral rows with small hairs between posterior two dorsocentrals. Acrostichals short and sparse, in two rows that end before level of posterior pair of dorsocentral bristles, leaving prescutellar area bare. Scutum with one well-developed presutural and one postsutural (prealar) supra-alar bristle, one postalar and no intra-alar bristle. Notopleuron high, approximately an equilateral triangle, with two long bristles and no hairs, anterior bristle contiguous to notopleural suture, posterior one conspicuously shifted dorsally. Postpronotal lobe bare except one reclinate, more or less developed (sometimes hairlike) bristle, and usually a small hair below it. Scutellum 2.5–3.0× as broad as long, disc bare, dorsally convex, with one or two pairs of marginal

bristles. Posterior pair long and convergent, anterior pair, if present, short (half as long as posterior pair to small and hairlike). Subscutellum slightly developed. Pleuron bare except for posterodorsal katepisternal bristle (no hairs in front of it), an irregular row of hairs connecting this bristle with setulose lower portion of katepisternum, and a tiny proepimeral bristle (difficult to see). Katepisternal bristle strongly inclined forward. Coxopleural streak absent. Spiracles small, posterior spiracle without hairs or bristles. Proepisternum simple, without vertical carina and free from prosternum. Prosternum bare, slightly expanded anteriorly, about as broad as first flagellomere, widely separated from fore coxae by membranous area.

Legs (Fig. 1). Relatively slender compared to stout body, and paler than ground colour of body. Coxae normal, fore coxa with two dorsoapical bristles, mid coxa with two bristles and hind coxa with one bristle on outer surface. Mid coxal prong present. Femora not unusually thickened, diameter of fore femur slightly greater than diameter of hind femur, which is slightly greater than diameter of mid femur. Fore femur (Fig. 3D) slightly sexually dimorphic: with an anteroventral row of 2–6 and posteroventral row of 6–9 bristles in both sexes, bristles of anteroventral row or both rows stronger in male than in female. Antero- and posteroventral bristles mostly erect and longer than diameter of fore tibia, distal-most bristle of posteroventral row enlarged and curved forward; fore femur otherwise with one enlarged dorsal bristle at 2/3. Mid and hind femur simple, without outstanding bristles. Tibiae slender, without preapical or ventroapical bristles, hind tibia with a posteroapical comb of bristles (visible only under high magnification). Setulae of ventral surface of male fore tibia semierect, fairly strong in some species. Tarsi simple, without outstanding hairs or bristles. Tarsal claws simple.

Wing (Fig. 3E). Unmarked, well-developed, wing length *c.* 2.0–2.5× width. Wing membrane microtrichose throughout, slightly to moderately infuscate; veins brown and microtrichose. Costa with well-defined subcostal and humeral breaks, extending to apex of M, but distinctly weaker in last sector; costa in second and basal portion of third sector with well-spaced bristles slightly longer and stouter than regular hairs (Fig. 3E: csp); no distinctly enlarged bristles before subcostal break. Subcosta running close to R_1, fading away in distal half far before reaching costa. R_1 short, ending in basal fourth of wing. R_{2+3} long, ending in distal fifth of wing. R_{4+5} almost ending at wing apex, slightly convex anteriorly. M ending slightly behind wing apex, nearly straight in last sector. CuA_1 fading away before reaching wing margin. A_1 strongly developed and tubular, fading away in distal fifth; A_2 absent. Cell dm narrow, separated from cell bm by oblique bm-cu. Cell cup closed, distally convex. Anal lobe of wing not prominent; alula of moderate size, with fringe of long hairs. Upper and lower calypter vestigial. Halteres brown.

Abdomen (Fig. 1). Ovoid, about as long as head plus thorax, with six pairs of functional spiracles in both sexes. Tergites sparsely setulose, with medium-sized hairs, and a few enlarged bristles posterolaterally (on all tergites) and posteromedially (on tergites 4 and 5 only). Tergites 1 and 2 completely fused, boundary indicated by a weak suture laterally. Syntergite 1 + 2 slightly desclerotized mediobasally, slightly longer than tergite 3. The following three tergites (tergites 3–5) of approximately the same length. Tergite 6 fused to tergite 5 in male (indicated by a double set of spiracles). Spiracles 1–6 situated in pleural membrane (spiracles 5 and 6 of male more or less incorporated into lateral portion of syntergite 5 + 6). Pleural membrane of segments 3–5 sparsely setulose. Sternites 1–5 narrow, width only about one-third width of abdomen, sparsely beset with medium-sized hairs. Sternite 1 very short and weakly sclerotized, sternite 2 longer than following sternites.

Male terminalia (Fig. 4). Male sternites 5, 6 and 7 fused, with boundaries of individual sternites obliterated (Figs 4A; 6D), often with process at hind margin of lateral or ventral portions (Fig. 6D: prv). Intersegmental membrane behind syntergite 5 + 6 dorsomedially with peculiar ring-shaped sclerite (enlarged, dorsally shifted, nonfunctional left spiracle 7?) (Fig. 4C: rs). Male sternite 8 very short and transverse, laterally articulated at apices with epandrium and anteromedially with posterior margin of synsternite 5 + 6 + 7. Hypopygium symmetrical. Epandrium (Fig. 4A, B) saddle-shaped, anteroventrally with a pair of long, surstyluslike processes (Fig. 4A: vp) and posterior to each process with a short, dorsally directed cleft above insertion area of surstylus, separating off a posteroventral lobe (Fig. 4B: vl). Epandrium dorsally sometimes with a pair of broad anterior apodemes (Fig. 4B: ap). Main surface of epandrium sparsely bristled in posterior half. Epandrial process articulated with epandrium in about half of the species, apically tapered or expanded, with only short hairs or teeth. Subanal plate (= sclerotized area ventral to anus, Fig. 4A, D: sa) variably developed and sometimes hardly sclerotized, low (short) or high (long), medially divided by a distinct suture, laterally usually continuous with epandrium (in one species separate from epandrium and fused to base of surstylus). Cercus absent (incorporated into subanal plate?). Surstylus articulated with epandrium, apically more or less expanded or curved posteriorly, margin with few to many long bristles and sometimes one or two stout, toothlike bristles. Subepandrial sclerite (sternite 10) not developed. Hypandrium Y-shaped (Figs 4E; 7E), with robust and heavily sclerotized anterior apodeme; posterior arms running medially of epandrial wall posteriorly, articulated with anteroventral margin of epandrium and with bases of postgonites. Hypandrium in one species with a long, slender, forked, ventral process. Postgonites (Fig. 4D: pg) usually well developed (absent in one species), with bristles, some of which are usually stout and toothlike. Base of postgonite posteriorly fused with ventral (anterior) margin of subanal plate, its movability very restricted. Phallus (Figs 4F; 6F; 7D) with long, slender and strongly sclerotized phallapodeme. Basiphallus stout and well sclerotized with conspicuous, simple or apically forked epiphallus. Distiphallus short, membranous, tubular, directed anteriorly, in some areas with microtrichia or small spicules. Ejaculatory apodeme
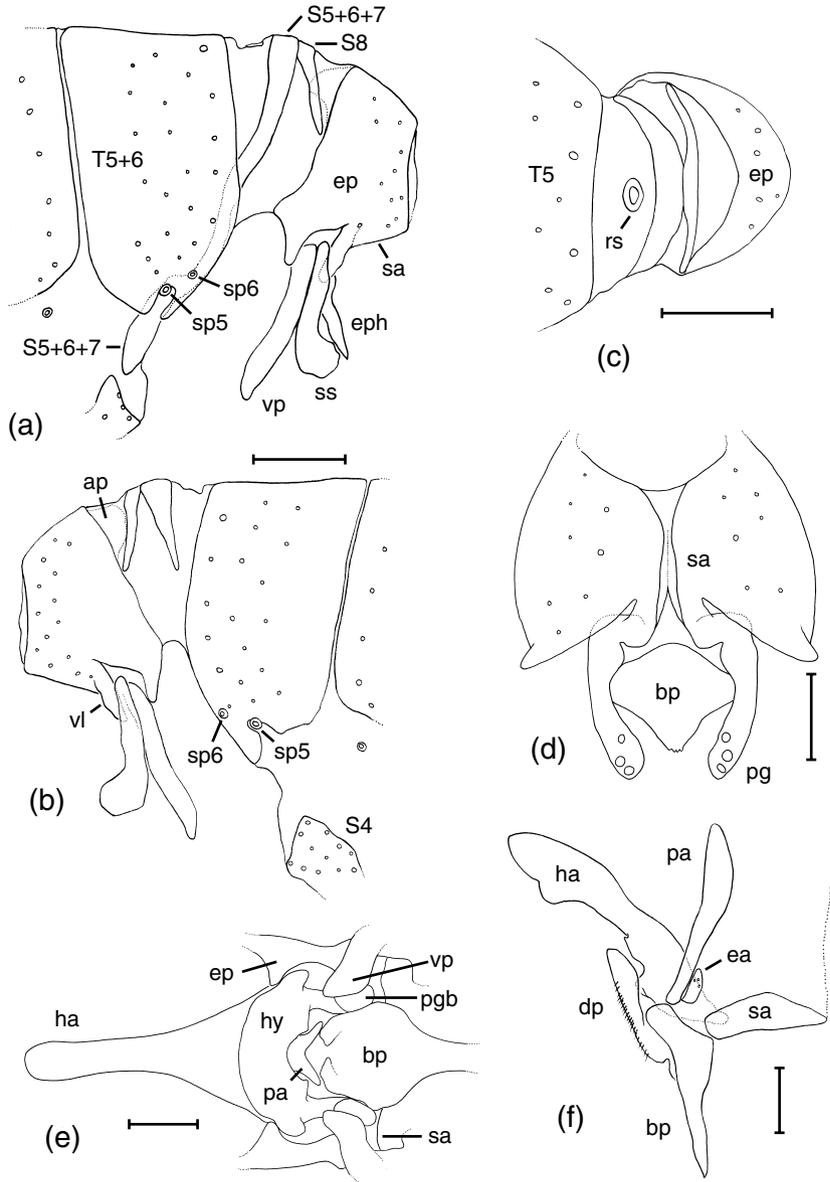
Fig. 4. *Inbiomyia* spp., male terminalia (bristles omitted). A–C, *I. mcalpineorum*, terminalia: A, left lateral; B, right lateral; C, dorsal. D–E, *Inbiomyia* sp. (Costa Rica): D, epandrium and postgonites, ventral; E, hypandrium and associated structures, ventral. F, *I. mcalpineorum*, phallic complex (postgonites omitted), left lateral. Scale: 0.1 mm (A–C), 0.05 mm (D–F). ap, apodeme of epandrium; bp, basiphallus; dp, distiphallus; ea, ejaculatory apodeme; ep, epandrium; eph, epiphallus; ha, hypandrial apodeme; hy, hypandrium; pa, phallapodeme; pg, postgonite; pgb, base of postgonite; rs, ring-shaped sclerite; S, sternite; sa, subanal plate; sp, spiracle; ss, surstylus; T, tergite; vl, posteroventral lobe of epandrium; vp, anteroventral process of epandrium.

(Fig. 4F: ea; Fig. 6G) very small and weakly sclerotized, closely associated with base of phallus and easily overlooked.

Female terminalia (Fig. 7A–C). Ovipositor extremely truncate and nontelescopic. Tergite 6 about half as long as tergite 5; tergite 7 very short and sometimes divided medially, but almost as broad as previous tergite. Tergite 8 broad, roughly trapezoidal with broadly rounded corners, in some species with broad anterior apodeme. Segments 9, 10 and cerci completely reduced. Female sternites 1–5 of approximately same width. Sternites 6 and 7 almost 2× as wide as preceding sternites, laterally almost reaching corresponding tergites, sometimes sternite and tergite 7 narrowly fused laterally. Sternite 8 virtually absent, sometimes visible as small, very faintly sclerotized, medially divided plate. Abdominal sternum membranous behind sternite 7, forming pouch bearing field of scales. Scales

(Fig. 7C) at margins of field with simple to trifid apex, elsewhere spatulate with crenulate apical margin, apices directed anteriorly. Reproductive tract (Fig. 5A, B) with two spermathecae. Spermathecal ducts short, narrowed near base and near apex, slightly and gradually dilated in middle section. Surface structure of ducts simple, indistinctly annulated through most of their length, inserting laterally on thecae. Thecae tyre-shaped to ovoid with terminal invagination, moderately sclerotized, with striate surface. Spermathecal ducts joining vagina separately. Another pair of ducts (probably from accessory glands) joining vagina posterior to spermathecal ducts. Accessory glands (or their ducts) slender and tubular, without obvious peculiarities. Vagina apparently (observed in two species) with delicate and easily overlooked membranous pouch (ventral receptacle?).
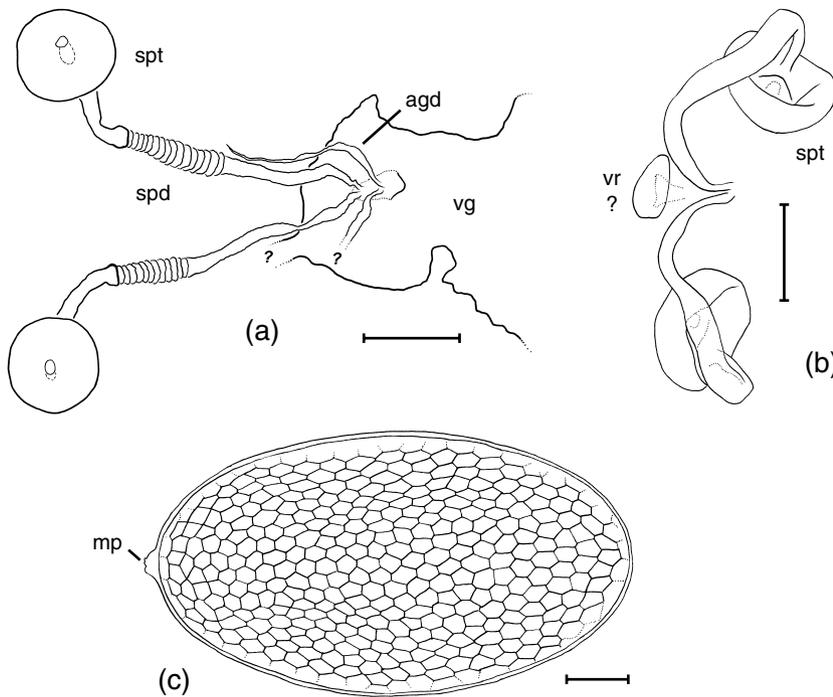
Fig. 5. *Inbiomyia* spp. A–B, female reproductive system: A, *I. mcalpineorum*, dorsal (surface structure of spermathecae not shown); B, *Inbiomyia* sp. (Colombia), spermathecae and ventral receptacle(?), ventral (spermathecae collapsed during preparation). C, Egg, dorsal, *Inbiomyia* sp. (Colombia). Scale: 0.05 mm. agd, duct of accessory gland; mp, micropyle; spd, spermathecal duct; spt, spermatheca; vg, vagina; vr, ventral receptacle.

Internal anatomy. Hindgut with four rectal papillae (observed in one species from Colombia).

Egg (Fig. 5C). Eggs were obtained by dissection from five species, with mature eggs per female varying from one to four. Egg morphology appears uniform across the genus. Size large compared to abdomen, shape elliptical in dorso-ventral view (length 0.39–0.48 mm, width 0.21–0.27 mm, length/width ratio 1.67–1.86), extremely flattened (thickness estimated at *c.* 0.05 mm). Ventral surface completely transparent, membranous, unornamented; dorsal surface thicker but not tough, reticulated, unpigmented. Reticulation polygonal (predominantly hexagonal) and not raised above surface; surface texture coarsely granulose. Micropyle simple, on small projection at anterior pole of egg.

Etymology. The generic name acknowledges the important contribution to research on Neotropical insects made by INBio of Costa Rica.

Biology. Very little is known about the biology of *Inbiomyia*. Adults are apparently microbial grazers, as can be concluded from the substantial amounts of fungal, algal (including diatoms) and probably bacterial material found in the guts of dissected specimens. However, the proboscis shows no conspicuous modifications for microbial grazing. Most specimens of *I. mcalpineorum* and two specimens of another species were collected by pan trapping and sweeping in treefalls in cloud or rain forest. Otherwise most material was collected in Malaise traps in primary rain or cloud forest. The larval biology of *Inbiomyia* is completely unknown. The egg morphology is highly

unusual for Acalyptratae and reminiscent of macrotype eggs of Tachinidae. The large size and low number of mature eggs in gravid females indicates a K-strategy of reproduction.

Biogeography. *Inbiomyia* is known currently from two Central American countries (Guatemala, Costa Rica) and six South American countries (French Guiana, Venezuela, Colombia, Ecuador, Peru, Bolivia). Based on these records it appears that the genus is distributed throughout tropical parts of the Neotropical region. *Inbiomyia* occurs from sea level to about 2000 m, but most species (excluding the type species *I. mcalpineorum* and two closely related species from South America) are restricted to lower elevations.

Inbiomyia mcalpineorum sp.n.

Holotype. ♂. COSTA RICA: Prov. Alajuela, Sarapiquí, Hacienda La Cayuga, 1500–1600 m, 22.ix.−20.x.2004, Malaise, L_N_241900_518500, #78706 (*Porras & Solís*) (INBC).

Paratypes. 29 ♂♂, 32 ♀♀. COSTA RICA: Prov. Alajuela, 2 ♂♂, 4 ♀♀, Volcán Tenorio, N slope nr. Bijagua Biol. Stn., 700 m, 17–18.vi.2000, pans in treefall (*Buck & Marshall*) (DEBU); 4 ♂♂, 8 ♀♀, same data except 18.vi.2000 (DEBU); 4 ♂♂, 4 ♀♀, same data except 19.vi.2000 (DEBU); 1 ♂, 1 ♀, Upala, Bijagua, Albergue Heliconias, trail to Lag. Danto, 1100 m, 17.iii.−17.iv.2000, Malaise, L_N_423760_298100, #59702 (*Gutiérrez*) (INBC); 1 ♂, Arenal Natl. Pk., Sector Cerro Chato, San Carlos,

1100 m, 25.ix.−22.x.1999, Malaise, L_N_269500_460900, #53935 (*Carballo*) (INBC); 1 ♂, 3 ♀,♀, same as previous except 14.iii.−24.iv.2001, L_N_460900_269500, #62075 (INBC). Prov. Cartago, 1 ♂, Dulce Nombre, Vivero Linda Vista, 1400 m, vi–viii.1993 (*Hanson*) (INBC); Prov. Guanacaste, 1 ♀, V. Miravalles, Cabro Muco Stn., 1100 m, 23.vi.−6.vii.2003, Malaise, L_N_299769_411243, #74091 (*Azofeifa et al.*) (INBC). Prov. Heredia, 2 ♂♂, 16 km SSE La Virgen, 10°16′N, 84°5′W, 1050–1150 m, 9–21.ii and 21.ii.−9.iii.2001, transect (*INBio-OET-ALAS*) (INBC). Prov. Limón, 1 ♀, Hitoy Cerere Biol. Ref., Espavel Trail, 560 m, 11.iii.−1.iv.2003, Malaise #8, L_N_410200_569800, #73580 (*Gamboa et al.*) (INBC). Prov. Puntarenas, 3 ♂♂, 1 ♀, Monteverde Biol. Res., 1500 m, 14.vi.2000, treefall sweep and pans (*Buck*) (DEBU); 2 ♂♂, 1 ♀, same data except sweeping treefall and trail (DEBU); 1 ♂, same data except 13–14.vi.2000, pans along stream (*Buck*) (DEBU); 1 ♀, same locality, ii.1980, cloud forest (*Mason*) (CNCI); 6 ♂♂, 5 ♀♀, Coto Brus Z.P., Las Tablas, trail to La Neblina, 1400 m, 6.xii.2000–6.i.2001, Malaise, L_N_597500_317800, #61360 (*Alfaro*) (INBC); 1 ♂, trail to Cerro Pittier, 600 m NW of station, 1750 m, 16.ix.1996, Malaise, L_N_331250_577150, #8525 (*Maroto*) (INBC). Prov. San José, 2 ♀♀, Zurquí de Moravia, 10°3′N, 84°1′W, 1600 m, vi.1993 (*Hanson*) (DEBU).

Description. Adult (Figs 1; 3). Wing length 1.61–1.71 mm (♂), 1.66–1.81 mm (♀). Sclerotized portions of head dark brown excluding prementum, which is pale brown. Antenna and palpus dark brown, almost concolorous with frons. Frons besides usual long inclinate orbital bristle with 2–3 orbital setulae and a pair of ocellar setulae. Thorax including pleuron dark brown, katepisternum slightly and gradually becoming paler ventrally. Dorsocentral line with 1–3 hairs between posterior two dorsocentral bristles; acrostichal rows of hairs extending posteriorly to at least level of postsutural dorsocentral bristle (at most half-way between levels of posterior two dorsocentrals). Scutellum with anterior pair of bristles small and subequal to acrostichal hairs. Legs pale to medium brown, fore coxa, mid and hind femur often darkened. Both antero- and posteroventral rows of bristles of fore femur (Fig. 3D) darker and slightly stouter in male than in female; bristles of posteroventral row longer in female. Distal three-quarters of male fore tibia with well-developed row of short, semierect, black, ventral bristles. Wing (Fig. 3E) somewhat infuscate. Cs2 3.4–4.2× as long as Cs3; Cs3 1.5–2.0× as long as Cs4.

Male terminalia (Figs 5A–C, F; 6; 7D, E). Synsternite 5 + 6 + 7 with a broad posterior process on its ventral portion (Fig. 6D: prv). Ring-shaped sclerite well developed. Epandrium dark brown, dorsally with a pair of well-developed anterior apodemes (Fig. 6B: ap), ventrally continuous with subanal plate, which is well sclerotized and concolorous with epandrium. Subanal plate nearly forming a right angle with posterolateral margin of epandrium in lateral view. Perianal field elliptical (Fig. 6C: pf). Ventral epandrial process (Fig. 6E) dark brown (excluding paler apex), articulated to a condylelike process of the epandrium (Fig. 6B); shape more

or less straight in lateral view, curved in anteroposterior view, medial surface with several medium-sized bristles; apical part with few *sensilla trichodea* only. Surstylus (Fig. 6B) yellowish brown (excluding darker base), moderately expanded distally, with a fringe of bristles arranged in a somewhat irregular row, and 2 bristles on outer surface. Hypandrium narrowly articulated with anteroventral corner of epandrium, with broad emargination between posterior arms (Fig. 7E). Postgonite (Fig. 6A) brown, directed anteriorly (Fig. 6B: pg), with slender stem and dilated apex; apex with a row of marginal bristles which become gradually stouter and more toothlike distally. Epiphallus long and slender, gradually tapering towards apex (Fig. 7D), straight in lateral view (Fig. 4F). Distiphallus (Fig. 6F: dp) relatively short, ventral surface with microtrichia and scattered spicules.

Female terminalia (Figs 5A; 7A–C). Tergite 7 distinctly narrowed medially, almost divided, laterally narrowly fused to sternite. Tergite 8 without anterior apodeme, slightly paler than preceding tergites (excluding heavily sclerotized anterior margin), posterior margin angulate, with or without shallow median emargination. Spermathecae well sclerotized, dark brown, tyre-shaped with small central invagination and laterally inserted duct.

Diagnosis. A key separating the species of *Inbiomyia* is provided in Buck (in press). *I. mcalpineorum* is the only species with long, anteriorly directed postgonites, surstyli that are only moderately expanded distally, but lack toothlike bristles, and a strongly angulate epandrium (posteroventral corner in lateral view). The female is the only species in which the tergite and sternite of segment 7 are fused.

Etymology. This species is dedicated to J.F. and D.K. McAlpine, who realized first that the original specimen of *Inbiomyia* belonged to an undescribed genus and probably a new family of Diptera.

Distribution. Known from every province in Costa Rica ranging from 560 to 1750 m above sea level.

Family Australimyzidae

On the basis of morphology, the sister group of *Inbiomyia* is Australimyzidae, a poorly known family restricted to the Australasian region. Currently, it includes only the type genus, *Australimyza*, with five described (and several undescribed) species. Here, characters of potential phylogenetic relevance, unmentioned by previous authors (Harrison, 1953, 1959; Griffiths, 1972), are discussed.

Australimyza Harrison, 1953

Species examined. Australimyza setigera Harrison, 1959 (New Zealand: South I., Banks Peninsula, Port Levy and South I., ∼15 km S Cheviot, Napenape; DEBU); *A. anisotomae* Harrison, 1953 (females only; New Zealand:
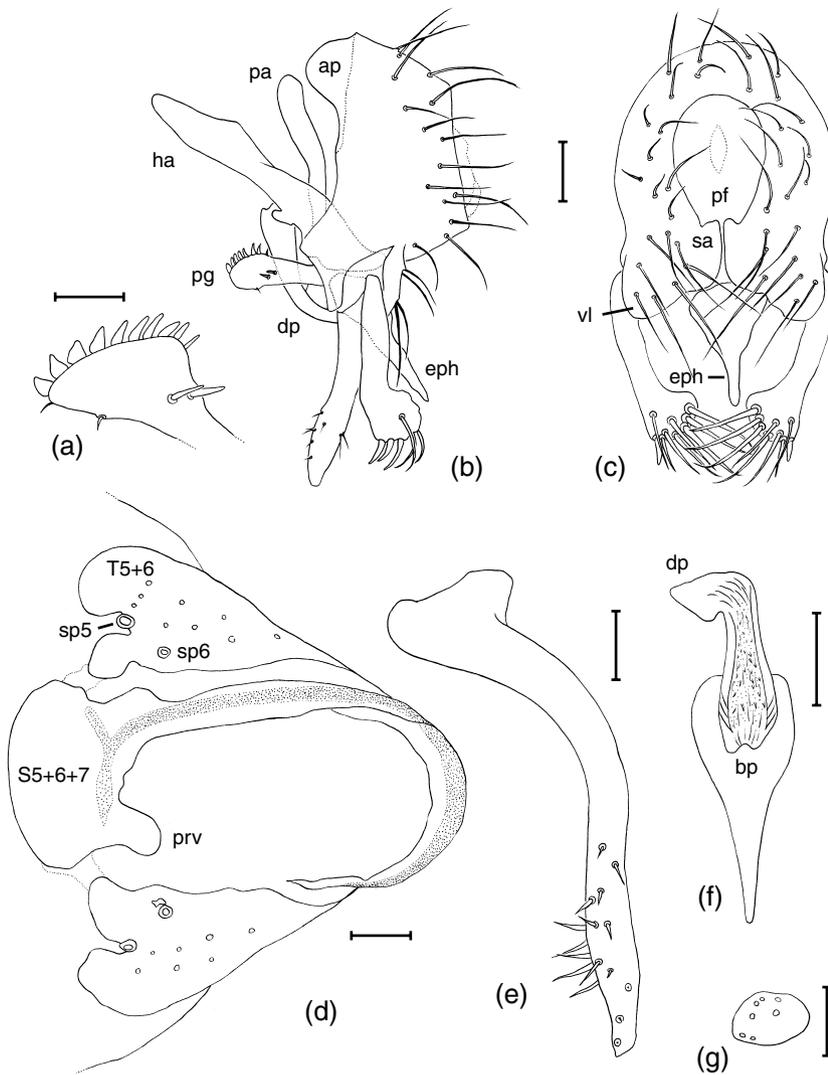
Fig. 6. *Inbiomyia mcalpineorum*, male terminalia. A, apex of left postgonite, outer surface; B, hypopygium, left lateral; C, hypopygium, posterior; D, segments 5–8, ventral; E, left ventral epandrial process, anterior; F, phallus, ventral; G, ejaculatory apodeme, posterodorsal. Scale: 0.05 mm (B–D, F), 0.025 mm (A, E, G). ap, anterior apodeme of epandrium; bp, basiphallus; dp, distiphallus; eph, epiphallus; ha, hypandrial apodeme; pa, phallapodeme; pf, perianal field; pg, postgonite; prv, posterior process of ventral portion of synsternite 5 + 6 + 7; S, sternite; sa, subanal plate; sp, spiracle; T, tergite; vl, posteroventral lobe of epandrium.

Campbell I.; CNCI); and *Australimyza* sp. A (Australia: Western Australia, Yalgorup Beach, Albany and Augusta; DEBU).

A general description of the genus and its species was provided by Harrison (1959). Griffiths (1972) detailed the male genitalia. The following morphological notes apply to all species that were examined except noted otherwise. The ptilinum and fine structure of the proboscis were studied only in *A. setigera*. Male and female genitalia were not examined in *A. anisotomae*.

Description. Adult. Head. Frontal orbits with row of proclinate setulae along inner margin. One inclinate setula in front of first orbital bristle. Interspaces between first, second and third orbital bristle with 1(−2) exclinate setula each (absent in *Australimyza* sp. A). Interfrontal setulae proclinate (omitted from fig. 405 in Harrison, 1959), more or less arranged in two rows, supra-antennal pair not enlarged. Inner occipital bristle small, inserted approximately at level of inner vertical bristle. Eye

densely haired, every second junction between ommatidia occupied by a hair. Ptilinal fissure well developed but short, not extending below level of upper margin of insertion area of antenna. Ptilinum extremely reduced and obviously nonfunctional, developed as simple fold that extends no more than one mid ocellus diameter into the head capsule. Surface of ptilinum covered in low scales as is typical in Schizophora. Tentorial pit undivided and anterior tentorial arm well developed (Fig. 9A). Arista two-segmented, with no trace of basal segment in *A. setigera* (three-segmented according to D.K. McAlpine, 2002), apparently three-segmented in *A. anisotomae* (not confirmed on cleared material). Proboscis with simple prementum, not swollen as in Carnidae. Stipes (Fig. 10H) with ventral appendage, lacinia bare, long and acuminate, medial surface with very fine serration. Labella simple, without the modifications of *Inbiomyia* or Carnidae: labellar lobes completely fused along middle and extending posteriorly, forming an acute angle with haustellum ventrally. Labella with five pairs of pseudotracheae. Fulcrum with internal 'filter apparatus'
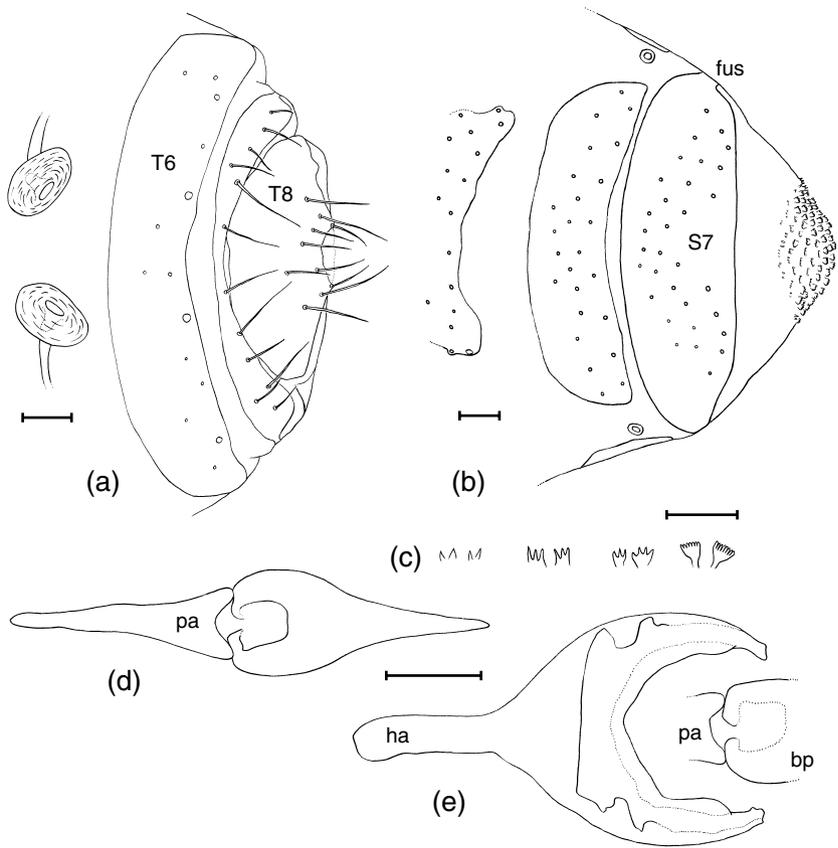
Fig. 7. *Inbiomyia mcalpineorum*, terminalia. A–C, female: A, terminalia and spermathecae, dorsal; B, terminalia, ventral (pouch behind sternite 7 extruded); C, ventral spicules of segment 8. D–E, male: D, phallapodeme and basiphallus, dorsal; E, hypandrium, ventral. Scale: 0.05 mm (all excluding C), 0.025 mm (C). bp, basiphallus; fus, area of fusion between tergite and sternite 7; ha, hypandrial apodeme; pa, phallapodeme; S, sternite; T, tergite.

(*sensu* Frey, 1921) consisting of five pairs of close-set setulae (Fig. 11H).

Thorax and wing. Proepisternal bristle very small, shifted anteriorly and closer to cervical sclerite than to fore coxa (this bristle apparently absent in *Australimyza* sp. A). Proepimeral bristle small. Prosternum bare, precoxal bridge absent. Coxopleural streak well defined. Subscutellum moderately developed. Wing with row of costal spinules extending to apex of R_{4+5}. I cannot confirm that A_2 is present as stated by J.F. McAlpine (1989).

Abdomen. With six pairs of spiracles in both sexes, spiracle 1 present (its presence was doubted by Griffiths, 1972).

Male terminalia (Fig. 8A, B). Sternite 7 not fused to sternite 8 (narrowly fused near mid-line in species examined by Griffiths, 1972). Sternite 8 extensively setulose, sternite 6 and syntergosternite 7 bare except for the usual anterior pair of *sensilla trichodea*. Epandrium narrow dorsally, but not medially divided as in the species examined by Griffiths (1972). No trace of a subepandrial sclerite, inner base of surstyli contiguous with hypandrium. Hypandrium with paired anterior apodemes (Fig. 8B: ha), the two arms broadly separated in *Australimyza* sp. A, but very close and touching basomedially in *A. setigera*. Lateral posterior arms of hypandrium running parallel to ventral margin of epandrium, reaching base of surstyli (Fig. 8A: hy). Hypandrial bridge above base of phallus present and broad in *Australimyza* sp. A, weak, narrow and medially

desclerotized in *A. setigera*. Pregonites variable: produced into a short, slender process with setulose apex in *Australimyza* sp. A; developed as a low bulge with two long bristles and a few setulae in *A. setigera* (Fig. 8B: pr). Postgonites firmly connected to base of phallapodeme dorsally and to pregonites ventrally (Fig. 8B: pg), not moveable. Forked base of phallapodeme together with postgonites tightly embracing basiphallus precluding movement. Basiphallus very simple, ringlike, with small, flat, broadly rounded epiphallus projecting above postgonites in *Australimyza* sp. A; epiphallus not developed in *A. setigera*. Distiphallus (Fig. 8B) flexible, ribbonlike and slightly coiled or curved, with a pair of sclerotized strips reinforcing lateral margins from base almost to apex. Posterior surface of distiphallus microtrichose; microtrichia sparse and very small in *A. setigera*, coarse and prominent in *Australimyza* sp. A.

Female terminalia. Sternites 4 and 5 simple in *Australimyza* sp. A, very wide and medially divided in *A. setigera*, apparently also wide in *A. anisotomae*. Ovipositor conspicuously shortened, hardly telescopic. Cerci small and short. Spermathecae mushroom-shaped (Fig. 8C, D), with short individual ducts, arising from very short common duct. Accessory glands paired (Fig. 8D: ag), much longer than spermathecae including ducts, apically dilated into membranous sac, basally joining vagina immediately behind spermathecal duct. Ventral receptacle not developed.
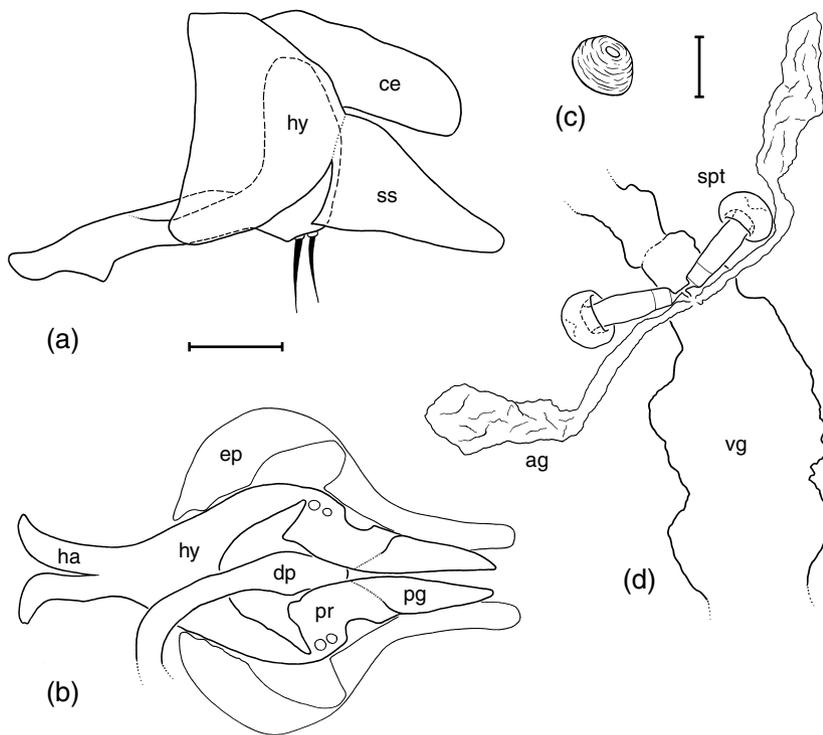
Fig. 8. *Australimyza setigera*, genitalia. A–B, male genitalia (phallapodeme, ejaculatory apodeme, distal portion of distiphallus and hairing omitted): A, lateral view; B, ventral view. C–D, female: C, spermatheca, dorsal; D, female reproductive system, dorsal. Scale: 0.05 mm. ag, accessory gland; ce, cercus; dp, distiphallus; ep, epandrium; ha, hypandrial apodeme; hy, hypandrium; pg, postgonite; pr, pregonite; spt, spermatheca; ss, surstylus; vg, vagina.

Phylogenetic relationships of Inbiomyiidae

Monophyly of the Carnoidea

The Carnoidea is one of the most poorly defined superfamilies in the Schizophora. Its putative sister group is the Opomyzoidea (J.F. McAlpine, 1989), which is equally poorly defined. J.F. McAlpine (1989) gives ten synapomorphies for the Carnoidea: (1) uppermost fronto-orbital bristle(s) exclinate; (2) lowermost fronto-orbital bristle(s) inclinate; (3) postocellar bristles relatively weak; (4) paravertical (= inner occipital) bristles present; (5) proepisternal bristle present; (6) proepimeral bristles present; (7) subcosta weakened or absent apically, contiguous or fused with R_1; (8) R_1 bare (reversal in *Apetaenus* Eaton, Canacidae s.l.); (9) epiphallus absent; (10) two spermathecae. None of these characters is very convincing. Characters (5) and (6) are difficult to polarize because they show a high degree of homoplasy. Characters (7) and (10) are present in most taxa of the sister group Opomyzoidea and could be a synapomorphy for the Carnoidea + Opomyzoidea (reversal in Acartophthalmidae). Characters (8) and (9) are probably plesiomorphic. Character (3) is subjective, and characters (2) and (4) are based on doubtful homology assumptions. In accordance with Brake (2000), I am interpreting the inclinate bristles of the frons as orbitals in Carnidae and as frontals in Milichiidae (see also characters 1–3 of the phylogenetic analysis below). According to this homologization, neither inclinate orbitals nor frontals are present in the Carnoidea ground plan. I concur with D.K. McAlpine (2006) that the paravertical bristles of

Canacidae (s.l.) are in fact postvertical bristles. Of the ten characters given by J.F. McAlpine (1989), I tentatively consider (1) as a synapomorphy of the Carnoidea. Two new putative synapomorphies are suggested here: (11) phallus flexible, unsclerotized, simple and elongate; (12) phallus microtrichose. These characters clearly are apomorphic with regard to the putative sister group Opomyzoidea and the Schizophora ground plan, and are present in most Carnoidea, except in some derived groups (Cryptochetidae, Milichiidae, Chloropidae, *Carnus*). Based on these characters, the monophyly of the Carnoidea is accepted tentatively as a working hypothesis.

Taxonomic limits of the Carnoidea

The selection of families included in Carnoidea is based on J.F. McAlpine (1989) with some exceptions: (i) Risidae have been shown recently to be an aberrant clade of Ephydridae (Freidberg *et al.*, 1998); (ii) Acartophthalmidae were considered the sister group of Clusiidae (Opomyzoidea) by many previous authors (e.g. Hennig, 1958, 1965, 1971; J.F. McAlpine, 1989); other authors (Hennig, 1939; Griffiths, 1972; Brake, 2000) referred the family to the Carnoidea; this view is followed here (see also discussion below); (iii) 'Tethinidae' are united with Canacidae because the former is paraphyletic with regard to the latter (see discussion below).

Australimyzidae were given family status by Griffiths (1972), which was followed by J.F. McAlpine (1989). However, Colless & McAlpine (1970, 1975, 1991) and

Grimaldi (1997) included *Australimyza* in the Carnidae and considered Australimyzidae a synonym of the latter. To resolve the relationship between these two families, the Carnidae is included in the present analysis not at the family level, but with its four extant genera *Neomeoneurites*, *Hemeromyia*, *Meoneura* and *Carnus*.

Cryptochetidae were included in Carnoidea by J.F. McAlpine (1989), but were referred to the superfamilies Ephydroidea and Lauxanioidea by others (e.g. Griffiths, 1972; D.K. McAlpine, 1976). I agree with J.F. McAlpine (1989) that there is no convincing evidence to include the Cryptochetidae in either the Ephydroidea (see also Hennig, 1971) or the Lauxanioidea (see also D.K. McAlpine, 1976). D.K. McAlpine's (*l.c.*) main argument for including Cryptochetidae in the Ephydroidea was the hypothetical relationship with the amber fossil *Phanerochaetum* Hennig and with the enigmatic extant genus *Librella* D.K. McAlpine, both of which share certain apomorphic characters with the Ephydroidea (e.g. pedicel with dorsal seam). Cryptochetidae, on the other hand, share several apomorphic characters with families of the Chloropidae family group (Carnoidea), which do not occur in Ephydroidea, namely: (1) connection of pedicel and first flagellomere of Milichiidae type (character 12 of phylogenetic analysis); (2) posterior tentorial pit divided (shared with Milichiidae, Chloropidae; a character not occurring in the Ephydroidea; character 9 of phylogenetic analysis); (3) wing venation in anal region of Milichiidae type (characters 34–36 of phylogenetic analysis).

Following Griffiths (1972), the Braulidae are considered here as a family of uncertain relationships. As a result of its highly autapomorphic morphology, this family is difficult to place in a phylogenetic analysis based on morphological characters alone.

Monophyly of taxa included in the phylogenetic analysis of Carnoidea

Monophyly of Inbiomyiidae. The monophyly of *Inbiomyia* is documented by many synapomorphies. The following list includes mostly characters that are unique within the superfamily Carnoidea. Further apomorphic characters that have evolved convergently in other Carnoidea taxa are mentioned below (see characters 3, 4, 9, 12, 13, 15, 16, 17, 23, 38, 40, 43 of phylogenetic analysis).

1. *Frons* (Fig. 3A) extremely short, with ocellar 'triangle' broadly attaining anterior margin of frons and ocellar tubercle approximately in middle of frons. Frons completely sclerotized through lateral expansion of ocellar plate. The primitive state in Schizophora is a somewhat weakened and flexible frontal vitta, which allows for slight lateral dilation when the ptilinum is inflated during emergence. The re-sclerotization of the frons in *Inbiomyia* is probably related to the reduction of the ptilinum, which apparently has become nonfunctional. A secondary sclerotization of the frons has occurred numerous times within Schizophora and, in some families, it has been achieved in a similar way as in *Inbiomyia* through enlargement of the ocellar plate (e.g. some Ephydridae, Canacidae and Chloropidae).

2. *Ptilinum* without armature of small scales or setulae, membranous. This condition is not known from any other Schizophora family. Even in species with a very reduced ptilinum (*Australimyza*, see below; Ephydridae: *Scatella* Robineau-Desvoidy, *Hyadina* Haliday, pers. obs.; some Sciomyzidae and Hippoboscidae, see Strickland, 1953), the armature of scales or setulae is retained. In other families, the scales are missing only when the ptilinum becomes completely sclerotized (Sciomyzidae: *Sepedon* Latreille, see Strickland, 1953).

3. *Posterior tentorial pit* (Fig. 9C) divided, upper portion drawn out horizontally toward eye margin. Divided tentorial pits occur in several families (see phylogenetic analysis), but in no other family is the upper portion drawn out horizontally.

4. *Arista* (Fig. 3A) extremely elongate, longer than head and thorax combined. This character state appears to be unique within the Acalyptratae.

5. *Prementum* with upcurved lateral margins bearing two pairs of bristles that cross over dorsally above the labrum (Fig. 3A: cr). The prementum of other Acalyptratae lacks cruciate bristles that are crossed dorsally. The lateral margins of the prementum of certain Carnidae genera are upcurved even more strongly than in *Inbiomyia*, but the shape of the prementum differs significantly (short and bulbous vs. elongate and slender in *Inbiomyia*).

6. *Labellar lobes* (Fig. 3C) slender and pointing in almost opposite directions, not fused to each other along midline. This configuration appears to be unique within the Acalyptratae. In other families, the labellar lobes are at least partially (usually more or less completely) fused along the midline and their apices are pointing approximately in the same direction.

7. *Posterior notopleural bristle* conspicuously shifted dorsally (Fig. 1). This very unusual character has developed independently in some other Acalyptratae families (e.g. in the Ephydridae: Ilytheini, Hecamedini).

8. *Katepisternal bristle* sloping forward (Fig. 1). Usually in Acalyptratae the katepisternal bristle (posterior one if more than one is present) is directed dorsally or slopes slightly posteriorly. An anteriorly directed katepisternal bristle has developed independently in Coelopidae (D.K. McAlpine, 1991b) and some Pseudopomyzidae (*Pseudopomyzella* Hennig).

9. *Mid tibia* without ventroapical bristle. A clearly differentiated ventroapical mid-tibial bristle is present in the ground plan of the Schizophora and all Acalyptratae families. Rarely, it is quite small (Chyromyidae: virtually absent in small species; Teratomyzidae: absent in *Teratomyza* Malloch) or missing (Sphaeroceridae: *Opacifrons* Duda).

10. *Abdominal sternites* lacking the usual pair of anterior *sensilla trichodea* in both sexes. The presence of a pair of anterior sensory setulae on each sternite is a very

conservative character within the Schizophora (M.R. Wheeler, 1960). The distribution of this character throughout the Schizophora has not been studied thoroughly, but I know of no other taxa lacking these setulae.

11. *Male tergite 5* (e.g. Fig. 6D) with two pairs of spiracles (pertaining to segments 5 and 6). This condition is unknown from the Schizophora, but it has developed independently in the 'Aschiza' family Lonchopteridae.

12. *Synsternite 5 + 6 + 7* (Fig. 4A, B). The fusion of pregenital sclerites represents a widespread trend in Schizophora. The sclerites most commonly involved in the fusion are sternites 6 through 8 (sometimes including remnants of corresponding tergites), while sternite 5 remains separate. In *Inbiomyia*, sternite 8 is articulated to synsternite 5 + 6 + 7, and sternite 5 has become involved in the fusion process.

13. *Male sternite 8* (Fig. 4A) well defined but very short, reduced to a linear, transverse band. This condition is rare in Schizophora because sternite 8 usually serves as a muscle attachment and therefore is relatively large in most taxa. Reductions have occurred independently in various Acalyptratae families, most notably in the Ephydroidea.

14. *Ring-shaped sclerite* (Fig. 4C: rs) behind male tergite 5. This peculiar, weakly developed sclerite might represent a modified nonfunctional left spiracle 7. A comparable condition can be observed in certain male Sphaeroceridae, where the right spiracle 7 is greatly enlarged, nonfunctional and has shifted ventrally into the genital pouch.

15. *Ventral epandrial process* (e.g. Fig. 4A). Epandrial lobes, which are sometimes difficult to distinguish from lengthwise divided (duplicated) surstyli (e.g. Fig. 12A), have developed independently in a number of families, e.g. Odiniidae, Dryomyzidae, Asteiidae (*Leiomyza* Macquart), 'Tethinidae' and most Tephritoidea.

16. *Male cerci* absent (or incorporated in subanal plate). Even though the cerci are often reduced in Acalyptratae (i.e. very small and/or membranous and poorly defined), a clearly recognizable remnant almost always is present. However, some Sphaeroceridae have evolved a similar condition where cercal material forms a subanal plate, connecting the epandrial sides below the anus.

17. *Hypandrium* (Fig. 7E) with undifferentiated, bare pregenital area. In most Schizophora, each postgonite is articulated to a setulose, more or less differentiated (e.g. protuberant) portion of the hypandrium, which is called the pregonite (e.g. Fig. 8B: pr). In Inbiomyiidae, the hypandrium is completely devoid of setulae, and pregonites are not differentiated.

18. *Female terminalia* (e.g. Fig. 7A, B) extremely truncate; cerci, tergite and sternite 10 lost. An extreme shortening of the female ovipositor, involving the complete loss of cerci and segment 10, is very unusual within the Acalyptratae (e.g. Sphaeroceridae: *Pterogramma substriatum* group, see Smith & Marshall, 2004).

19. *Egg* (Fig. 5C) extremely flattened with chorion of upper surface firm; chorion of lower surface thin and membranous. This egg morphology is highly unusual for Acalyptratae and reminiscent of macrotype Tachinidae eggs.

Australimyzidae

Autapomorphies (plesiomorphic state in parentheses). (1) Fulcrum with internal 'filter apparatus', cf. Fig. 11(H) (absent). (2) Proepisternal bristle in a far forward position, distinctly closer to cervical sclerite than to base of fore coxa (not shifted forward, close to base of fore coxa). (3) Katepisternum with two dorsal bristles (one bristle). (4) Tarsomeres relatively short and stout (not shortened). (5) Tergite and sternite of male segment 7 fused, forming an asymmetrical, complete ring (not fused). (6) Ejaculatory apodeme extremely long, rodlike (not unusually long). (7) Hypandrial apodeme paired, cf. Fig. 8(B) (unpaired). (8) Hypandrial bridge present but partly desclerotized in some species (absent). (9) Coastal habitat (not coastal).

Characters (2), (7) and (8) are newly recognized as synapomorphies and should be studied on a larger array of species.

Neomeoneurites Hennig (Carnidae)

Autapomorphies (based on Hennig, 1972; T.A. Wheeler, 1994; plesiomorphic state in parentheses). (1) Ventral appendage of stipes absent (present). (2) Lacinia reduced (present). (3) Katepisternum with two dorsal bristles (one bristle). (4) Sternite 8 fused to right side of hypandrium (not fused). (5) Hypandrium with a pair of large posteroventral projections (without projections). (6) Surstyli greatly reduced, indistinguishably fused to epandrium (separate from epandrium). (7) Ovipositor greatly elongated, longer than remainder of body from head to posterior margin of segment 5 (moderately elongated). (8) Tergite 6 medially divided (entire). (9) Female tergites 6 and 7 with long anterior apodemes (without apodemes).

Hemeromyia Coquillett (Carnidae)

Autapomorphies (plesiomorphic state in parentheses). (1) Female spiracle 7 absent (present). (2) Female cercus very shortened, not longer than broad (elongate).

The monophyly of this genus is weakly supported, and it could prove to be paraphyletic with regard to *Meoneura* + *Carnus*. I could not find any autapomorphic characters in the male genitalia. Character (1) needs to be checked on more material as there might be plesiomorphic species that retain spiracle 7. Character (2) also occurs in *Carnus*, but both *Neomeoneurites* and *Meoneura* have slender cerci. I therefore consider the shortened cercus of *Carnus* a case of convergence.

Carnus Nitzsch (Carnidae)

Autapomorphies (plesiomorphic state in parentheses). (1) Postvertical bristles absent (present). (2) Proboscis with reduced labella (not reduced). (3*) Wing vein dm-cu absent (present). (4*) Wing dehiscent (not dehiscent). (5*) Physogastry (abdomen normal). (6) Male spiracle 7 absent (present). (7) Epandrium with dorsomedial suture from anterior to posterior margin (suture absent). (8) Hypandrium not directly connected to epandrium (articulated to each other). (9) Hypandrium on each side shield-like, projecting over base of postgonites and phallus (not projecting). (10*) Distiphallus extremely shortened and bare (long and microtrichose). (11) Female spiracle 7 absent (present). (12) Female cercus shortened (elongate). (13*) Ectoparasites of birds. (*Also mentioned by Grimaldi, 1997.)

Both Hennig (1972) and Sabrosky (1987) illustrated a spiracle 7 for the female of *Carnus hemapterus* Nitzsch. In the specimens examined here, no trace of spiracle 7 was detected.

Meoneura Rondani (Carnidae)

Autapomorphies (after Grimaldi, 1997; plesiomorphic state in parentheses). (1) Costal setulae of sector 1 long, *c.* 2.5× width of costal vein (no longer than 1.5× width of costal vein).

As already pointed out by Hennig (1972), *Meoneura* could well be paraphyletic with regard to *Carnus*. Grimaldi (1997) tentatively suggested autapomorphy (1) for *Meoneura*. However, certain undescribed species of the genus have costal setulae of the same size as in *Carnus*. No additional autapomorphies could be found during this study. Some species of *Meoneura* (apparently undescribed) share characters (6) and (11) of *Carnus*. If *Meoneura* is indeed paraphyletic, the sister group of *Carnus* might be found in these species.

Canacidae s.l. (including 'Tethinidae')

The monophyly of the Tethinidae is disputed (Griffiths, 1972; J.F. McAlpine, 1989). I agree with D.K. McAlpine (2006) that the Tethinidae, as defined currently (see Mathis & Munari, 1996), are almost certainly paraphyletic with regard to the Canacidae. I am therefore combining the two families for the current analysis. Canacidae is the older name and therefore has priority. Here, Canacidae in the traditional sense are referred to as Canacidae (s.str.) and the Canacidae + 'Tethinidae' as Canacidae (s.l.).

Autapomorphies (plesiomorphic state in parentheses). (1) Precoxal bridge present (absent). (2) Anepisternum with enlarged, upcurved seta in posterodorsal corner (upcurved seta absent or small and hairlike). (3) Vein A_2 long, present as a fold (absent). (4) Male sternite 6 reduced and medially divided (entire and not reduced). (5) Male tergite 6 fused with sternite 8, forming symmetrical pregenital sclerite (tergite 6 free). (6) Male sternite 7 lost, not incorporated into pregenital sclerite (present). (7) Postgonites firmly connected laterally to base of phallapodeme, distinctly anterior to basiphallus (articulated to phallapodeme at level of basiphallus). (8) Hypandrium forming sheath (phallic mantle) around postgonite and basiphallus (phallic mantle absent). (9) Halophilic (not halophilic).

For a discussion of characters (1), (2), (3), (5) and (6), see D.K. McAlpine (2006). Characters (4), (7) and (8) have never been recognized as synapomorphies of the Canacidae (s.l.) and therefore deserve further comment:

(4) Sternite 6. The ground plan condition can be observed in Apetaeninae (e.g. Papp, 1983: fig. 2), Zaleinae (some *Zalea* spp.) and many Canacidae (s.str.). In the other subfamilies, sternite 6 appears to be completely lost. The homology of the paired last ventral sclerite with sternite 6 is convincingly established by the presence of a pair of *sensilla trichodea*.

(7) Postgonite. Plesiomorphically in Carnoidea (and most Schizophora) the postgonites articulate with the base of the phallapodeme at the same level as the basiphallus. In the stem species of the Canacidae (s.l.), the base of the postgonite became extended anteriorly alongside the base of the phallapodeme, thus articulating in a distinctly more anterior position than the basiphallus (Fig. 12D). This is highly unusual for Schizophora, and similar conditions are only found in Syringogastridae (Diopsoidea) and Nerioidea. In the latter, however, the postgonite became completely fused to the phallapodeme. In the Canacidae (s.l.), the postgonite is connected firmly to the phallapodeme (precluding movement), but the two are not fused to each other. Posteriorly, the postgonites are often weakly sclerotized and mostly hidden within the phallic mantle (see below). Because of this complicated morphology, the postgonites have been misinterpreted sometimes as pregonites (Beschovski, 1994).

(8) Phallic mantle (Fig. 12C, D: pm). One of the most peculiar apomorphies of the Canacidae (s.l.) is the formation of a membranous, ventrally open fold around the postgonites and the base of the phallus. The origin of this fold is hypandrial and it involves the portion of the hypandrium that is differentiated as pregonites in many families of Schizophora. The mantle is formed by medial fusion of the 'pregonites' above the phallus. Griffiths (1972), who called this fold the 'aedeagal mantle', first recognized its phylogenetic significance in defining the Canacidae (s.str.). However, a homologous structure is present in all subfamilies of Canacidae (s.l.) and the character must therefore be considered as a synapomorphy of the Canacidae (s.l.). The phallic mantle is reduced secondarily in the genus *Pelomyia* Williston, forming merely a narrow bridge above the basiphallus, and was referred to as a 'gonopodal hood' by Foster & Mathis (2003). In the related genus *Pelomyiella* Hendel, the phallic mantle is developed normally as in other subfamilies. A perplexingly similar membranous fold is also present in most Odiniidae.

Here, the phallic mantle appears to envelop the base of the phallus only and no postgonites are apparent inside. In fact, the mantle might have originated from dorsomedially fused postgonites (as opposed to pregonites) in this family. At present, I consider the phallic mantle of the Canacidae (s.l.) as nonhomologous to the similar structure in Odiniidae, but further study is required.

Sister group of Canacidae (s.str.). Based on the relatively large male syntergosternite 6 + 8 and misinterpreted homology of the postvertical bristles (see D.K. McAlpine, 2006), the Zaleinae have been considered to be more closely related to the Canacidae (s.str.) than have other subgroups of the 'Tethinidae' (D.K. McAlpine, 1982; Freidberg, 1995). I disagree for two reasons: a large, setose tergite 6 probably is a plesiomorphy, and the apomorphic presence of two pairs of surstyli in *Zalea* D.K. McAlpine appears to link this genus to other 'Tethinidae' (especially the Tethininae). Without further analysing canacid subfamily relationships, the Apetaeninae seem the most likely sister group to the Canacidae (s.str.), supported by the following putative synapomorphies (plesiomorphic states in parentheses). (1) Antennae broadly separated, inserted on more or less protuberant facial tubercle (antennae contiguous, not on facial tubercle, usually in slightly depressed foveae). (2) Clypeus distinctly enlarged and anteriorly produced (clypeus small, not produced). (3) Prementum apically distinctly emarginate (more or less straight). (4) Tentorial arms of head capsule enormously developed and strongly sclerotized, cf. Fig. 9E: ta (inconspicuous and weakly sclerotized).

Acartophthalmidae

Autapomorphies (plesiomorphic state in parentheses). (1) Male spiracle 7 absent (present). (2*) Male sternites 6 and 8 fused to form a symmetrical pregenital sclerite (not fused). (3) Female spiracle 7 absent (present). (*Misinterpreted by Griffiths, 1972; see discussion of character 39 in phylogenetic analysis below.)

Cryptochetidae

Autapomorphies (plesiomorphic state in parentheses). (1) Arista dorsoapical and strongly reduced (dorsobasal, not reduced). (2) Ocellar bristles absent (present). (3) Orbital bristles absent (present). (4) Ocellar triangle setulose (bare). (5) Dorsal cornuae of fulcrum reduced as in Fig. 11D (not reduced). (6) Long axis of thorax shortened (not shortened). (7) Propleuron in its entirety oriented perpendicular to long axis of body, facing occiput (oriented at least in part parallel to long axis of body and facing laterally). (8) Katepisternum bare (with at least one dorsal bristle and several setulae). (9) Main bristles of scutum reduced (not reduced). (10) Scutellum with sharp-edged posterior margin (rounded). (11) Abdominal spiracles lost in both sexes except for spiracle 6 (spiracles 1–5 present). (12) Male sternites 6–8 lost (present). (13) Phallus rigid, sclerotized and bare (flexible, largely membranous, microtrichose). (14) Ovipositor modified for piercing (simple). (15) Larvae endoparasitic in scale insects (larvae free-living).

Milichiidae

Autapomorphies (after Brake, 2000; plesiomorphic state in parentheses). (1) Three pairs of exclinate orbital bristles (latero-reclinate). (2) Two pairs of inclinate frontal bristles (frontal bristles absent; see also character 1 of phylogenetic analysis). (3) Frons with a pair of setulae between supra-antennal setulae (= anterior pair of interfrontals) and frontal orbits (not differentiated). (4) Lunule with a pair of setulae (bare). (5) Labella with four pairs of pseudotracheae (with more than four pairs). (6) Postgonite absent (present).

Chloropidae

Autapomorphies (after Andersson, 1977; plesiomorphic state in parentheses). (1) First and second pair of orbital bristles latero-proclinate (latero-reclinate). (2) Propleuron with sharp, vertical carina (carina absent). (3) Hind tibia with a 'tibial organ', see Andersson (1977) (absent). (4) Subcosta reduced in apical half (present). (5) Vein bm-cu absent (present). (6) CuA_1 slightly sinuate near middle of penultimate sector (straight). (7) Cell *cup* absent (present). (8) Male tergite 6 absent (present).

Characters used in the phylogenetic analysis of Carnoidea

Fifty-eight characters were used for the analysis of Carnoidea relationships (Table 1). Characters are polarized on the basis of outgroup comparison with Clusiidae and 'Heleomyzidae'. Clusiidae is one of the most plesiomorphic families of the Opomyzoidea, the putative sister group of the Carnoidea. According to J.F. McAlpine (1989), the Sphaeroceroidea (including 'Heleomyzidae') + Ephydroidea is the sister group of the Carnoidea + Opomyzoidea. Certain clades currently placed in the paraphyletic 'Heleomyzidae' represent the least derived groups within the Sphaeroceroidea.

Head

Note on homology of orbital bristles (cf. characters 1–3). Considering that the addition or loss of orbital bristles apparently took place near the anterior margin of the frons, orbital bristles should be homologized from the vertex forward. My homologization of the individual orbital bristles therefore differs from Grimaldi (1997). Grimaldi considered the presence of inclinate orbital bristles a synapomorphy for the Carnidae + Australimyzidae (in both groups the anterior pair is inclinate). However, the inclinate pair is the third one from behind in Australimyzidae, but

Table 1. Character matrix for the Carnoidea with Clusiidae and 'Heleomyzidae' as outgroups. Character 48 is ordered, characters 9, 10, 30, 31, 40, 52, 53 and 54 are considered irreversible.

Taxon	1 1234567890	2 1234567890	3 1234567890	4 1234567890	5 1234567890	12345678
'Heleomyzidae'	0??0?00000	0000000000	0000?0??00	0000000000	000000?00?	00000000
Clusiidae	0?00000000	0010000000	0000000000	0000010000	0000001000	00001010
Acartophthalmidae	0000000011	0000000000	0000000010	0000010331	0210001110	01011110
Canacidae (s.l.)	0?00000000	0000000000	0001000100	1000100201	2010001111	00001011
Cryptochetidae	0321000011	1110001001	2111202111	1001100001	2220021010	01111010
Milichiidae	0210000011	0100011000	2110100011	1001100111	1000001200	00011120
Chloropidae	0210000011	0000011000	2001200101	1011210311	1000001200	00011120
Australimyzidae	01?0100100	1000000000	1000101011	1000010000	0201120111	11001001
Inbiomyiidae	0121000110	1110111002	1010100011	1000010321	0211120110	11?01000
Neomeoneurites	10001110??	0?00111011	1??0101000	1000010101	0?00020110	001010?0
Hemeromyia	1110112010	0001100011	2010010011	1000011100	0100011110	01101010
Meoneura	1110112011	0001100111	2010010011	1111211310	1110011110	00111010
Carnus	1110112011	0001100111	2010010011	1111211310	1210010200	01111010

the fourth one from behind in *Neomeoneurites*, the sister group of the rest of Carnidae.

1. *Fourth orbital bristle from behind*: 0, absent; 1, inclinate to medio-reclinate. The presence of four pairs of orbital bristles is a synapomorphy for Carnidae. A fourth pair of orbitals evolved independently more than once within Canacidae s.l. (some Canacidae (s.str.), *Horaismoptera* Hendel, some Tethininae). I am following Brake (2000) in interpreting the inclinate bristles of the lower frons of Milichiidae as frontal bristles, not orbitals.

2. *Third orbital bristle from behind*: 0, latero-reclinate to reclinate; 1, inclinate to medio-reclinate; 2, exclinate to latero-proclinate; 3, absent. Outgroup comparison for this character is inconclusive because multiple character states occur (Clusiidae: inclinate and reclinate; 'Heleomyzidae': usually absent, otherwise reclinate). The single pair of long, inclinate orbitals in Inbiomyiidae (Fig. 3A: or) is homologized with the third pair of orbitals in other families. The first and second pairs in Inbiomyiidae are vestigial (reduced to small setulae, Fig. 3A: ors). This reduction in size appears to be linked to the extreme shortening of the frons in Inbiomyiidae.

3. *Second orbital bristle from behind*: 0, latero-reclinate to reclinate; 1, exclinate to latero-proclinate; 2, absent. In the Carnidae ground plan, the first pair of orbitals is latero-reclinate. In 'Heleomyzidae', the orientation varies from reclinate to exclinate.

4. *Ocellar bristles*: 0, present; 1, absent or minute. A loss of ocellar bristles has occurred independently in Inbiomyiidae and Cryptochetidae.

5. *Inner occipital (paravertical) bristles*: 0, absent; 1, present. Inner occipitals are present in Carnidae, Australimyzidae and some Milichiidae (e.g. *Phyllomyza* Fallén). The character is equivocal in Cryptochetidae because the bristles on the vertex are uniform in size and therefore difficult to homologize.

In 'Heleomyzidae', the inner occipitals vary from well developed to not differentiated.

6. *Antennal foveae*: 0, absent or shallow, not well defined; 1, deep and sharply defined.

7. *Facial carina*: 0, absent; 1, broad; 2, narrow. Characters 6 and 7: The presence of deep antennal foveae is a synapomorphy of the Carnidae. In *Neomeoneurites*, the carina separating the foveae is broad and sclerotized; in higher Carnidae (*Hemeromyia*, *Meoneura*, *Carnus*), it is very narrow and medially desclerotized. In some species of *Hemeromyia* the facial carina is secondarily poorly developed and the antennal foveae are relatively shallow.

8. *Ptilinum*: 0, well developed and functional; 1, very small (length less than first flagellomere), apparently nonfunctional. The reduction of the ptilinum is a putative synapomorphy of the Inbiomyiidae + Australimyzidae. Very few examples for this character state have been reported in the Schizophora (Strickland, 1953). However, reduced ptilina are easily overlooked (only detectable through clearing of head capsule), and might be more widespread than thought. A brief survey of some non-Carnoidea families revealed similarly reduced ptilina in two Ephydridae genera (*Scatella picea* (Walker), *Hyadina albovenosa* Coquillett).

9. *Posterior tentorial pit*: 0, elongate and entire; 1, divided into basal and distal pits, connected at most by faint scar. The transition from 0 to 1 is considered to be irreversible. To my knowledge, this phylogenetically interesting character has not been mentioned in the previous literature. In the Schizophora ground plan, the posterior tentorial pit is drawn out ventrolaterally forming an elongate sulcus that stretches from near the occipital foramen towards the ventrolateral corner of the postgena (Fig. 9A: pt). The tentorial process (Fig. 9A: tp), a short, usually medially directed, process that ends blindly in the head cavity, arises from its base
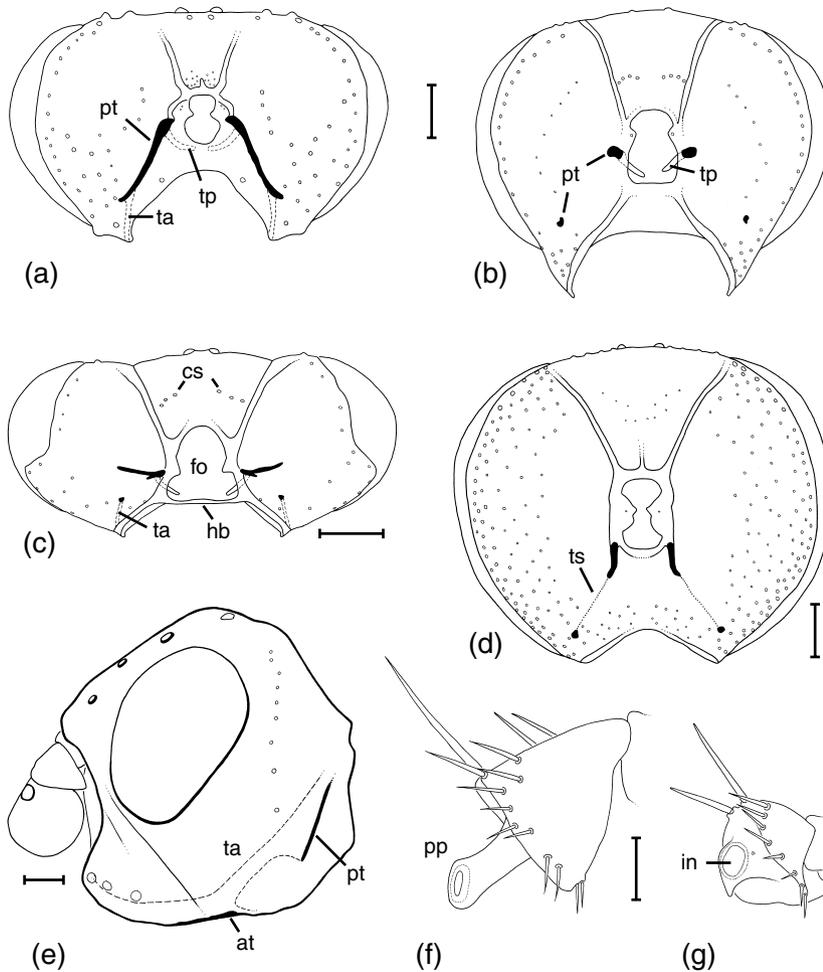
Fig. 9. Carnoidea, heads and pedicels. A–D, occiput: A, *Australimyza setigera*; B, *Appalates* sp. (Chloropidae); C, *Inbiomyia mcalpineorum*; D, *Cryptochetum iceryae* (Cryptochetidae). E, *Listriomastax litorea*, head capsule, lateral (Canacidae). F–G, left pedicels, lateral: F, *Pholeomyia* sp. (Milichiidae); G, *Australimyza setigera*. Scale: 0.1 mm (A–E), 0.05 mm (F, G). at, anterior tentorial pit; cs, sockets of supracervical setulae; fo, occipital foramen; hb, hypostomal bridge; in, insertion area of first flagellomere; pp, process of pedicel; pt, posterior tentorial pit; ta, anterior tentorial arm; tp, tentorial process; ts, scarlike connection between posterior tentorial pits.

near the occipital foramen (Bonhag, 1951). The anterior tentorial arm (Fig. 9A, E: ta) arises from the opposite extreme ventrolaterally on the postgena, connecting it with the anterior tentorial pit. Internally, the drawn out posterior tentorial pit is reinforced by a distinct ridge between the insertion points of the tentorial process and the tentorial arm. In most Carnoidea and a few other families (Agromyzidae, Fergusoninidae, Sphaeroceridae, Strongylopthalmyiidae), the sulcus becomes obliterated between the two ends, i.e. the anterior tentorial arm and the tentorial process now arise from two separate pits (Fig. 9B, C). In some families (e.g. Cryptochetidae), a connection between the two pits is indicated faintly by a scarlike weakening of the cuticle (Fig. 9D: ts).

10. *Tentorial arm*: 0, distinct and sclerotized; 1, absent or filiform and translucent (desclerotized); if present only detectable under high magnification. The transition from 0 to 1 is considered to be irreversible. The anterior tentorial arm is developed moderately in the Schizophora ground plan. Within Carnoidea, this condition is expressed in the Australimyzidae (Fig. 9A: ta) and several Canacidae (s.l.) subfamilies (Tethininae, Pelomyiinae, Horaismopterinae and Zaleinae). In taxa with a divided posterior tentorial pit, the tentorial arm is absent or strongly reduced. In the Apetaeninae + Canacidae (s.str.), the tentorial arm is secondarily very strongly developed (Fig. 9E).

11. *Eye pubescence* (in centre of eye): 0, absent or sparse (i.e. with < 50% of the ommatidial junctions occupied by a hair); 1, present and dense (50% or more ommatidial junctions occupied by a hair). This character is of limited phylogenetic value because of the high degree of homoplasy in Schizophora. Sparsely pubescent eyes can be found in many Acalyptratae families, e.g. in Acartophthalmidae. Densely pubescent eyes evolved several times independently within Carnoidea (Canacidae s.l.: Zaleinae, three genera of Tethininae; several lineages of Chloropidae).

12. *First flagellomere connection with pedicel*: 0, inserted laterally on small process of pedicel projecting little into first flagellomere; 1, inserted apically on long process projecting deeply into first flagellomere. In most Schizophora, the first flagellomere articulates laterally on a small process of the pedicel (e.g. Fig. 9G), which is also the assumed ground plan condition for Carnoidea. Apomorphically, the process of the pedicel becomes elongated (e.g. Fig. 9F), extending

deeply into the first flagellomere, and the latter articulates apically or apicolaterally on the pedicel. This condition has developed independently in Milichiidae, Cryptochetidae and Inbiomyiidae. Outside Carnoidea, a very similar flagellar connection is found in Pseudopomyzidae and Sphaeroceridae.

13. *Arista*: 0, inserted dorsobasally on first flagellomere; 1, inserted dorsoapically. A dorsoapical arista was considered part of the Schizophora ground plan by J.F. McAlpine (1989: 1426). However, based on outgroup comparison with the Syrphoidea, which possess a dorsobasal arista, it is more parsimonious to interpret the dorsoapical insertion as apomorphic (see also Cumming *et al.*, 1995). Dorsoapically inserted aristae have evolved independently in Inbiomyiidae, Cryptochetidae, Clusiidae and Nerioidea (Pseudopomyzidae, Neriidae).

14. *Prementum, shape*: 0, not short and swollen; 1, short and swollen.

15. *Prementum, lateral margin*: 0, not upcurved; 1, upcurved. Characters 14 and 15: Usually the prementum is more or less flat in Schizophora. Within Carnoidea, the lateral margins of the prementum become strongly upcurved in Inbiomyiidae (Fig. 3A), Carnidae and Canacidae (s.str.). A strongly swollen prementum has developed in higher Carnidae (*Hemeromyia*, *Meoneura*, *Carnus*) as well as Canacidae (s.str.).

16. *Stipes, ventral appendage*: 0, present (Fig. 10B); 1, absent.

17. *Lacinia*: 0, well developed (longer than broad); 1, strongly reduced. Characters 16 and 17: The loss of these structures is apomorphic for Chloropidae + Milichiidae (Brake, 2000). It has also occurred, apparently convergently, in *Neomeoneurites* and Inbiomyiidae (Fig. 10G). The ventral appendage of Clusiidae is small and difficult to see, as noted already by Frey (1921).

18. *Labrum, internal knoblike projection*: 0, absent; 1, present. The dorsal wall of the labrum bears a peculiar internal process in *Meoneura* and *Carnus* (Fig. 11K), a synapomorphy linking these two genera.

19. *Labella, outer surface*: 0, membranous or weakly sclerotized, not shining; 1, extensively sclerotized and shining. Plesiomorphically, the outer surface of the labella is membranous or weakly sclerotized and dull in Carnoidea. In Carnidae, the outer labellar surface is sclerotized and shining.

20. *Labella*: 0, labellar lobes extended posteriorly behind connection point with haustellum and fused along midline (i.e. with notch between haustellum and labella in lateral view); 1, labellar lobes very short, not extended posteriorly (no notch in lateral view); 2, labellar lobes largely free, tapered distally and pointing laterally. Two apomorphic states for this character occur in the Carnoidea. In Carnidae, the posterior portion of the labella is reduced, with no notch to haustellum (Hennig, 1972). In Inbiomyiidae, the labellar lobes are separate and widely divergent (Fig. 3C) (see autapomorphies of the family above).

21. *Number of pseudotracheae*: 0, numerous (seven or more pairs); 1, reduced (five or six pairs); 2, extremely reduced (four or less pairs). The reduction in the number of pseudotracheae is a common trend in Schizophora (Frey, 1921), and is in general probably related to the reduction of body size. A reduction to four or less pairs of pseudotracheae apparently has happened at least three times within Carnoidea. Only Acartophthalmidae and certain lineages of Canacidae (s.l.) have retained the plesiomorphic state of seven or more pairs.

22. *Fulcrum, upper plate*: 0, with basal group of one to four sensilla; 1, without sensilla. Plesiomorphically, in Schizophora, the upper (posterior) plate of the fulcrum bears a group of four porelike sensilla (sometimes reduced to three or one) near the dorsal cornuae (e.g. Fig. 11A–C, E, G, H–J). These sensilla have been lost in Cryptochetidae and Milichiidae (Fig. 11D, F).

23. *Fulcrum, lower plate*: 0, with numerous setulae in two longitudinal rows; 1, number of setulae strongly reduced. In the Schizophora ground plan, the lower (anterior) plate of the fulcrum bears two longitudinal rows of well-developed setulae (e.g. Fig. 11A–C, E, H).
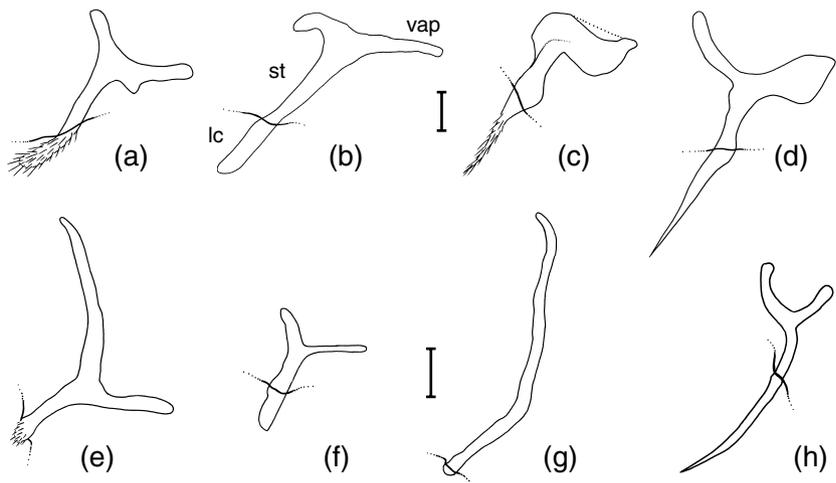

Fig. 10. Carnoidea, left maxilla (excluding palpus), lateral. A, *Acartophthalmus nigrinus* (Acartophthalmidae); B, *Paracanace hoguei* (Canacidae); C, *Pseudorhicnoessa* sp. (Canacidae); D, *Pelomyia intermedia* (Canacidae); E, *Cryptochetum iceryae* (Cryptochetidae); F, *Hemeromyia* sp. (Carnidae); G, *Inbiomyia mcalpineorum*; H, *Australimyza setigera*. Scale: 0.025 mm. lc, lacinia; st, stipes; vap, ventral appendage of stipes.
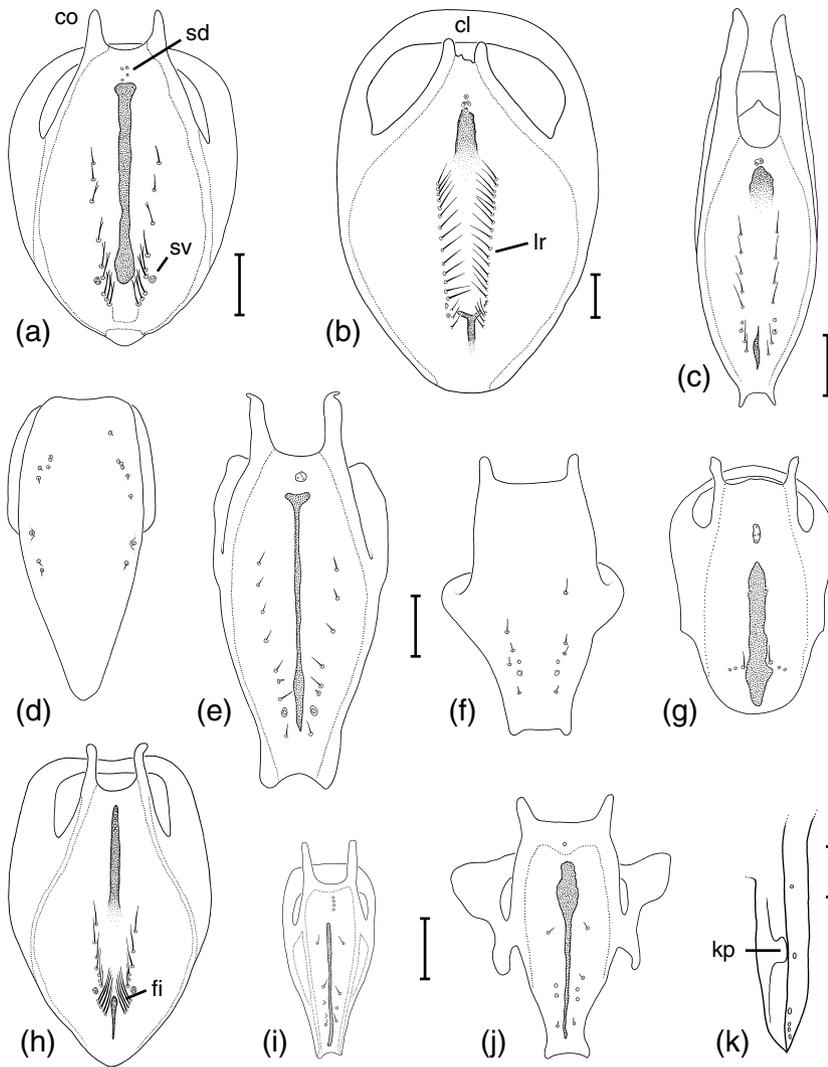
Fig. 11. Carnoidea, mouthparts. A–J, fulcra, dorsal: A, *Acartophthalmus nigrinus* (Acartophthalmidae); B, *Listriomastax litorea* (Canacidae); C, *Neopelomyia rostrata* (Canacidae); D, *Cryptochetum iceryae* (Cryptochetidae); E, *Apotropina* sp. (Chloropidae); F, *Phyllomyza* sp. (Milichiidae); G, *Inbiomyia mcalpineorum*; H, *Australimyza setigera*; I, *Meoneura triangularis* (Carnidae); J, *Carnus hemapterus* (Carnidae). K, *Carnus hemapterus*, labrum, lateral. Scale: 0.05 mm (A–J), 0.025 mm (K). cl, clypeus; co, dorsal cornuae; fi, 'filter apparatus' (*sensu* Frey, 1921); kp, knoblike, internal, dorsal projection of labrum; lr, longitudinal row of setulae of lower plate of fulcrum; sd, group of sensilla of upper plate of fulcrum; sv, group of sensilla of lower plate of fulcrum.

The setulae become reduced in number in Inbiomyiidae, Carnidae, Cryptochetidae, Milichiidae (and also in certain lineages within Canacidae (s.l.) and Chloropidae) (Fig. 11D, F, G, I, J).

Thorax

24. *Precoxal bridge*: 0, absent; 1, present. Precoxal bridges have developed independently at least three times within the Carnoidea: in Canacidae (s.l.) (secondarily reduced in some Zaleinae), Chloropidae, Cryptochetidae and in one lineage within the Milichiidae (Brake, 2000). Certain derived lineages of 'Heleomyzidae' (e.g. Blaesochaetophorini) also have a precoxal bridge (D.K. McAlpine, 1985).

25. *Anepisternum*: 0, setulose and outstanding bristle(s) at posterior margin; 1, bare; 2, setulose but without outstanding bristles. This character was inconsistently polarized by J.F. McAlpine (1989) (bare anepisternum as autapomorphy for Australimyzidae; set(ul)ose anepisternum as autapomorphy for Canacidae s.l.). An outstanding anepisternal bristle is part of the Carnoidea ground plan according to this analysis. In 'Heleomyzidae', all three character states occur.

26. *Anepisternum, upcurved seta near ventral margin*: 0, absent; 1, present. This unique bristle is a synapomorphy for the higher Carnidae (*Hemeromyia, Meoneura, Carnus*).

27. *Katepisternum*: 0, with one bristle; 1, with two to three bristles; 2, bare. The presence of a single katepisternal bristle as part of the Carnoidea ground plan (J.F. McAlpine, 1989) is confirmed by the present analysis. In 'Heleomyzidae', the number of katepisternal bristles is variable.

28. *Scutellum, disc*: 0, bare; 1, with at least a few setulae. The setulose scutellum comes out as a tentative synapomorphy of the Chloropidae family group (reversals in Milichiidae and many subgroups of Canacidae s.l.). The scutellum is bare or setulose in different tribes of the 'Heleomyzidae'.

29. *Costa, humeral break*: 0, absent; 1, present. The absence of a humeral break was believed to be part of the ground plan of the Carnoidea (J.F. McAlpine, 1989). However, J.F. McAlpine did not include Acartophthalmidae in the Carnoidea. If this family is included, then the humeral break becomes part of the Carnoidea ground plan (reversals in Canacidae s.l., Chloropidae and *Neomeoneurites*).

30. *Subcosta*: 0, complete; 1, apically desclerotized. The transition from 0 to 1 is considered to be irreversible. The apex of the subcosta usually is sclerotized, if it is well separated from the apex of R_1 (e.g. 'Heleomyzidae', Clusiidae, Acartophthalmidae). In some Canacidae (Canacidae s.str., Apetaeninae) and in *Neomeoneurites*, it is well sclerotized despite being closely approximated to the apex of R_1.

31. *Subcosta apex*: 0, strong and broadly separated from apex of R_1; 1, very close to apex of R_1 or evanescent. The transition from 0 to 1 is considered to be irreversible. Acartophthalmidae is the only Carnoidea in which the apex of the subcosta is separated broadly from the apex of R_1. An approximation of the two veins has taken place several times within the Schizophora. This step is considered to be irreversible because there are no indicators that reversals have occurred anywhere within the Schizophora.

32. *Vein M*: 0, strong throughout; 1, weakened in distal sector. The weakening of the distal sector of M is a synapomorphy for *Meoneura + Carnus*.

33. *Vein bm-cu*: 0, present; 1, absent. The loss of bm-cu is a synapomorphy for *Meoneura + Carnus* and has occurred convergently in Chloropidae and most Cryptochetidae (according to van Bruggen, 1960, bm-cu is present in *Cryptochetum capense* van Bruggen).

34. *Vein $CuA_2 + A_1$*: 0, present, strong at least in basal third; 1, absent or abbreviated and foldlike. A loss of $CuA_2 + A_1$ has occurred at least three times independently in the Carnoidea. Vein $CuA_2 + A_1$ is well developed in the ground plan of the Canacidae (s.l.) (preserved in the Apetaeninae and Horaismopterinae), but has been lost in most subfamilies.

35. Vein CuA_2 (closing vein of cell *cup*): 0, present, convex (at least slightly); 1, present, straight; 2, absent. A straight CuA_2 is a synapomorphy for the Chloropidae family group. In Milichiidae, all three character states occur. Based on Acartophthalmidae as an outgroup, Brake (2000) considered a convex CuA_2 the ground plan condition for this family. According to the present analysis, the convex CuA_2 of some Milichiidae must be considered a reversal.

36. *Vein A_2*: 0, moderately to strongly developed; 1, absent. A foldlike A_2 was considered to be a ground plan character of the Carnoidea by J.F. McAlpine (1989: 1476), but, erroneously, he attributed a clearly discernible A_2 to the Carnidae and Australimyzidae, in which this vein is completely absent. I agree with D.K. McAlpine (2006) that, as a result of the isolated occurrence of A_2 in Canacidae (s.l.), Cryptochetidae and Milichiidae, it is more parsimonious to assume that it represents a new development and hence a synapomorphy of the Chloropidae family group (reversals occur in several Milichiidae genera and Chloropidae).

Abdomen

37. *Pleural membrane*: 0, bare; 1, with setulae rising from sclerotized bases. A setulose pleural membrane is a synapomorphy for the higher Carnidae.

Male terminalia

38. *Tergite 6*: 0, free and large, size subequal to tergite 5; 1, present and free but notably reduced (distinctly smaller than tergite 5); 2, fused with sternite 8; 3, absent. Transition costs between character states are specified in Table 2. Within the Carnoidea, the plesiomorphic condition, a fully developed, free tergite 6 subequal in size to tergite 5, is preserved only in Australimyzidae and Cryptochetidae. Reduction or loss of the tergite has occurred in several lineages. In the stem species of Canacidae (s.l.), tergite 6 became fused to sternite 8 (D.K. McAlpine, 2006). Griffiths (1972) interpreted the pregenital sclerite of Canacidae (s.str.) wrongly as consisting of tergite 6 only. The composite nature of this sclerite is evidenced by the fact that the limits of the two sclerites are discernible still in some groups (e.g. *Paracanace hoguei* Mathis & Wirth). The two sclerites furthermore differ by the presence (tergite 6) vs. the absence (sternite 8) of discal setae.

39. *Sternite 6*: 0, present and free; 1, fused to synsternite 7 + 8; 2, fused to sternite 5 and 7; 3, fused to sternite 8. Sternite 6 is free in the ground plan of Carnoidea. A fusion of sternites 6, 7 and 8 has occurred twice (*Meoneura + Carnus* and Milichiidae + Chloropidae).

40. *Tergite 7*: 0, present; 1, absent. The transition from 0 to 1 is considered to be irreversible. Tergite 7 was lost numerous times within the Schizophora, including at least three times within the Carnoidea. Most taxa in the outgroups Clusiidae and 'Heleomyzidae' also lack tergite 7 (preserved in *Clusia czernyi* Johnson, pers. obs.; *Scoliocentra villosa* (Meigen) and *Anastomyza* sp., cf. D.K. McAlpine, 1985: figs 67, 87).

Table 2. Step matrix for character 38.

	To			
	0	1	2	3
From				
0	–	1	1	1
1	1	–	1	1
2	∞	∞	–	1
3	∞	∞	∞	–

41. *Sternite 7*: 0, present and not fused to sternite 8; 1, completely fused to sternite 8, forming a symmetrical or nearly symmetrical dorsal pregenital sclerite; 2, absent. Transition costs between character states are specified in Table 3. In the Carnoidea ground plan, sternite 7 is present, separate from (not fused to) sternite 8, and asymmetrically placed on the left side of the abdomen. In the stem species of Canacidae (s.l.), sternite 7 was lost. Some authors (Wirth, 1987; Mathis & Munari, 1996; Brake, 2000) speculated that the symmetrical pregenital sclerite of Canacidae might include remnants of sternite 7, but I agree with D.K. McAlpine (2006) that there is no evidence to support this. In two other lineages (*Meoneura* + *Carnus*, Milichiidae + Chloropidae), sternite 7 became fused with sternite 6 and 8, also resulting in a secondarily symmetrical pregenital sclerite. A symmetrical pregenital sclerite furthermore developed in Acartophthalmidae through fusion of sternites 6 and 8, but in this case does not include sternite 7. The sternite 7 of Acartophthalmidae is preserved as a separate but poorly sclerotized sclerite on the left side of the abdomen (see Andersson, 1977: fig. 6A, correcting the wrong interpretation of Griffiths, 1972, which was followed by Brake, 2000).

42. *Segment 7, spiracles*: 0, present and more or less symmetrically placed; 1, present, right spiracle shifted onto ventral surface; 2, absent. Transition costs between character states are specified in Table 4. Plesiomorphically, the spiracles of segment 7 are present and more or less symmetrically placed in the pleural membrane. In the stem species of the higher Carnidae (*Hemeromyia*, *Meoneura*, *Carnus*), the right spiracle 7 is shifted medially onto the ventral surface of the abdomen. A loss of spiracle 7 occurred at least six times within the Carnoidea: in Acartophthalmidae, Cryptochetidae, Australimyzidae + Inbiomyiidae, *Carnus*, some species of *Meoneura*, at least one species of *Hemeromyia* (according to Griffiths, 1972; spiracle present in all species examined by myself).

43. *Sternite 8*: 0, present, setulose; 1, present, bare; 2, absent. In its primitive condition, sternite 8 is extensively setulose. However, in most Carnoidea with setulose sternite 8, the number of setulae is very small (excluding Australimyzidae). A complete loss of setulae is only observed in groups in which sternite 8 becomes

Table 3. Step matrix for character 41.

From	To		
	0	1	2
0	–	1	1
1	∞	–	1
2	∞	∞	–

Table 4. Step matrix for character 42.

From	To		
	0	1	2
0	–	1	1
1	1	–	1
2	∞	∞	–

secondarily fused with other sclerites, or when sternite 8 is very small (Inbiomyiidae, Fig. 4A).

44. *Hypandrial apodeme*: 0, without slender anterior apodeme; 1, with slender anterior apodeme(s). The hypandrium has no anterior apodeme or only a very short and broad apodeme in the ground plan of the Carnoidea. A slender apodeme (e.g. Fig. 4E) is a synapomorphy for Inbiomyiidae + Australimyzidae.

45. *Hypandrium/epandrium connection*: 0, hypandrium articulated to anterior margin of epandrium (both movable against each other), point of connection removed from surstylus (if present); 1, hypandrium rigidly connected to ventral margin of epandrium, extending posteriorly to base of surstylus. In the ground plan of Schizophora and Carnoidea, the connection between the epandrium and hypandrium is flexible and restricted to a small area (e.g. Fig. 12A), enabling muscle-mediated movement of the two sclerites against each other. At its articulation point, the hypandrium often bears a more or less developed condylar process. In most Acalyptratae families, the surstylus is broadly separated from the epandrial–hypandrial articulation (e.g. Fig. 12A). In Inbiomyiidae and Australimyzidae, the hypandrium is rigidly connected to the epandrium along its ventral margin and extends posteriorly to the base of the surstyli (Figs 4E; 8B). This is one of the primary synapomorphies linking Inbiomyiidae with Australimyzidae. Outside the Carnoidea, a rigid epandrial–hypandrial connection occurs only in the Sphaeroceroidea (Chyromyidae, Sphaeroceridae, a few tribes of 'Heleomyzidae') and the Curtonotidae.

46. *Subepandrial sclerite*: 0, present, not or only narrowly connected to epandrium; 1, present, broadly connected posteriorly to epandrium between cerci and surstyli; 2, absent. A variably shaped subepandrial sclerite is part of the ground plan of Schizophora and Carnoidea. A very unusual modification has taken place in the stem species of the higher Carnidae (*Hemeromyia* + *Meoneura* + *Carnus*). Here, the subepandrial sclerite is broadly fused with the posterior margin of the epandrium on each side between the cerci and the surstyli (Fig. 12B: fus). Both immediate outgroups (*Neomeoneurites* and Inbiomyiidae + Australimyzidae) lack subepandrial sclerites. Therefore, the unusual subepandrial sclerite of the higher Carnidae seems to represent a neomorphic structure that developed
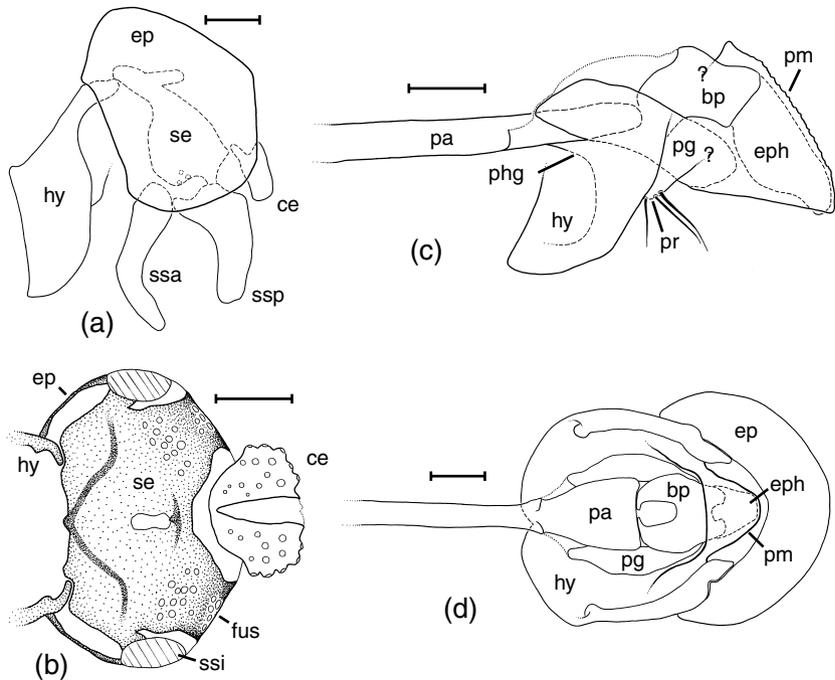
Fig. 12. Carnoidea, male genitalia: A, *Zalea horningi* group, epandrium, hypandrium and associated structures, lateral (Canacidae); B, *Meoneura vagans*, epandrial complex, ventral (Carnidae); C, *Zalea horningi* group, hypandrial complex, lateral (distiphallus omitted); D, *Zalea horningi* group, male genitalia, dorsal. Scale: 0.05 mm. bp, basiphallus; ce, cercus; ep, epandrium; eph, epiphallus; fus, area of fusion between subepandrial sclerite and epandrium; hy, hypandrium; pa, phallapodeme; pg, postgonite; phg, phallic guide; pm, phallic mantle; pr, pregonite; se, subepandrial sclerite; ssa, anterior surstylus; ssi, insertion area of surstylus; ssp, posterior surstylus.

through re-sclerotization of the membranous roof of the epandrial cavity.

47. *Phallapodeme*: 0, separate from hypandrium; 1, connected or fused to hypandrium. Outgroup evidence for this character is equivocal. Both character states occur in Sphaeroceroidea (including 'Heleomyzidae') and Opomyzoidea. In Clusiidae, the phallapodeme always is fused to the hypandrium, but this might not be the ancestral state for Opomyzoidea. I agree with Griffiths (1972: 164) that it appears most plausible to postulate a free and rodlike phallapodeme (not connected to the hypandrium through a phallic guide or phallapodemic plate) for the Carnoidea ground plan, because this state appears to be difficult to derive from the fused condition observed in other families. However, the present analysis polarizes the character differently with a free phallapodeme as the derived condition.

48. *Distiphallus shape*: 0, rigid and moderately elongate, sclerotized; 1, flexible and slender (more or less ribbon-shaped), largely or completely desclerotized; 2, truncate, membranous. This character is ordered.

49. *Distiphallus vestiture*: 0, bare; 1, microtrichose. Characters 48 and 49: The ancestral state in Carnoidea appears to be a very simply structured, flexible, slender, microtrichose distiphallus. This character combination is apomorphic with regard to other Acalyptratae superfamilies and is considered a defining character of the Carnoidea. Grimaldi (1997) interpreted this condition as synapomorphic for the Carnidae (including *Australimyza*) based on outgroup comparison with the Milichiidae, which have a bare and truncate distiphallus. According to the present analysis, the bare and truncate distiphallus is a synapomorphy of

Milichiidae + Chloropidae, and the condition found in Carnidae (excluding *Carnus*), Acartophthalmidae, Canacidae (s.l.) and Inbiomyiidae + Australimyzidae is representative of the Carnoidea ground plan.

50. *Ejaculatory apodeme*: 0, small; 1, enlarged. Based on outgroup comparison and the distribution of character states within the Carnoidea, a small ejaculatory apodeme appears to be the ground plan condition for the superfamily. Both character states occur in the 'Heleomyzidae' and the Clusiidae. According to Owen Lonsdale, University of Guelph, Canada (pers. comm.), a small ejaculatory apodeme is the ground plan condition for Clusiidae.

Female terminalia

51. *Ovipositor*: 0, long and telescopic; 1, shortened. A truncate ovipositor is one of the synapomorphies of Inbiomyiidae + Australimyzidae.

52. *Segment 7, spiracles*: 0, present; 1, absent. The transition from 0 to 1 is considered to be irreversible. Spiracle 7 is present in the ground plan of the Carnoidea, and was lost five times independently within the superfamily.

53. *Cerci*: 0, separate from each other; 1, completely fused. The transition from 0 to 1 is considered to be irreversible. Fused cerci evolved independently in the Carnidae and Cryptochetidae.

54. *Spermathecae, morphology*: 0, well developed and sclerotized; 1, rudimentary and weakly sclerotized, or absent. The transition from 0 to 1 is considered to be irreversible. Sclerotized spermathecae appear to be

part of the Carnoidea ground plan. Desclerotized spermathecae have evolved at least three times independently within the Carnoidea.

55. *Spermatheca number*: 0, three; 1, two. Three spermathecae are present in the ground plan of the Schizophora (J.F. McAlpine, 1989) and also the Sphaeroceroidea (some 'Heleomyzidae' have four or two). The presence of two spermathecae is a putative synapomorphy for the Carnoidea + Opomyzoidea (J.F. McAlpine, 1989).

56. *Spermathecal ducts*: 0, uncoiled; 1, rolled into a single, tightly packed regular coil. In the Carnoidea ground plan, the spermathecal ducts are relatively short and uncoiled. Tightly packed, regular coils have evolved independently in the stem species of Milichiidae + Chloropidae (Sturtevant, 1926; Brake, 2000) and in Acartophthalmidae. Some species of *Meoneura* (pers. obs.) have very long and coiled spermathecal ducts, but the coils are irregular and not tightly packed.

57. *Ventral receptacle*: 0, absent (or inconspicuous?); 1, present and distinct but not pocketlike; 2, well developed, pocketlike. A well-developed, pocketlike ventral receptacle is a synapomorphy of Milichiidae + Chloropidae (Sturtevant, 1926).

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58. *Life habits*: 0, not halophilic; 1, halophilic. Halophily has evolved independently in Canacidae (s.l.) and Australimyzidae.

Results of phylogenetic analysis. The analysis yielded two most parsimonious trees (Fig. 13; tree length 152, CI = 0.46, RI = 0.59, RC = 0.27), which differ only in the position of the Acartophthalmidae. The ingroup consists of three principal clades: the Chloropidae family group (Canacidae s.l., Cryptochetidae, Milichiidae, Chloropidae), Inbiomyiidae + Australimyzidae and a monophyletic Carnidae in the traditional sense (including *Neomeoneurites, Hemeromyia, Meoneura, Carnus*). Bremer support (noted in Fig. 13) was high for all three clades, except for the basal node of the Chloropidae family group (Canacidae s.l. + (Cryptochetidae, Milichiidae, Chloropidae)). The sister group relationship between Carnidae and Inbiomyiidae + Australimyzidae is very weakly supported and is based merely on the reduced number of pseudotracheae and the absence of a subepandrial sclerite (regained in the higher Carnidae).

Discussion

Family status of Inbiomyiidae

Four different possibilities of classifying *Inbiomyia* are compatible with the present phylogenies: (i) both *Inbiomyia* and *Australimyza* are included in a redefined Carnidae; (ii) *Inbiomyia* is included as a genus in Australimyzidae without erecting a new family group taxon; (iii) a new (a) subfamily or (b) family is erected for the genus. The first option is discussed and rejected below (see 'Relationships of Australimyzidae'). Considering the high number of autapomorphies that have evolved in the stem lineage of *Inbiomyia*, and considering the different biogeography of *Australimyza* and *Inbiomyia*, it appears that the two lineages separated early in the evolution of the Carnoidea. No fossils of either *Australimyza* or *Inbiomyia* are known and so no time estimate can be given for the separation of the two clades. In order to uphold consistency with the current degree of division at the family/subfamily level in Schizophora classification, a new family group taxon for *Inbiomyia* is appropriate and justified. In the absence of objective criteria for assigning absolute ranks for taxa above the species level, practical considerations play an important role. Australimyzidae including 'Inbiomyiinae' would be an unwieldy group that cannot be defined on the basis of external characters as is usual for Schizophora. In the author's opinion, the erection of a new family is therefore justified and necessary.

Phylogeny of the Carnoidea

The main difference between the present phylogeny and previous phylogenetic hypotheses (Griffiths, 1972; J.F. McAlpine, 1989; Grimaldi, 1997; Brake, 2000) lies in the placement of the Australimyzidae, Cryptochetidae and Acartophthalmidae.

Relationships of Australimyzidae. The genus *Australimyza* was described originally as a genus of Milichiidae (Harrison, 1953). After the Carnidae were separated from Milichiidae (Hennig, 1965), Colless & McAlpine (1970) referred *Australimyza* to the Carnidae. Based on the primitive condition of the male pregenital segments (cf. characters 38–41), male genitalic characters (cf. character 47) and the absence of synapomorphies linking *Australimyza* to Milichiidae or any other Acalyptratae family, Griffiths (1972) rejected a closer relationship between this genus and Milichiidae. He considered *Australimyza* to be a genus of uncertain relationships and erected for it a new family in a separate 'prefamily' (corresponding to the rank of superfamily as used in J.F. McAlpine, 1989). Colless & McAlpine (1975, 1991) acknowledged Griffiths' (*l.c.*) proposal of a new family, but maintained that their 'studies tend to confirm its position in Carnidae'. J.F. McAlpine (1989) accepted family status for Australimyzidae and considered it to be related to Carnidae. Reviewing Carnidae phylogeny, Grimaldi (1997) again placed *Australimyza* in this family, but his supposed synapomorphies for Carnidae + *Australimyza* are plesiomorphies (characters 48, 49; see discussion above), are based on wrong homology assumptions (characters 1, 2; see discussion above), are based on incorrect observations (number of dorsocentral bristles) or are equivocal (presence of 'inner frontal'
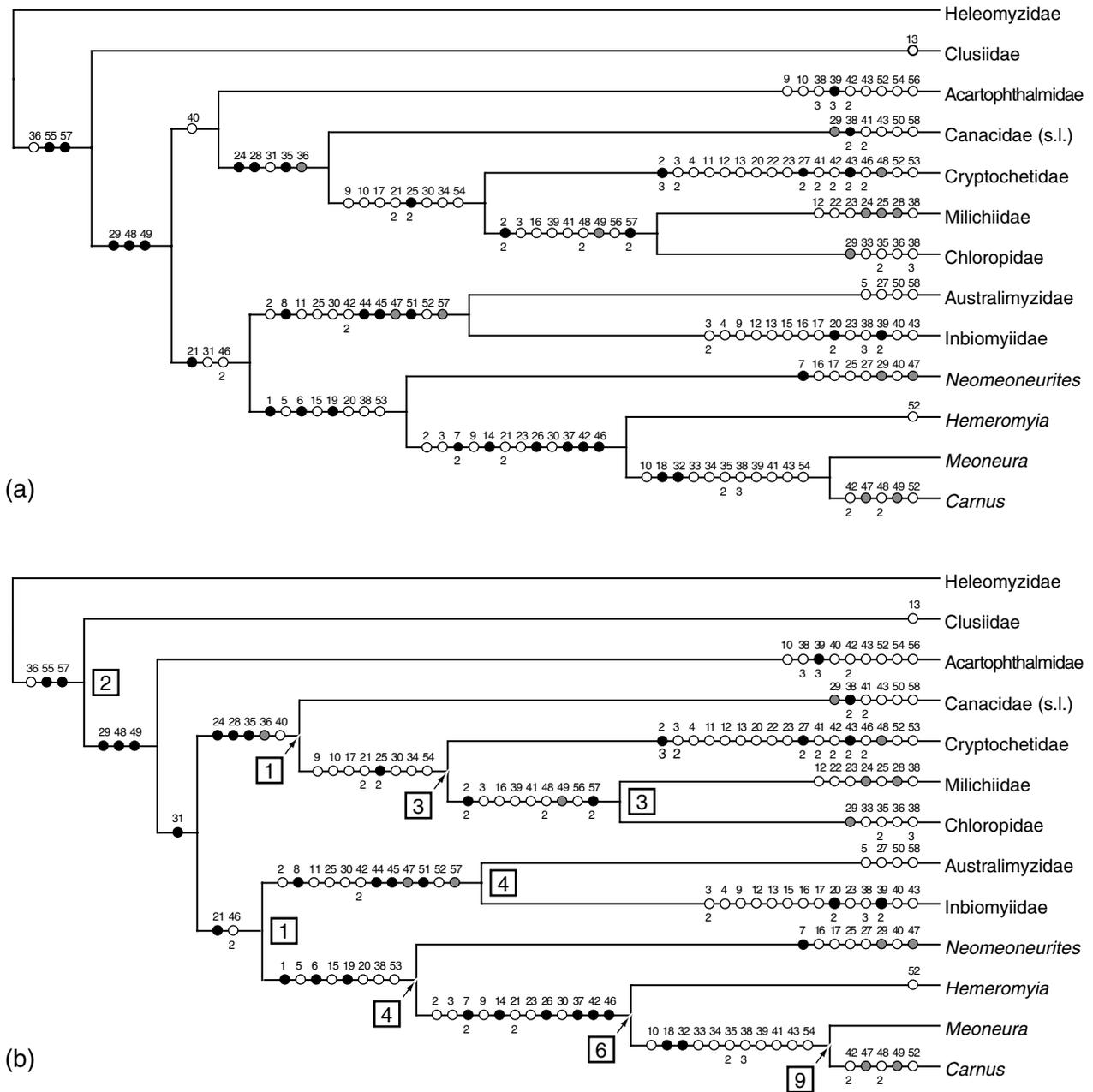
Fig. 13. Phylogeny of the Carnoidea with Clusiidae and Heleomyzidae as outgroups. The two most parsimonious trees are shown. Filled circles represent unambiguous changes, open circles represent convergent characters and shaded circles represent reversals. States for multistate characters are given below the circles. Bremer support values are shown in rectangles beside each consensus node. (Note: ancestral states for characters 2 and 47 are uncertain).

[= interfrontal?] setae). The present analysis places *Australimyza* as the sister group of *Inbiomyia*, in a strongly supported relationship. However, the sister group relationship between Australimyzidae + Inbiomyiidae and Carnidae is supported only by homoplasious characters within Carnoidea (characters 21, 46 in both cladograms; 31 in cladogram a). Expansion of Carnidae to include both *Australimyza* and *Inbiomyia* appears to be unjustifiable.

Relationships of Acartophthalmidae. Previously, Acartophthalmidae have been considered either part of the Carnoidea (Hennig, 1939; Griffiths, 1972; Brake, 2000) or related to Clusiidae (Hennig, 1958, 1965, 1971; J.F. McAlpine, 1989). The former view has become more widely accepted (Thompson, 2005) since Brake's (2000) review of the phylogeny of the Chloropidae family group. Brake (*l.c.*) postulated a sister group relationship between

the Acartophthalmidae and Milichiidae + Chloropidae based on two synapomorphies: Firstly, the very long and regularly coiled spermathecal duct observed in all three families, and, secondly, the symmetrical synsternite 7 + 8. As discussed above (see character 41), the pregenital sclerite of Acartophthalmidae consists of fused sternites 6 + 8 (sternite 7 is free), and therefore is not homologous to the pregenital sclerite (synsternite 6 + 7 + 8; incorrectly termed synsternite 7 + 8 by Brake, *l.c.*) of Milichiidae and Chloropidae. According to the current analysis, the coiled spermathecal duct evolved independently in Acartophthalmidae and Milichiidae + Chloropidae. The shortest trees that place Acartophthalmidae and Milichiidae + Chloropidae together as sister groups are four steps longer than the two most parsimonious trees yielded in the present analysis. A close relationship between Acartophthalmidae and Milichiidae + Chloropidae can therefore be rejected with confidence. Unfortunately, the sister group of the Acartophthalmidae remains unknown.

Relationships of Cryptochetidae. The reasons for including this family in the Carnoidea (as opposed to Ephydroidea or Lauxanioidea) were discussed earlier. Only J.F. McAlpine (1989) has provided a phylogenetic hypothesis, proposing Chloropidae as the sister group of Cryptochetidae. The present analysis agrees with most previous authors (e.g. Sturtevant, 1926; Hennig, 1971; Griffiths, 1972; Brake, 2000) in that the sister group of Chloropidae is the Milichiidae. Although a sister group relationship between Cryptochetidae and Milichiidae + Chloropidae has never been suggested, it is well supported through synapomorphies of the head capsule (characters 9, 10), proboscis (characters 17, 21), wing venation (character 34) and spermathecal structure (character 54). The hypothesis of J.F. McAlpine (1989) is largely the result of an incorrect assessment of the Chloropidae ground plan. Most synapomorphies allegedly linking the two families are not present in the Chloropidae ground plan and evolved only within this family (i.e. reduced vibrissae; densely setulose frons, scutum and scutellum; reduction of main bristles of scutum; enlarged, strongly convex and margined scutellum; notopleuron with several bristles posteriorly; for a description of the Chloropidae ground plan, see Andersson, 1977). Other putative synapomorphies are based on incorrect observation (i.e. a propleural carina is undeveloped in Cryptochetidae) or mistaken homology (tibial organ of the posterodorsal surface of the hind tibia; see Andersson, 1977). The tibial organ of Chloropidae (examined in *Thaumatomyia glabra* (Meigen)) consists of a patch of extremely dense microtomentum (i.e. not of true setae). The superficially similar tibial patch in *Cryptochetum* Rondani, however, consists solely of setulae (which have sockets unlike the trichia that form the microtomentum). The precoxal bridge, another synapomorphy mentioned by J.F. McAlpine (1989), is considered here to be a synapomorphy of the whole Chloropidae family group because of its presence in the Canacidae (s.l.) (reversal in

Milichiidae). Cryptochetidae share more apomorphic characters with Milichiidae than with Chloropidae. Based on the present matrix, the shortest tree that places Cryptochetidae and Chloropidae as sister groups is five steps longer than the most parsimonious trees. The shortest tree with Cryptochetidae and Milichiidae as sister groups, on the other hand, is just three steps longer.

Supplementary material

Acknowledgements

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