1.1. Morphology and terminology of adult Diptera (other than terminalia)

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1. INTRODUCTION – Bernhard Merz

General remarks. The following chapter deals with important morphological terms of adult Diptera. It is intended to give the reader an overview of those parts of Diptera, which are currently used in classification and identification.

This chapter does not have the scope to treat all the morphological terms of Diptera. Those characters and structures which occur only in single families or which are otherwise very rarely exhibited, are explained in an appropriate manner in the respective chapters.

Adult morphology has been for a long time confusing because students of Diptera followed their own concepts and terminology. The readers
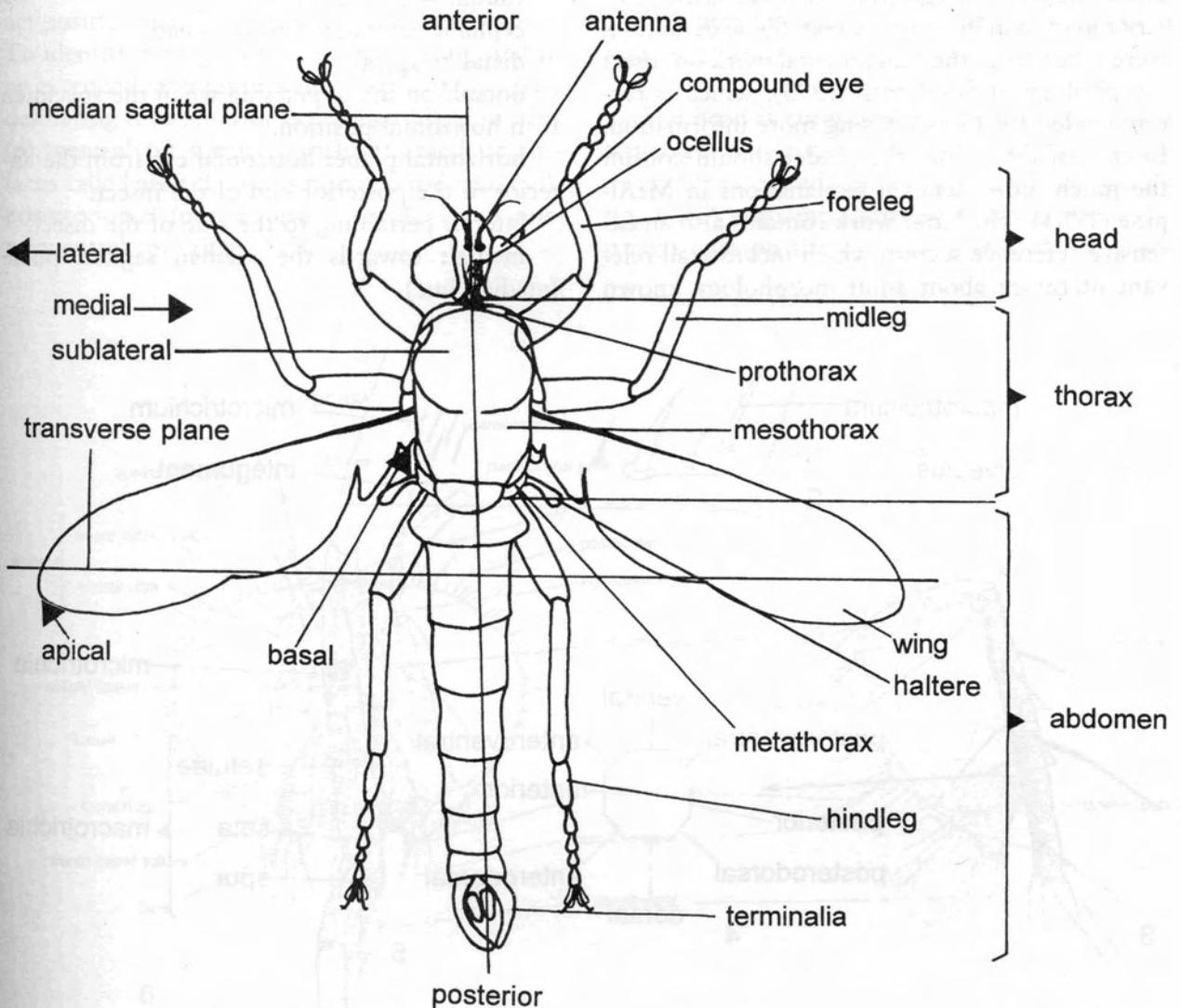
Fig. **1.1.** General organisation and orientation of a Diptera. A generalized fly, *Machimus rusticus* (Meigen) (Asilidae), to show orientation and anatomical planes.

of the "Die Fliegen der palaearktischen Region" by Lindner (1949 and other volumes) are aware of this problem constantly when dealing with different families. However, McAlpine (1981) has produced an excellent account on adult morphology in the "Manual of Nearctic Diptera". In this work, a congruent terminology for the whole order was proposed. Presently, most scientific papers follow McAlpine (e.g., Colless and McAlpine 1991; Barraclough 1995; Andersson 1997; Oosterbroek 1998). Logically, the present "Manual" also follows as far as possible his terminology, and new terms and definitions are given only when required by recent investigations.

In order to facilitate the use of the present book, the terms are given in an alphabetical glossary rather than in a prosaic text. Some definitions were taken from the fundamental work on insect morphology of Snodgrass (1993), which is recommended for users needing more information. In case of difficulties the reader should consult the much more detailed explanations in McAlpine (1981). The latter work contains also an extensive reference section which includes all relevant literature about adult morphology known up to that time. An excellent analysis of the terms and evolution of the antennae of the Brachycera was most recently published by Stuckenberg (1999). For lack of time the results of his studies cannot be incorporated in the present chapter.

Orientation and relationships of the body parts (Figs 1, 3–4, 6). The bilateral symmetry in adult Diptera has consequences on the relative position of the morphological and anatomical parts. Thus, the most important directions and planes are explained here:
anterior: in the direction of the head.
apical: at the tip.
basal: at the base.
caudal = posterior.
cephalic: pertaining to the head.
distal = apical.
dorsal: on the upper side when the specimen is in horizontal position.
horizontal plane: horizontal cut from the anterior to the posterior end of the insect.
lateral: pertaining to the side of the insect.
medial: towards the median sagittal plane (median line).
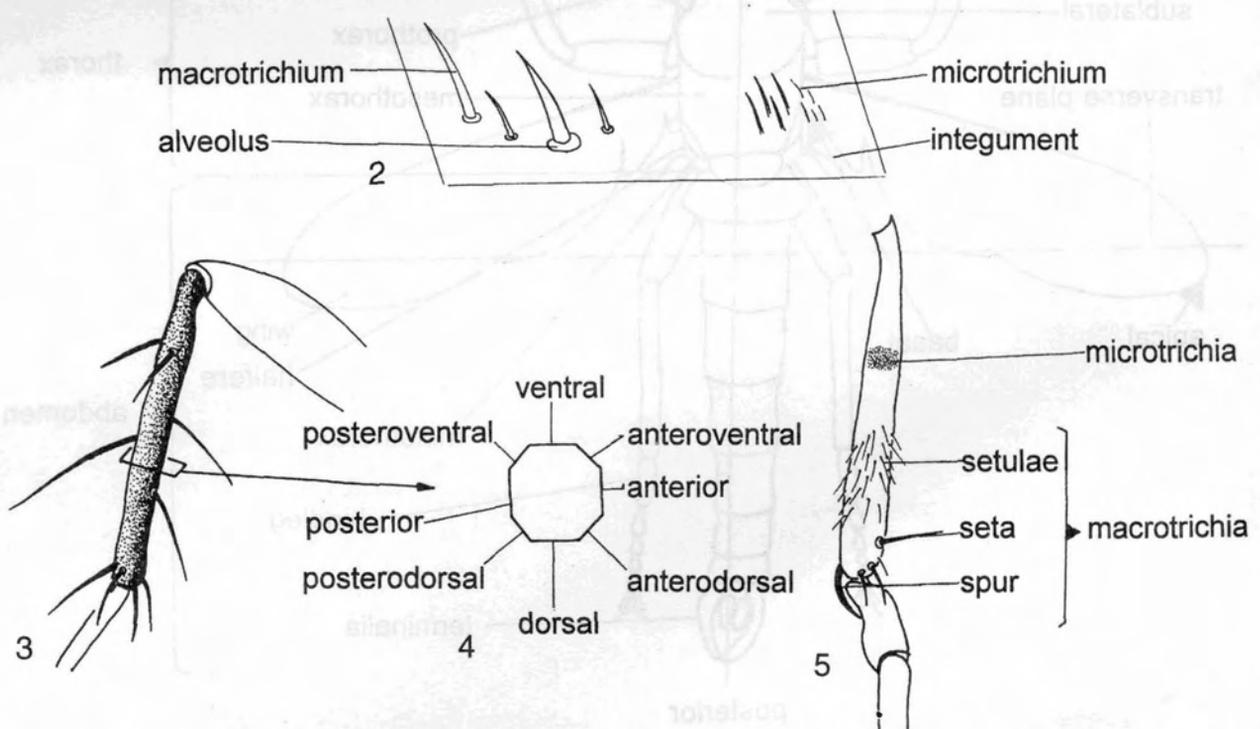
Figs 1.2–5. Types of cuticular outgrowths and their orientation. 2: types of cuticular outgrowths; 3–4: schematic tibia in anterior view with vertical section; 5: types of macrotrichia on a schematic tibia of a Sphaeroceridae.

median sagittal plane: dorso-ventral cut from the anterior to the posterior end through the central axis, dividing the insect into two symmetric parts.

posterior: in the direction of the terminalia.

proximal = basal.

sublateral: the zone between the side and the central axis of the insect.

transverse plane: dorso-ventral cut through the lateral axis (for example from wing-tip to wing-tip).

ventral: on the lower side, when the specimen is in horizontal position.

The legs of Diptera are often armed with outgrowths (macrotrichia, microtrichia). Their exact position may be important for identification. To identify their position, the leg is supposed to be extended laterally at a right angle to the body, delimiting thus anterior (a), dorsal (d), posterior (p), ventral (v) surfaces, with intermediate surfaces called after their position anterodorsal (ad), posterodorsal (pd), anteroventral (av) and posteroventral (pv) (Figs 3–5).

Principal structures of adult Diptera (Fig. 1). As in other insects, the Diptera have an external skeleton and their body is divided into three main regions: **Head, thorax** and **abdomen.** Each region bears appendages and/or organs which will be explained below.

Each thoracic and abdominal segment is divided into three parts, which in turn may further be subdivided into smaller sclerites (see chapter "thorax" for a detailed explanation of the individual sclerites):

pleurum: usually the membranous part of each segment between tergum and sternum.

tergum: the sclerotized, rigid dorsal part of each body segment.

sternum: the sclerotized ventral part of each body segment.

The **head** is composed of the following main structures and organs:

antenna: paired sense organ of 3–16 (rarely up to 36) segments, situated between the compound eyes on the anterior aspect of the head.
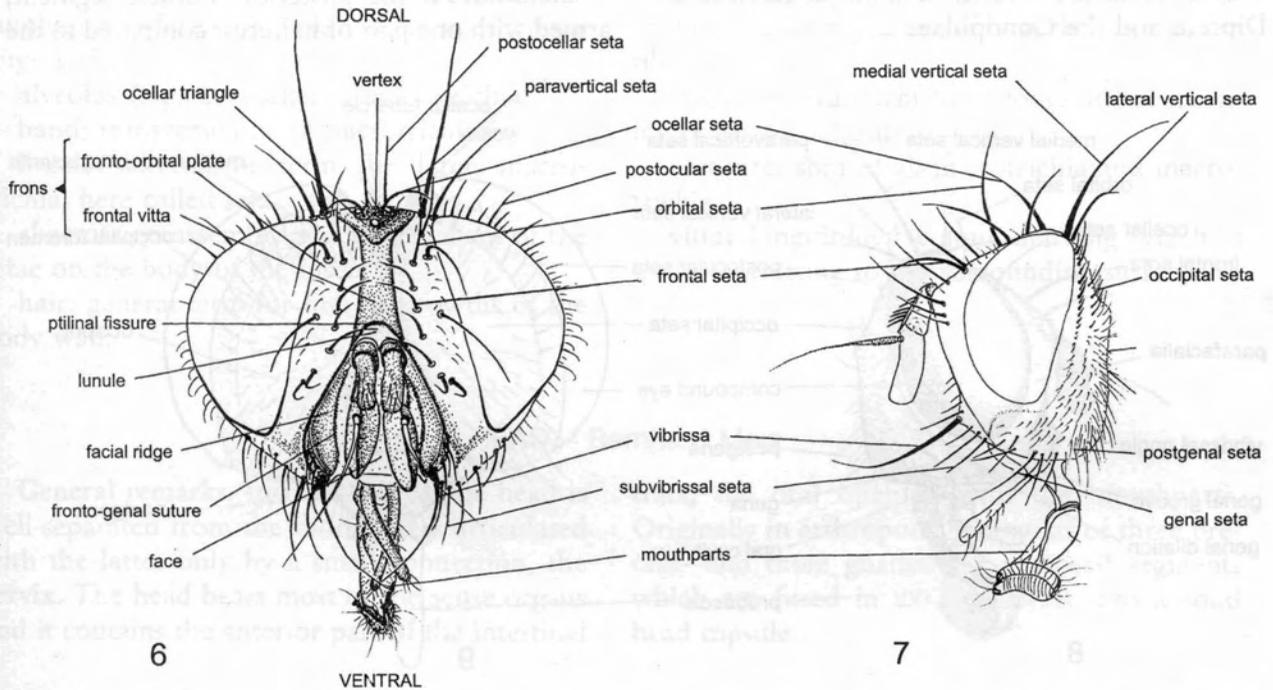
Figs **1.6–7.** *Blondelia nigripes* (Fallén) (Tachinidae): structures and chaetotaxy of the head. 6: anterior view; 7: lateral view.

Definitions and shape of the different parts are described below.

compound eye (Figs 1, 8–9, 13–14): paired sense organ for visual stimuli, composed of a varying number of ommatidia; shape elliptical or spherical, sometimes with indentations or notches; usually very large in raptorial species or in species with epigamic behaviour. They may occupy most or all of the lateral surface of the head; compound eyes are partly reduced in some subterranean, in cave-dwelling or parasitic species. For more detailed information, see below.

head capsule: strongly sclerotized fused product of the former segments of the head. The head capsule is divided into different sclerites which are explained below.

mouthparts (Figs 6–7): from the phylogenetic point of view, the extremities of anterior three segments of the head are modified into feeding organs: paired mandibles, paired maxillae and an unpaired labium. In the Diptera, they exhibit a very wide range of modifications, as shown below.

ocellus: optical sense organ, situated on the dorsal aspect of the head between the compound eyes, the frons and the vertex. Usually 3 ocelli are arranged in a triangular shape on the ocellar triangle or ocellar tubercle, but reductions to 2, 1 or 0 ocelli are known in some nematocerous Diptera and the Conopidae.

oral cavity (Fig. 8): opening on the ventral aspect of the head, incorporating the mouthparts. The oral margin, which separates the oral cavity from the gena, may be covered by some setae which are important for identification (e.g., Ephydridae).

subcranial cavity = oral cavity.

The **thorax** (Fig. 1) is composed of 3 segments, each one with one pair of **legs** (**fore leg** on prothorax, **mid leg** on mesothorax and **hind leg** on metathorax) on the ventral side for locomotion.

halter: the reduced, highly specialised, club-like metathoracic wing; it serves as balancing organ to maintain stability in flight.

wing: as the name of the order indicates, Diptera have developed usually only the anterior, mesothoracic pair of wings as functional flight organ; shape, surface, structure and venation are subject to high variation and are important for classification and identification.

mesothorax: the large second segment of the thorax of Diptera, situated between pro- and metathorax; it is divided into prescutum, scutum and scutellum; usually carrying the anterior pair of wings.

metathorax: the posterior thoracic segment, armed with one pair of halteres; compared to the
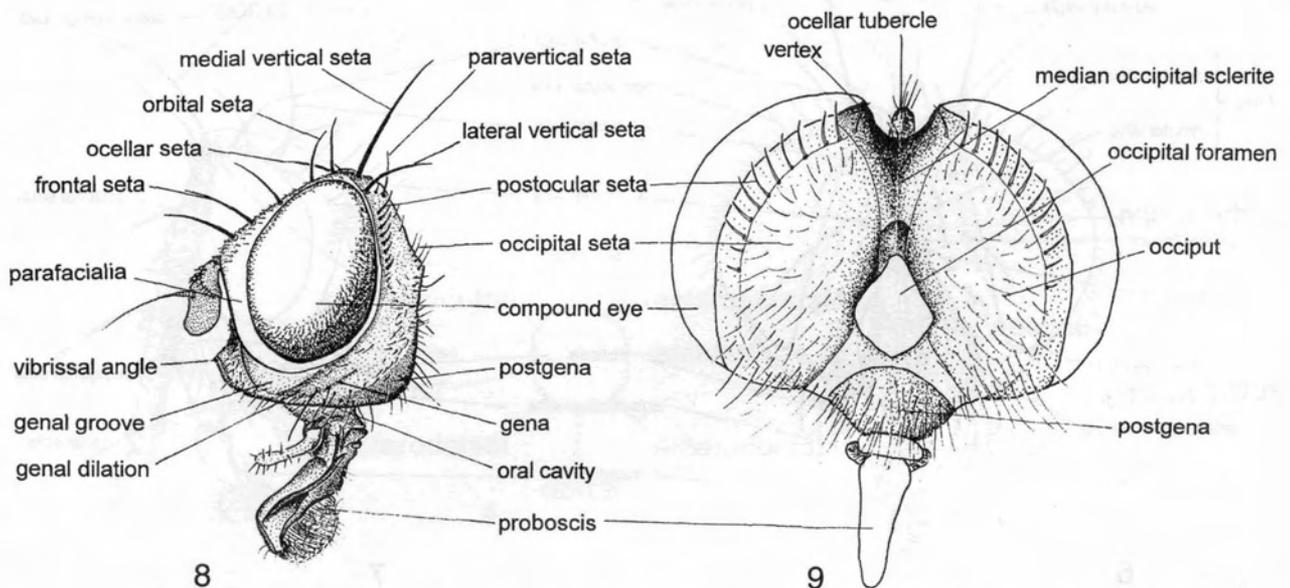
Figs 1.8–9. Structures and chaetotaxy of the head. 8: *Orellia falcata* (Scopoli) (Tephritidae), lateral view. 9: *Paritamus melanopus* (Meigen) (Asilidae), posterior view.

mesothorax usually rather small; with one pair of stigmata.

prothorax: the anterior thoracic segment, usually little developed.

The **abdomen** is distinctly segmented and originally comprising 8–9 pregenital segments, depending on taxon and sex, and the genital segments, the **terminalia** (Fig. 1) which are used during copulation. The number of pregenital segments is reduced in some taxa.

Male terminalia consist principally of claspers for holding the females terminalia and of the aedeagus with appendages for sperm transfer. They are extremely modified within the Diptera. A special account on these structures is given in the next chapter.

The general structure of the **female terminalia** usually is simpler than that of the males, but regarding the diversity of substrates for egg deposition, the terminalia may be highly modified. Detailed explanations are given in the next chapter.

The **skeleton** of Diptera is – compared with that in other orders (Hymenoptera, Coleoptera) – usually rather weakly sclerotized. It bears a number of surface structures and ornamentations (Figs 2, 5):

alveolus (Fig. 2): socket of macrotrichia.

band: transverse line of microtrichiosity.

bristle: alternative term for large macrotrichia, here called seta.

chaetotaxy: assembly and arrangement of the setae on the body of the insect.

hair: general term for fine outgrowths of the body wall.

macrotrichia (Figs 2, 5): general term for larger projections of the cuticle which possess alveoli. Depending on their size they are termed setulae, setae or spurs.

microtomentose: old term for microtrichose.

microtrichia (Figs 2, 5): usually minute projections of the cuticle that lack alveoli. They are usually hair-like or scale-like under compound or scanning electron microscopy. They may cover parts of the wing membrane, making them look darker, or parts of the body, producing a dull or mat appearance.

microtrichose: parts of the body surface which are covered with microtrichia giving a dull appearance. In McAlpine (1981) this structure is called pruinose and pollinose. These terms, however, do not give an indication on the origin of the dull appearance.

pollinosity: old term for microtrichose.

pruinosity: old term for microtrichose.

seta (Fig. 5): strong, rigid hair at a defined position. The setae usually have names according to the sclerite of insertion. The arrangement and number of the setae give in total the chaetotaxy.

setulae (Fig. 5): small, soft setae, usually rather unordered on various parts of the body; the individual setulae do not have specific names.

spur (Fig. 5): stout, mostly curved macrotrichium, usually present only at the apex of the tibia.

stripe: general term for a longitudinal marking of microtrichosity.

vestiture: sum of all microtrichia and macrotrichia.

vitta: longitudinal colour marking which is quite contrasting to the surrounding surface.

2. HEAD – Bernhard Merz

General remarks. In the Diptera, the head is well-separated from the thorax. It is articulated with the latter only by a small connection, the **cervix.** The head bears most of the sense organs and it contains the anterior part of the intestinal tract, the oral opening with the mouthparts. Originally in arthropods, it consists of three preoral- and three gnathal (= postoral) segments which are fused in extant species into a solid head capsule.

rostrum

10

eye bridge

callus

12

occiput

ocellar tubercle

11

compound eye

14

antennal socket

13

mystax

facial tubercle

15

16

fronto-orbital seta

antennal groove

facial carina

labrum

clypeus

18

clypeo-labral membrane

17

medial postocellar seta

postocellar seta

interfrontal seta

vibrissa

19
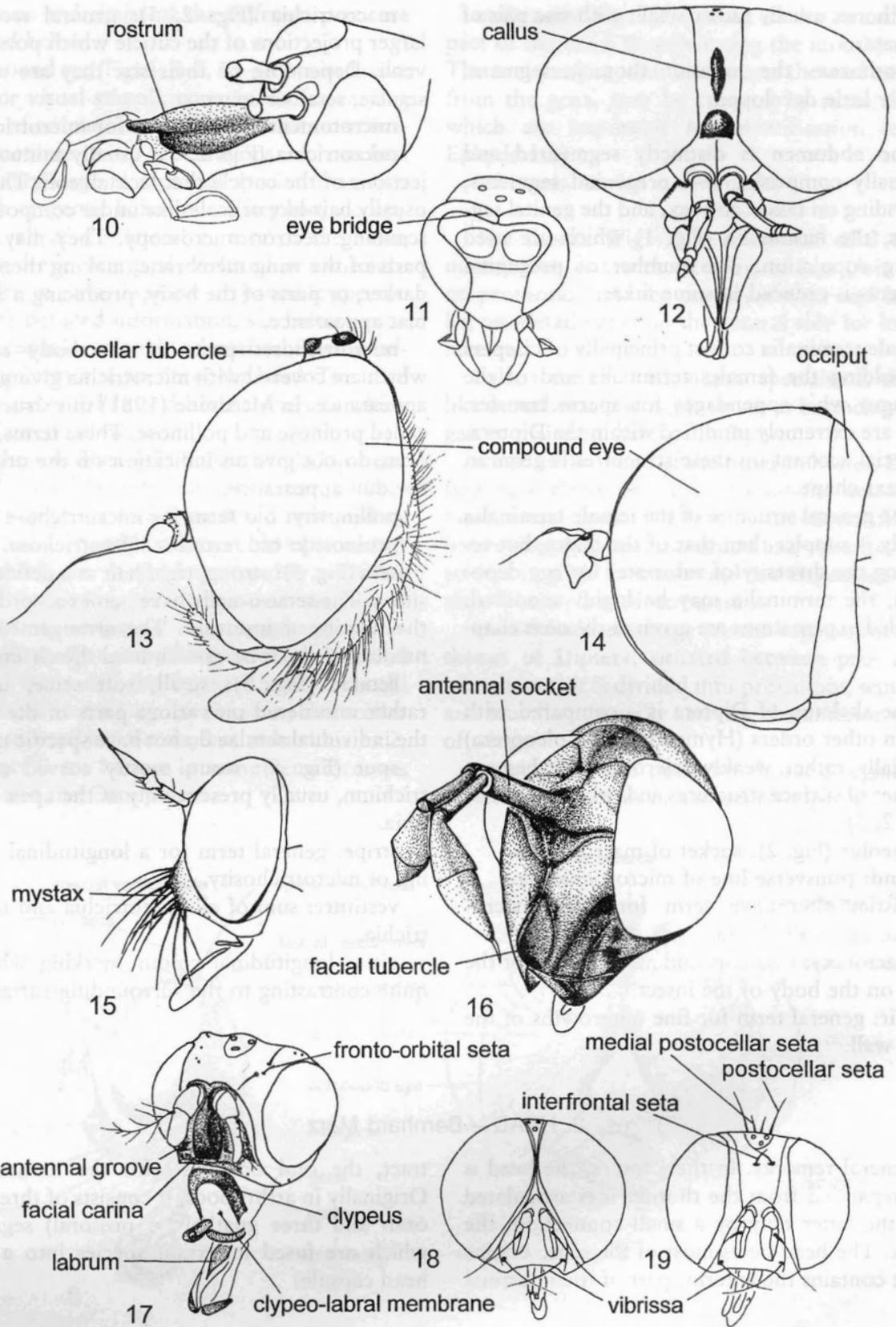
Head plates and structures

antennal groove (Fig. 17): paired longitudinal invagination on the face.

callus (Fig. 12): shiny area on the frons or face, most conspicuous in females of Tabanidae, Therevidae and some other orthorrhaphous Diptera, rarely in Cyclorrhapha or nematocerous Diptera.

cheek = gena. Gena and cheek are here treated as synonyms, although McAlpine (1981) proposed to divise the cheek in the gena dorsally and the subgena, a hairless stripe along the oral cavity, ventrally.

face (Fig. 6): sclerotized area which is delimited dorsally by the antennal sockets, ventrally by the fronto-clypeal suture and laterally by the fronto-genal suture or – if it is absent – by the compound eyes. This plate may be small in blood sucking (Culicidae, Ceratopogonidae, Tabanidae) or raptorial Diptera (Empididae, Hybotidae), but is well-developed in Cyclorrhapha; often with antennal groove and facial carina, sometimes with a facial tubercle.

facial carina (Fig. 17): longitudinal keel on the face, separating the antennal grooves.

facial ridge (Fig. 6): small sclerite which lies between the parafacialia and the fronto-genal suture; present only in Cyclorrhapha.

facial tubercle (Fig. 16): protuberance in the center of the face, dorsally of the oral cavity; present in some Syrphidae, rarely in other families.

frons (Fig. 6): dorsal plate which is delimited dorsally by the vertex, ventrally by the antennal sockets or lunule and laterally by the compound eyes. The frons includes the frontal and orbital or fronto-orbital plates laterally and the frontal vitta medially; dorsally in the middle often with ocellar triangle or ocellar tubercule; the frons may be reduced to a small triangle above the lunule in holoptic specimens (see there) or well developed, rectangular to square in dichoptic specimens.

frontal plate: paired sclerite of the frons which separates the compound eyes from the frontal vitta anteriorly; only present in species where frontal and orbital plates are well differentiated (e.g., Agromyzidae, Tephritidae).

frontal vitta (= mesofrons) (Fig. 6): central area of the frons, delimited laterally by the frontal and orbital or fronto-orbital plates.

fronto-genal suture (Fig. 6): separates the face from the facial ridge in Cyclorrhapha.

fronto-orbital plate (Fig. 6): only differentiated in Cyclorrhapha. In the plesiomorphic condition, it is a single, strong, paired sclerite which runs along the compound eyes; in the apomorphic condition, these plates are divided into an anterior portion (frontal plate) and a posterior portion (orbital plate).

gena (= cheek) (Fig. 8): laterally situated, paired sclerite which is delimited dorsally by the compound eyes, ventrally by the oral margin, anteriorly by parafacialia and vibrissal angle and posteriorly by the postgena.

genal dilation (Fig. 8): well-sclerotized, usually hairy part of the gena just posterior of the vibrissal angle; well-developed in many Cyclorrhapha (e.g., Tachinidae).

genal groove (Fig. 8): small to large, rather weakly sclerotized area at the ventral end of the ptilinal fissure just at the junction of the parafacialia with the gena; present only in Cyclorrhapha.

lunule (Fig. 6): crescentic sclerotized area between ptilinal fissure and antennal sockets; well-developed in Schizophora; a lunule-like structure is present in some aschizous Diptera (e.g., Syrphidae).

mesofrons = frontal vitta.

Figs 1.10–19. Special structures and macrotrichia of the head. 10: *Tipula maxima* Poda (Tipulidae), oblique view; 11: Sciaridae, anterior view; 12: *Hybomitra montana* (Meigen) (Tabanidae), anterior view; 13: *Chrysopilus auratus* (Fabricius) (Rhagionidae), lateral view; 14: *Pipunculus campestris* Latreille (Pipunculidae), lateral view; 15: *Paritamus melanopus* (Meigen) (Asilidae), lateral view; 16: *Ceriana conopsoides* (Linnaeus) (Syrphidae), oblique view; 17: *Drosophila funebris* (Fabricius) (Drosophilidae), oblique view; 18: schematic Calyptrata male, frontal view; 19: schematic Calyptrata female, frontal view.

median occipital sclerite (Fig. 9): medial area of the occiput.

mystax (Fig. 15): term used only in the Asilidae, which refers to the central, strongly convex and setose portion of the face.

occipital foramen (Fig. 9): connecting opening between head and cervix, through which the nerves, haemolymph, and intestinal tract are leading.

occiput (Figs 9, 14): posterior part of the head, delimited by the vertex dorsally, the compound eyes laterally and the postgena ventrally below the occipital foramen; shape variable, ranging from strongly convex in many nematocerous Diptera, straight in many families of Cyclorrhapha, to concave in Pipunculidae and Bombyliidae.

ocellar triangle (Fig. 6): prominent area on the frons bearing the ocelli; covers most of the frons in the Chloropidae, but not projecting beyond the lateral margins of the ocelli in most other families.

ocellar tubercle (Figs 9, 13): ocelli are situated in some nematocerous and orthorrhaphous Diptera (e.g., Bibionidae, Rhagionidae, Asilidae) on a conspicuous, projecting ocellar triangle.

orbital plate: paired sclerite of the frons which separates the compound eyes from the frontal vitta posteriorly; only present in taxa with a differentiation of the fronto-orbital plate in a frontal and an orbital plate.

parafacialia (incorrectly parafacial, Fig. 8): paired sclerite which is the continuation of the
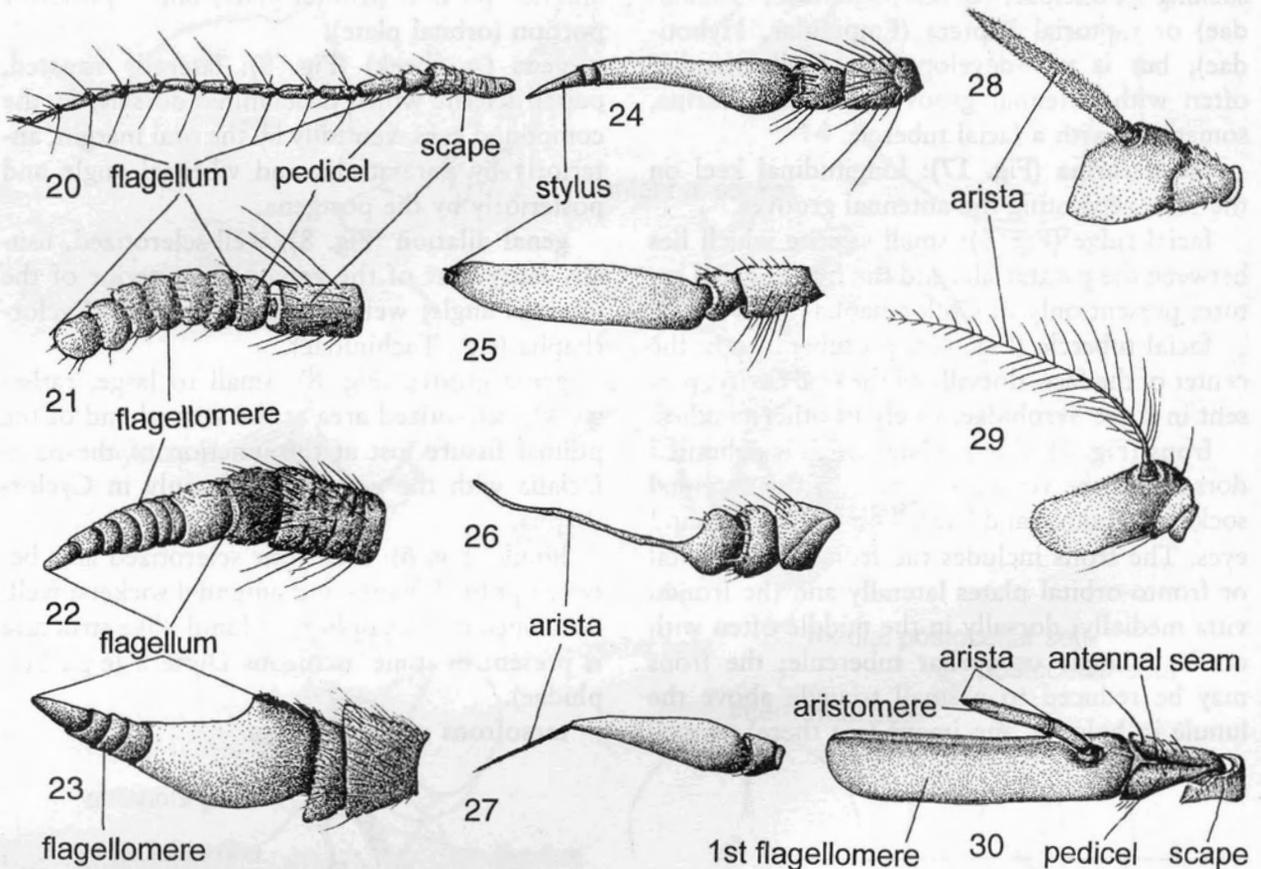
Figs 1.20–30. Antennae, lateral view. 20: *Tipula maxima* Poda (Tipulidae); 21: *Bibio* sp. (Bibionidae); 22: *Coenomyia ferruginea* (Scopoli) (Coenomyiidae); 23: *Hybomitra montana* (Meigen) (Tabanidae); 24: *Rhamphomyia anthracina* Meigen (Empididae); 25: *Ancylorrhynchus glaucius* (Rossi) (Asilidae); 26: *Rhagio notatus* (Meigen) (Rhagionidae); 27: *Platypalpus nigritarsis* (Fallén) (Hybotidae); 28: *Hendelia beckeri* Czerny (Clusiidae); 29: *Minettia czernyi* Freidberg et Yarom (Lauxaniidae); 30: *Onychogonia suggesta* (Pandellé) (Tachinidae).

fronto-orbital plates, anteriorly along the compound eyes to the gena. Medially it is bordered by the ptilinal fissure.

postcranium = occiput.

postgena (Figs 8–9): ventral continuation of the occiput below the occipital foramen, bordered laterally by the genae and ventrally by the oral cavity.

ptilinal fissure (= ptilinal suture) (Fig. 6): synapomorphy of the Schizophora; adults evert their ptilinium while emerging; it is retracted inside the head capsule before the integument is hardened, thus leaving a fissure, which makes a half-circle along the parafacialia and around the lunule.

ptilinal suture = ptilinal fissure.

rostrum (Fig. 10): term of Tipulomorpha and Bibionomorpha for the produced, cylindrical face and mouthparts.

vertex (Figs 6, 9): upper margin of the head, separating the frons and compound eyes from the occiput.

vibrissal angle (Fig. 8): produced ventral continuation of the facial ridge; present in many Cyclorrhapha.

vibrissal ridge = facial ridge.

Compound eyes. The compound eyes (Figs 1, 8–9, 13–14) are highly variable in size and shape. Usually they have a uniform dark reddish to black colour, but in Tabanidae, Syrphidae, Tephritidae, Sciomyzidae and some other families they may have crossbands or spots of different colours. The compound eyes may be bare or setulose on the intersections of the ommatidia. The presence of these setulae may be of taxonomic importance and is best seen against a black background. Some species exhibit a strong sexual dimorphism in the shape of the compound eyes (e.g., males of most Cyclorrhapha have much larger eyes than females). In some Bibionidae, the eyes may be divided into a dorsal and a ventral section.

dichoptic (Fig. 19): eyes clearly separated on the frons, usually more or less parallel-sided.

eye bridge (Fig. 11): the compound eyes are fused above the antennae, forming a bridge in some nematocerous Diptera (e.g., Sciaridae, Scatopsidae).

facet: exterior surface of an ommatidium.

holoptic (Fig. 18): males of many orthorrhaphous Diptera and many Cyclorrhapha have the compound eyes continuous between the antennal base and the occiput for a distance, thus, the frons may be reduced to a small triangle. Holoptic eyes are often related to epigamic or territorial behaviour. They are rarely found in females (e.g., some Hybotidae).

ommatidium: unit of the compound eye. The number of ommatidia varies from species to species; size of ommatidia on dorsal and ventral side may differ (e.g., Empididae).

Antennae

antennal seam (= antennal cleft) (Fig. 30): longitudinal cleft on dorsal or posterodorsal side of pedicel; probably a synapomorphy for Calyptrata, rarely present in some acalyptrate Diptera.

antennal cleft = antennal seam.

antennal socket (Fig. 16): insertion place of the antennae on the head capsule; usually little developed, but very prominent in some Syrphidae.

arista (Figs 26–30): term of orthorrhaphous Diptera and Cyclorrhapha; usually situated dorsally in the basal half of the first flagellomere in Cyclorrhapha, but in terminal or subterminal position in most orthorrhaphous Diptera; phylogenetically the arista is derived from the last 3 flagellomeres (Stuckenberg 1996). It is composed by 3 aristomeres. The arista is slender – in contrast to the stylus. It may be only microscopically pubescent or shorter or longer setulose dorsally and ventrally. The separation between stylus and arista is sometimes indistinct.

aristomere (Fig. 30): segment of the arista. The first two aristomeres are usually short, the third aristomere is usually much longer.

flagellomere (Figs 21–23): single segment of the flagellum. In the plesiomorphic condition, Diptera have 8 flagellomeres (Stuckenberg 1996). In nematocerous Diptera the flagellomeres are rather uniform in shape, often with whorls of hairs distally. They are highly modified in males of some families (e.g., Tipulidae, Chironomidae, Ceratopogonidae). In orthorrhaphous Diptera and Cyclorrhapha, the number of flagellomeres

is reduced as the result of a fusion of certain flag-ellomeres. Excellent transformation series supporting this hypothesis are seen in extant Vermileonidae (Stuckenberg 1996).

1st flagellomere (Fig. 30): the very conspicuous 3rd antennal segment of most orthorrhaphous Diptera and Cyclorrhapha; usually much longer than the basal two segments together; it is regarded as the fusing product of flagellomeres 3–8 of plesiomorphic nematocerous Diptera (Stuckenberg 1996). Shape, colour and setulae of the 1st flagellomere are important for identification in many families; it possesses either a terminal style or a dorsal arista.

flagellum (Figs 20–23): all antennal segments following scape and pedicel form the flagellum. It is composed by a number of flagellomeres, which may be one segmented (1st flagellomere) in many orthorrhaphous Diptera and most Cyclorrhapha, or up to 14 segmented in some nematocerous Diptera (Limoniidae, Canthyloscelidae). An extreme case is seen in Rachiceridae where the flagellum consists of up to 36 flagellomeres.

pedicel (Figs 20–21, 30): second antennal segment; either shorter or longer than the flagellomeres; contains the Johnston's organ, which bears receptors for detecting movements of the flagellum; in Cyclorrhapha and few other families on the posterodorsal side with the antennal seam; often setulose or with conspicuous setae dorsally.

scape (Figs 20–21, 30): first or basal antennal segment. In most orthorrhaphous Diptera this segment is very small, sometimes almost invisible; the distal end of the scape may be furnished with some longer setulae.

stylus (Figs 24–25): the rigid fusing product of the flagellomeres following the 1st flagellomere (e.g., Stratiomyidae, Asilidae). It is situ-
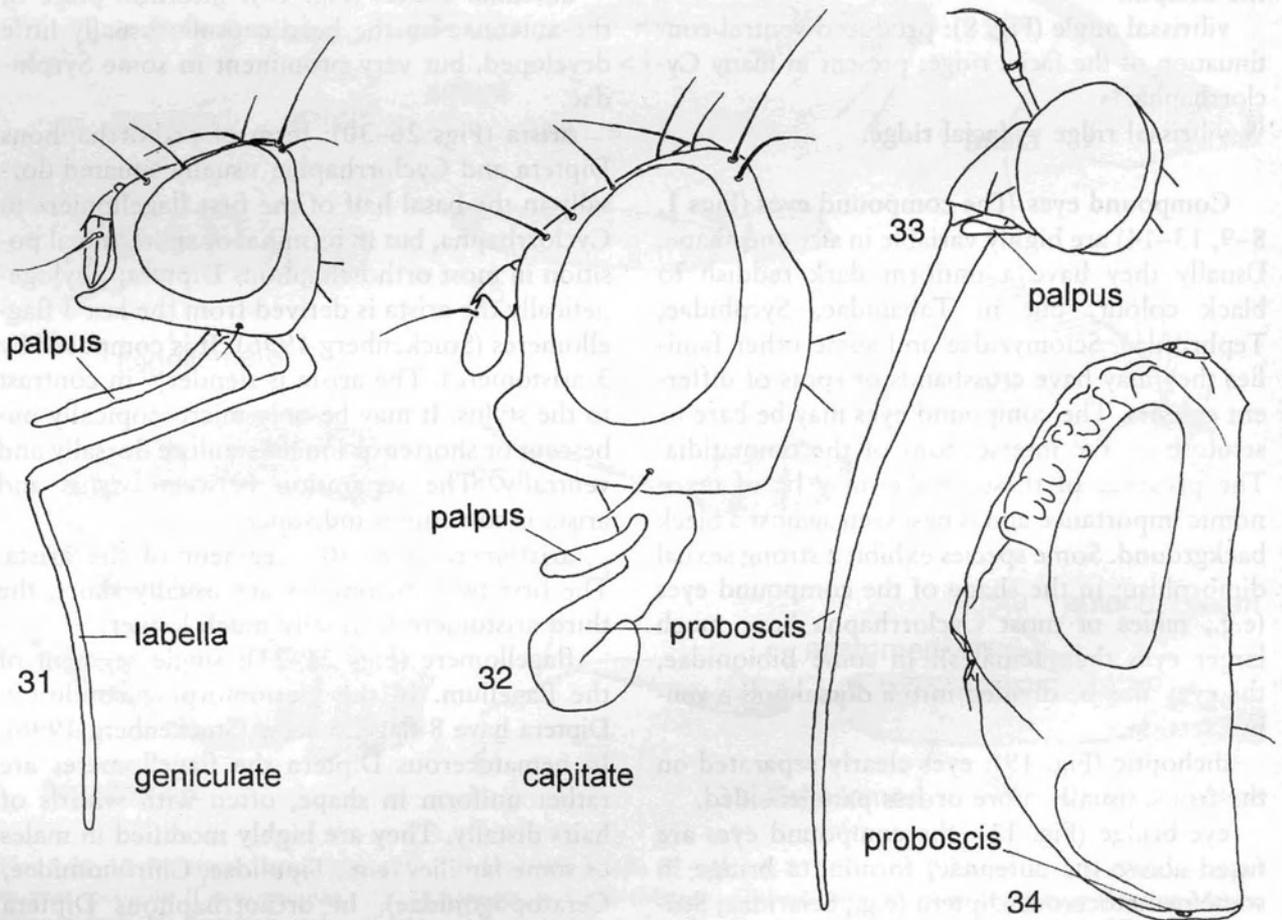
Figs 1.31–34. Outline of head profile. 31: *Myopites lelae* Dirlbek (Tephritidae); 32: *Orellia falcata* (Scopoli) (Tephritidae); 33: *Lampromyia canariensis* Macquart (Vermileonidae); 34: *Oestrus ovis* Linnaeus (Oestridae).

ated either terminal or subterminal and may consist of 1 to 5 segments. The separation between arista and stylus is sometimes indistinct.

Mouthparts. The mouthparts of Diptera exhibit a very wide range of modifications, but all are able only to take up dissolved food. Therefore, the mandibles, if they are present, are modified to a stylet-like blade which cannot break up solid food. In most blood-sucking and raptorial taxa the individual mouthparts are very long and narrowly built allowing them to pierce skin or cuticle. Some orthorrhaphous Diptera and most Cyclorrhapha have the mouthparts modified into a sucking organ which enables the fly to absorb liquid by capillary pressure.

During the evolution of Diptera, the individual structures of the mouthparts have undergone strong differentiations and adaptations. Generally speaking, evolution led to reductions, and the remaining, functional structures have been transformed considerably. In females of most blood-sucking nematocerous Diptera all structures of the mouthparts (labrum, mandibles, maxillae, labium, hypopharynx) are still present, whereas Cyclorrhapha have the mandibles entirely reduced, as well the maxillae except for the maxillary palpus. Also the labium, which is the largest mouthpart, consists of a reduced number of sclerites.

capitate (Fig. 32): type of proboscis with labellum short, square to slightly rectangular.

cardo: basal part of the maxilla; present only in some nematocerous Diptera.

clypeo-labral membrane (Fig. 17): connecting membrane between clypeus and labrum.

clypeus (Fig. 17): part of the head capsule, situated between face and labrum; reduced to a small, U-shaped sclerite in Cyclorrhapha. In contrast, the clypeus is rather large and shield-shaped in nematocerous and most orthorrhaphous Diptera. In blood-sucking species, the clypeus is enlarged and the face reduced.

food channel: enclosed proximally by the labrum and distally by the hypopharynx.

geniculate (Fig. 31): type of proboscis bent at an obtuse angle with labellum elongate, thin, of about the same length as the prementum.

hypopharynx (Figs 35, 38–40): unpaired medioventral postoral lobe of the gnathal region of the head anterior to the labium; this sclerite is present throughout the order. It is stylet-shaped and encloses the salivary channel.

labellum (Figs 31, 39–40): structure of the labium at its distal end; best developed in non-piercing species. Ontogenetically the labellum derives from the paired, united, two-segmented labial palpi. The labellum consists of two membranous, cushion-like lobes. They bear small, sclerotized, trachea-like grooves, the pseudotracheae, which radiate from the terminus of the food channel.

labium (Figs 35, 38–40): unpaired, posterior piece of the mouthparts forming a sheath for the other mouthparts; present in all Diptera. The glossa and the paraglossa are entirely absent, the postmentum may be present or absent, the palpi are fused and form the labellum; the prementum is well-developed.

labrum (Figs 17, 35, 38–40): sclerite which is derived from a single preoral lobe and encloses the anterior part of the food channel. Its shape may vary considerably among taxa.

lacinia (Fig. 37): inner endite lobe of the stipes of maxillae. Developed as part of the piercing organ in piercing nematocerous and orthorrhaphous Diptera (e.g., Asilidae, Tabanidae).

mandible (Figs 35–36): anterior pair of the mouthparts; only functional in females of some families of nematocerous and few orthorrhaphous Diptera (Athericidae, Rhagionidae, Tabanidae). They are either blade-like (in non-piercing species) or slender, stylet-like and then often serrate (in piercing species).

maxilla (Figs 35, 37–40): medium pair of the mouthparts; composed of a basal cardo and a distal stipes with the lacinia and the maxillary palpus (usually only called "palpus"). It is usually a stylet-like piercing organ which is present in many nematocerous and some orthorrhaphous Diptera (Tabanomorpha, Asilomorpha).

maxillary palpus = palpus.

palpus (= maxillary palpus) (Figs 31–33, 35, 37–40): structure of the maxilla, situated distally of the stipes; 5–segmented in many nematocerous Diptera, but reduced to 1–2 segments in

most orthorrhaphous Diptera and Cyclorrhapha; the only part of the maxilla which is still present in the latter taxa. The palpus may exhibit sexual dimorphism (e.g., Tabanidae). Its shape, chaetotaxy and colour is important for identification.

postmentum (Fig. 40): proximal structure of the labium.

prementum (Fig. 40): distal structure of the labium, usually forming a sheath for the other mouthparts. It bears distally the labellum.

proboscis (Figs 8, 32–34): tubular sucking organ; in Diptera, this term refers to all structures which form together the mouthparts.

pseudotracheae (Fig. 40): trachea-like grooves at the inner end of the labellum. They allow the

Diptera to take up liquid by capillar pressure. In Stomoxyini (Muscidae) they are secondarily sclerotized and become part of the piercing organ.

salivary channel: exit of the salivary glands, surrounded by the hypopharynx. Saliva is used to liquefy solid food in non-piercing species, and to inject anticoagulantia in blood-sucking species.

stipes (Fig. 37): distal structure of the maxilla, bearing the palpus in almost all Diptera, and bearing the lacinia in taxa with piercing mouthparts.

tormae: small sclerite, present in the lateral angles between labrum and clypeus and only de-
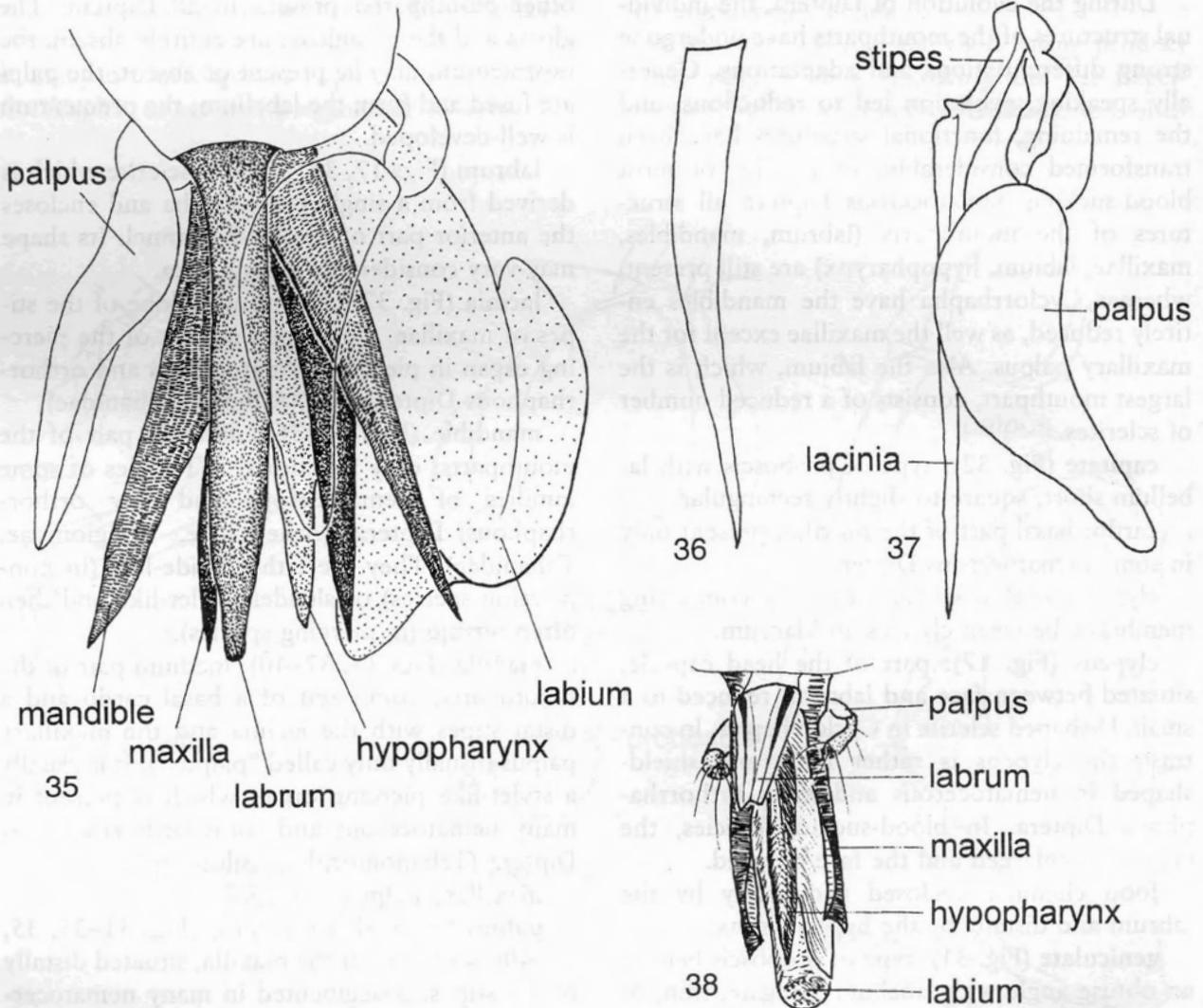
Figs 1.35–38. Mouthparts. 35–37: *Tabanus bromius* (Linnaeus) (Tabanidae): 35: schematic illustration, 36: mandible, 37: maxilla. 38: *Paritamus melanopus* (Meigen) (Asilidae).

veloped in species with piercing mouthparts (nematocerous and some orthorraphous Diptera).

Chaetotaxy. The number and arrangement of the setae is crucial for identification of Diptera. In particular the orthorrhaphous Diptera and Cyclorrhapha exhibit a very wide range of different bristling, whereas the chaetotaxy is less important in the nematocerous Diptera. The colour of the setae varies from black to white, and their orientation may be **proclinate, reclinate, inclinate** (= converging, incurved) or **eclinate** (= diverging, outcurved). The shape of the seta may be either **acuminate** (narrowing evenly from socket towards the tip) or **lanceolate** (narrowing very abruptly at the tip).

frontal seta (Figs 6–8): 1–15 pairs of usually black setae on the frontal plate, either proclinate, reclinate or inclinate; only present in families with a differentiation of the fronto-orbital plates into a frontal and an orbital plate; if two pairs are present, they are often called anterior and posterior frontal setae.

fronto-orbital seta (Fig. 17): term used in cases where no distinction between frontal and orbital setae is possible; their number is low (1–4 pairs) in most acalyptrate Diptera, whereas it may be high in some Cyclorrhapha.

genal seta (Fig. 7): one, rarely more pairs of anteroventrally directed setae on the ventral side of the gena. In some families, they are very conspicuous, whereas in others they are hardly longer than the surrounding genal setulae.

inner vertical seta = medial vertical seta.

interfrontal seta (Fig. 19): 1–7 pairs of inclinate setae on the frontal vitta, usually a single pair is situated in the upper third of the frons in the Calyptrata, but they may form a row which narrows towards the lunule in Milichiidae and Chloropidae.
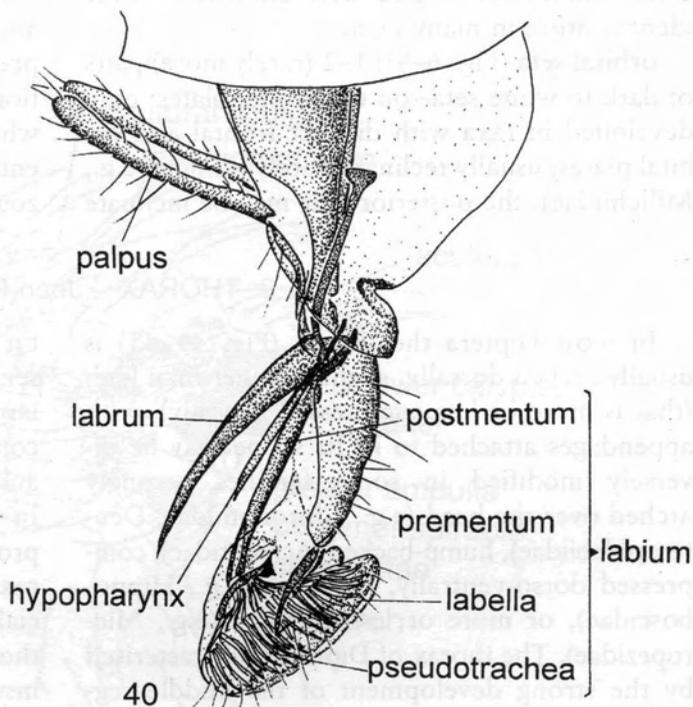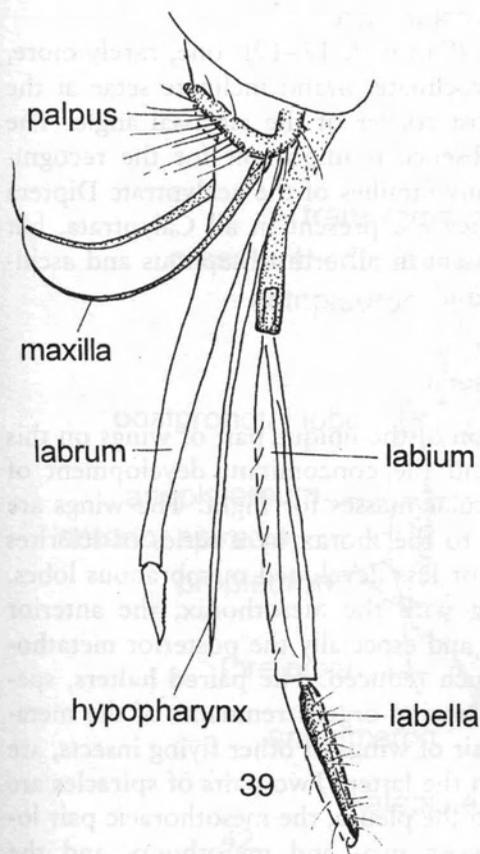
Figs 1.39–40. Mouthparts. 39: *Rhamphomyia anthracina* Meigen (Empididae); 40: *Sarcophaga variegata* (Scopoli) (Sarcophagidae).

lateral vertical seta (outer vertical setae of McAlpine 1981) (Figs 7–8): one pair of usually dark, eclinate setae on the vertex, usually just in the continuation of the margin between compound eye and frontal plate; present in some Hybotidae and most Schizophora.

medial postocellar seta (Fig. 19): few taxa have a small pair of setae just medial to the postocellar setae.

medial vertical seta (inner vertical setae of McAlpine 1981) (Figs 7–8): one pair of usually long setae which is inclinate or upright, situated on the vertex usually somewhat medial to the continuation of the line formed by the compound eye and the frontal plate.

occipital seta (Figs 7–9): stronger setae on the occiput; usually they are unordered, but they may form a regular row in the upper half, just posterior of the postocular setae in Tachinidae and some other families. Their number and colour may be important for identification.

ocellar seta (Figs 6–8): usually one pair, rarely 2–3 pairs of proclinate, rarely upright or eclinate setae on the ocellar triangle between the ocelli. Their length, colour and orientation is used for identification in many taxa.

orbital seta (Figs 6–8): 1–2 (rarely more) pairs of dark to white setae on the orbital plates; only developed in taxa with distinct frontal and orbital plates; usually reclinate, rarely eclinate (e.g., Milichiidae), the posterior pair may be inclinate

in some taxa. In case of two pairs present, they may be called anterior- and posterior orbital setae.

outer vertical seta = lateral vertical seta.

paravertical seta (Figs 6, 8): usually 1–2 pairs of small, but conspicuous upright to inclinate setae on the vertex, situated between medial vertical and postocellar setae. Present only in few families of Cyclorrhapha.

postgenal seta (Fig. 7): longer seta on the postgena. The number is usually variable.

postocellar seta (Figs 6, 19): one pair of strong setae on the vertex just posterior of the ocellar triangle. They may be eclinate, upright or inclinate. Their orientation defines some families of the acalyptrate Diptera.

postocular seta (Figs 6, 8–9): one to several rows of white or dark setae on the posterior side of the compound eyes just in the continuation of the vertex. The number of these setae in one row is usually variable.

subvibrissal seta (Figs 6–7): one to few pairs of setae just posterior the vibrissae, situated along the oral margin.

vibrissa (Figs 6–7, 18–19): one, rarely more, pairs of proclinate or/and inclinate setae at the anteriormost corner of the vibrissal angle. The presence/absence is important for the recognition of many families of the acalyptrate Diptera whereas they are present in all Calyptrata, but entirely absent in all orthorrhaphous and aschizous Diptera.

3. THORAX – Jean-Paul Haenni

In most Diptera the thorax (Figs 41–45) is usually arched dorsally, slightly longer than high (that is more or less compressed laterally), with appendages attached to it. Its shape may be diversely modified in some families, strongly arched over the head (e.g., Chironomidae, Deuterophlebiidae), hump-backed (Acroceridae), compressed dorso-ventrally, quadrate (e.g., Hippoboscidae), or more or less elongate (e.g., Micropezidae). The thorax of Diptera is characterised by the strong development of the middle segment, the **mesothorax**, which occupies most of its dorsal and lateral surfaces in connexion with

the insertion of the unique pair of **wings** on this segment and the concomitant development of large muscular masses for flight. The wings are connected to the thorax by a series of sclerites and more or less developed membranous lobes. In contrast with the mesothorax, the anterior **prothorax** and especially the posterior **metathorax** are much reduced. The paired **halters**, specialised balancing organs remnants of the metathoracic pair of wings of other flying insects, are inserted on the latter. Two pairs of **spiracles** are opening on the pleura, the mesothoracic pair located between pro- and mesothorax and the

41 — *Tipula trivittata* Say (Tipulidae), lateral view.

Labels (clockwise): presutural scutum, paratergite, basalare, prescutal pit, postpronotum, antepronotum, anterior spiracle, cervical sclerites, propleuron, fore coxa, anepisternum, katepisternum, mid coxa, trochanter, transverse suture, postsutural scutum, wing base, scutellum, anepimeron, mediotergite, halter, anatergite, katatergite, metanotum, posterior spiracle, metanepisternum, metepimeron, metakatepisternum, katepimeron, meron, hind coxa.

42 — Calliphoridae sp., lateral view.

Labels: transverse suture, presutural scutum, notopleuron, postpronotal lobe, anepisternum, anterior spiracle, propleuron, fore coxa, anepimeron, katepisternum, mid coxa, postsutural scutum, insertion of wing, scutellum, lower calypter, halter, greater ampulla, posterior spiracle, meral setae, katepimeron, meron, hind coxa.

Figs 1.41–42. Thorax, lateral view. 41: *Tipula trivittata* Say (Tipulidae). 42: Calliphoridae sp. (41 after Alexander and Byers 1981, 42 after Lane and Crosskey 1993).

metathoracic pair between meso- and metatho-
rax. Each of the 3 thoracic segments bears a pair
of **legs** attached to the thorax by the **coxae**.

The dorsal part of the prothorax is the **prono-
tum** which is divided into an anterior **anteprono-**

tum (developed mainly in nematocerous Di-
ptera) and the posterior **postpronotum** of higher
Diptera, of which the lateral **postpronotal lobes**
are taxonomically important. Laterally the **pro-
pleuron** is situated in front of the anterior spir-
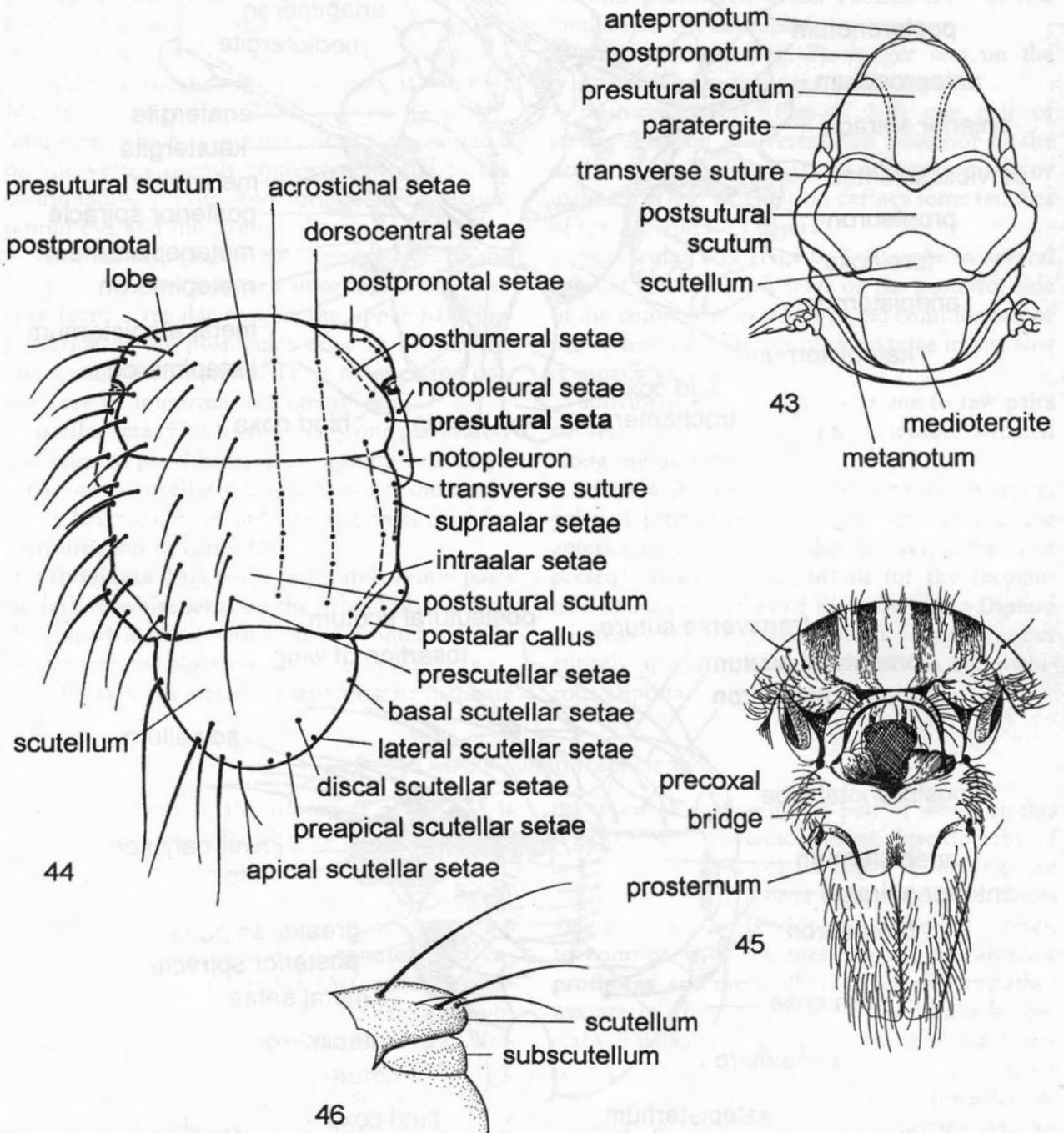
Figs 1.43–46. Thorax. 43: Tipulidae, dorsal view. 44: Tachinidae, dorsal view. 45: *Rhamphomyia (Megacyttarus) crassiros-
tris* (Fallén) (Empididae), anterior view. 46. *Cinochira atra* Zetterstedt (Tachinidae), lateral view of scutellar region (43–44
after Colless and McAlpine 1991, 45 after Collin 1961, 46 after Tschorsnig & Herting 1994).

acle and may be fused in some families with the ventral **prosternum** into a **precoxal bridge.**

The dorsal part of the mesothorax, the **mesonotum** is divided into an anterior **prescutum,** that is developed as such only in few nematocerous families, a **scutum** that occupies most of the dorsal thorax and is often more or less divided by a **transverse suture,** and a posterior **scutellum.**

The notum is bordered laterally in nematocerous Diptera by the **paratergite,** while in higher Diptera a sunken area, the **notopleuron,** extends between the postpronotal lobe and the wing base. The **postnotum** which lies posteroventrally of the scutellum may be divided into a dorsal **mediotergite** and 2 **laterotergites (anatergite** and **katatergite).** The pleural part of the mesothorax, the **mesopleuron** may be divided laterally by the **pleural suture** into an anterior **episternum** and a posterior **epimeron.** In turn, the episternum may be divided into a dorsal **anepisternum** and a ventral **katepisternum** while similarly the epimeron may be divided into a dorsal **anepimeron** and a

ventral **katepimeron.** Posteroventrally of the latter, lies the **meron.**

The dorsal part of the metathorax, the **metanotum,** is hardly visible between the postnotum and the first abdominal tergite. Laterally the **metapleuron** is divided into an anterior **metepisternum** and a posterior **metepimeron,** that are not always distinct. The latter may be fused behind the bases of the posterior coxae to form a **postcoxal bridge.**

The development of the individual pleural sclerites is very diverse throughout the order: reductions and fusions of sclerites may occur that are of taxonomic importance but may render their recognition difficult. Base of wing, halter, coxae and spiracles are the main landmarks that allow the localisation of the pleural sclerites. The **chaetotaxy** of thoracic sclerites is of great taxonomic importance especially in Cyclorrhapha but also in other divisions of the order. The names of the groups or rows of setae and setulae derive from that of the sclerite where they are inserted (see below).

Glossary
(most terms refer to structures that are shown on Figs 41–46)

anatergite: a pleural tergite of mesothorax between the scutellum and the halter. Together with katatergite it forms the laterotergite which is the lateral part of the postnotum.

anepimeron (= pteropleuron): a large pleural sclerite of the mesothorax, ventrally of the insertion of wing.

anepisternal cleft: pleural suture extending through the anterior margin of the anepisternum. It may be enlarged in certain nematocerous families (e.g., anepisternal membrane of Simuliidae).

anepisternum (= mesopleuron of former authors): a large pleural sclerite of the mesothorax generally occupying a central position, posteriorly of the anterior spiracle and anteroventrally of the base of the wing.

antepronotum: the most anterior dorsal part of prothorax, mainly developped in nematocerous families where it may form lateral enlarged antepronotal lobes (Tipulidae).

anterior spiracle: mesothoracic respiratory opening placed in the vicinity of the anterodorsal corner of the anepisternum, between pro- and mesothoracic sclerites.

greater ampulla (= subalar knob): a bulbous swelling of the anepimeron anteriorly of the articulation of the wing in Syrphidae and in Calyptrata.

basalare: small mesothoracic sclerite anteriorly of the insertion of wing.

cervix: membranous area joining the head to the thorax. The articulation is made through 3 pairs of cervical sclerites allowing the movements of the head.

coxopleural streak: suture-like depression separating the katepimeron from the meron in part of Calyptrata.

epimeron: posterior part of the mesopleuron, usually divided into a dorsal anepimeron and a ventral katepimeron.
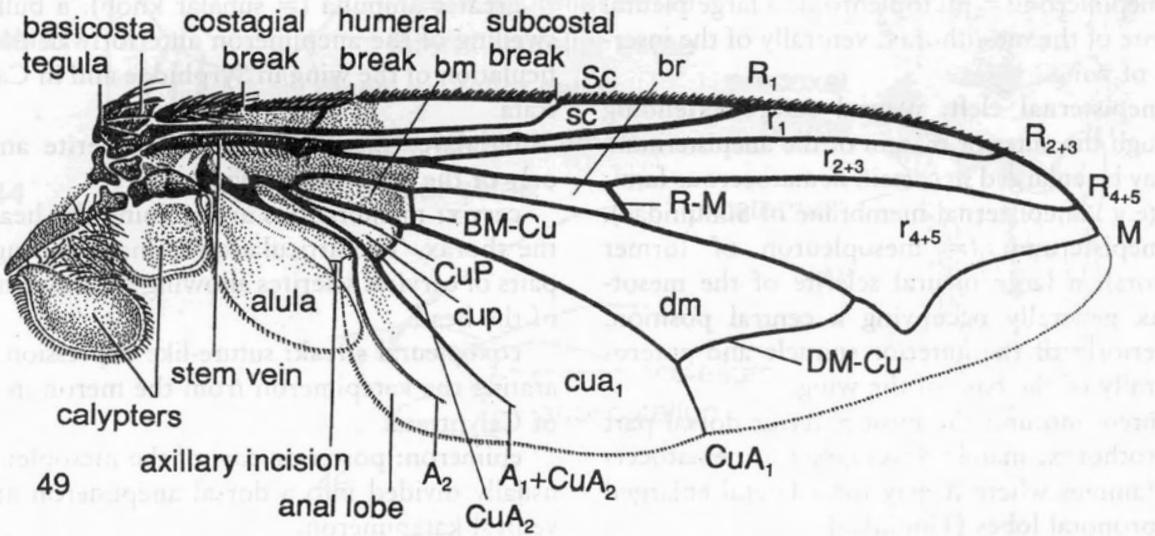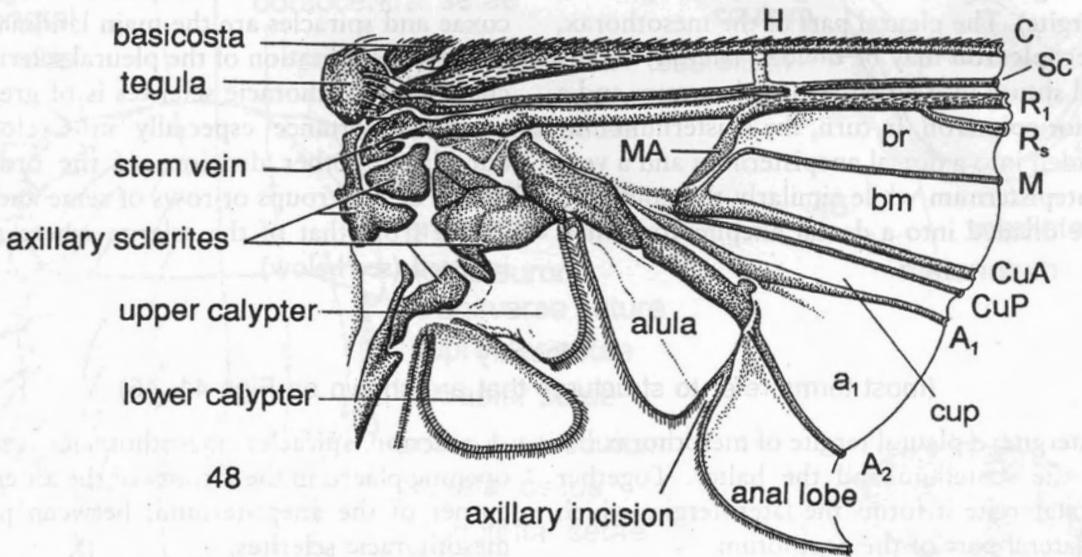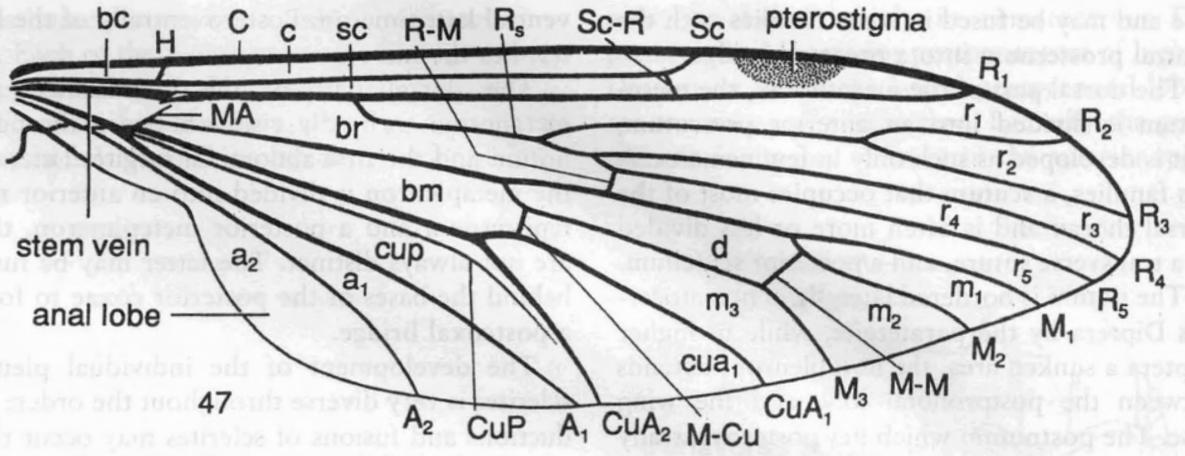
Figs 1.47–49. Wings. 47: venation of a hypothetical primitive Diptera. 48: *Tabanus americanus* Forster (Tabanidae), base of wing. 49: *Paralucilia wheeleri* (Hough) (Calliphoridae) (47–49 after McAlpine 1981).

episternum: anterior part of the mesopleuron, usually divided into a dorsal anepisternum and a ventral katepisternum.

halter: a paired balancing organ posteroventrally of the wing base, homologous with the metathoracic pair of wings of other winged insects. It is composed of a base, a stem or pedicel and a knob or capitulum (Fig. 59).

humeral calli = postpronotal lobes

humeral pits (see under prescutum)

humeri = **postpronotal lobes**

hypopleuron = meron

katatergite: a pleural sclerite of mesothorax dorsally of the posterior spiracle and anteriorly of the halter. Together with anatergite it forms the laterotergite.

katepimeron: a small mesopleural sclerite dorsally of the meron.

katepisternum (= sternopleuron, sternopleurum): a large pleural sclerite of the mesothorax between front and middle coxae, generally more or less triangular in shape. Its chaetotaxy is of great importance in many families of Diptera, especially in Cyclorrhapha.

laterotergite (= pleurotergite): a pleural sclerite of mesothorax, lateral part of the postnotum, located between base of wing and posterior spiracle. It may be divided into a posterior anatergite and an anterior katatergite.

mediotergite: mesothoracic sclerite, the dorsal part of the postnotum, ventrally of the scutellum. Its dorsal portion may be inflated to form the subscutellum (Tachinidae).

meron (= hypopleuron): a pleural sclerite posteroventrally of the posterior spiracle, between middle and hind coxae. In Calyptrata, the presence or absence of a row of meral setae is of great taxonomic importance at family level.

mesonotum: the dorsal part of the mesothorax, occupying most of dorsum of Diptera. It is divided into an anterior prescutum, a median much developed scutum (which may be itself divided by a transverse suture) and a posterior scutellum.

mesopleuron: pleuron of the mesothorax, divided by the pleural suture into an anterior episternum and a posterior epimeron. The mesopleuron occupies most of the pleural surface. The term mesopleuron has been used in a restricted sense by former authors to designate the anepisternum (dorso-anterior part of the mesopleuron in the present sense).

metanepisternum: a small pleural sclerite of metathorax posteroventrally of the posterior spiracle, the upper dorsal part of the metepisternum.

metanotum: dorsal part of the metathorax, generally hardly developed. In some families visible as a narrow band from halter to halter in front of the first abdominal tergite. May be produced posteriorly into a metanotal phragma inside of preabdomen (some families of nematocerous Diptera).

metapleural suture: a suture separating metepisternum and metepimeron of metapleuron.

metapleuron: a small pleural tergite of metathorax between hind coxa and halter, anteriorly of first abdominal segment. It may be divided into an anterior metepisternum and a posterior metepimeron.

metepimeron: posterior part of the **metapleuron**, separated from the metepisternum by the metapleural suture. In some families the metepimera are fused posteroventrally of the posterior coxae forming a postcoxal bridge.

metepisternum: anterior part of the metapleuron, separated from the metepimeron by the metapleural suture.

notopleuron: sunken area of the anterolateral region of the scutum, between postpronotal lobe and base of wing in higher Diptera. Its chaetotaxy is of major importance in Calyptrata.

paratergite: a narrow lateral tergite of the scutum in nematocerous Diptera extending from dorsally of the anterior spiracle to the base of the wing (Fig. 41).

pleural suture: a more or less distinct suture running ventrally from base of wing and separating the mesopleuron into an anterior episternum and a posterior epimeron. Relatively straight in nematocerous families, its course is sinuous in higher Diptera.

pleurotergite = laterotergite

postalar calli: a posterolateral paired region of the scutum between base of wing and anterior angle of scutellum, more or less separated from the scutum by a ridge. It is best developed in Cyclorrhapha Calyptrata, less so in acalyptrate and orthorrhaphous Diptera, and generally absent in nematocerous Diptera.

postcoxal bridge (see under metepimeron)

posterior spiracle: metathoracic respiratory opening placed on pleural membrane anteroventrally of the halter, between meso- and methorax. It may be more or less closed by lappets in Calyptrata (Sarcophagidae, Calliphoridae).

postnotum (= mediotergite, mesophragma): posterior part of mesothoracic notum, posteroventrally of the scutellum, best developed in nematocerous Diptera (e.g., Tipulidae), usually small in other groups. It may be more or less divided into a dorsal mediotergite and lateral laterotergites.

postpronotal lobes (= humeral calli, humeri) paired lobe of the anterolateral corner of thorax, part of the prothorax, best developed in higher

Diptera. Their chaetotaxy is of great taxonomic importance in Cyclorrhapha.

postpronotum: posterior part of the prothorax, generally weakly developed throughout the order except for the lateral postpronotal lobes.

postscutellum = subscutellum

postsutural scutum: the part of the scutum situated posteriorly of the transverse suture.

precoxal bridge: prothoracic sclerite anterior to the fore coxae resulting in some families from the fusion of the ventral prosternum with the pleural **proepisterna** (e.g., Empididae).

prescutal pits: (see under prescutum)

prescutal suture: (see under prescutum)

prescutum: anterior part of the mesonotum, generally indistinctly separated from the scutum, except in some nematocerous families where a prescutal suture may be developed laterally (Tipulidae, Psychodidae), or marked by prescutal pits (humeral pits) (Ceratopogonidae, Chironomidae).

presutural scutum: the anterior part of the scutum separated from the posterior postsutural
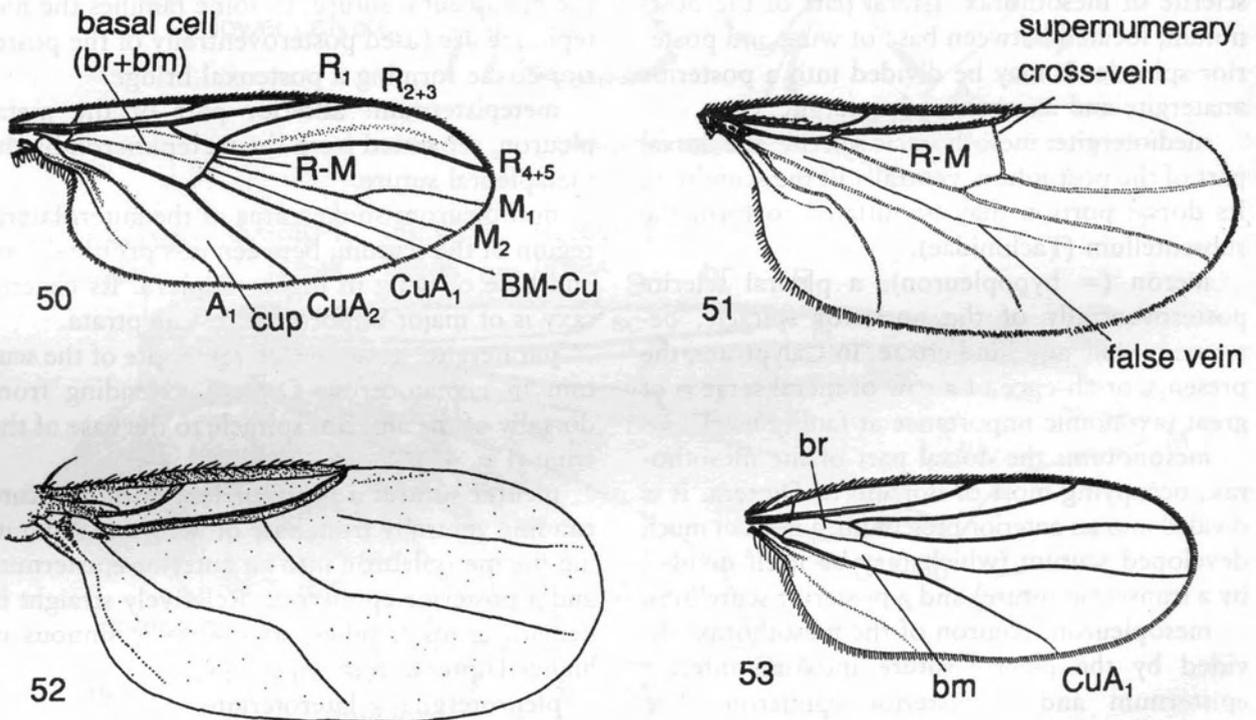
Figs 1.50–53. Wings. 50: *Mycetobia divergens* Walker (Mycetobiidae). 51: *Efcookella albitarsis* (Zetterstedt) (Scatopsidae). 52: *Metopina crassinervis* Schmitz (Phoridae). 53: *Drapetis* (*Crossopalpus*) *scissa* (Hybotidae) (50 after Peterson 1981, 51 after Haenni 1997, 52 after Disney 1998, 53 after Steyskal and Knutson 1981).

scutum by a more or less complete transverse suture.

proepimeron: small prothoracic sclerite, posterior part of the **propleuron**, anterobasally of the anterior spiracle. Its chaetotaxy is often of taxonomic importance.

proepisternum: small prothoracic sclerite, anterior part of the **propleuron** anteriorly to the anterior spiracle. Its chaetotaxy is often of taxonomic importance.

pronotum: the dorsal part of the prothorax, generally reduced to a narrow transverse band anteriorly of the notum. Its anterior part (antepronotum) is best developed in some nematocerous families (Tipulidae). In most higher Diptera the posterior part of the pronotum is enlarged into a pair of lateral postpronotal lobes (humeri, humeral calli) that form the anterior corners of the thorax.

propleuron: prothoracic pleural sclerite, anteroventrally of the anterior spiracle, dorsally of the front coxa. It may be divided into a distal proepimeron and a proximal proepisternum.

prosternum: ventral sclerite of the prothorax between the front coxae. Its shape and chaetosity is of taxonomic importance in acalyptrate Diptera and in Tachinidae. When fused with proepisterna it may form the precoxal bridge (e.g., Empididae).

pteropleuron = anepimeron

scutellum: the posterior part of the mesothorax, separated from the scutum by a deep suture and generally overwhelming the anterior part of the abdomen. It is generally rounded or triangular in shape, more or less cushion-like or flattened. Its chaetotaxy is of taxonomic importance.

scutum: the median dorsal part of the mesothorax, much developped in Diptera, occupying the greater part of the thorax in dorsal view. It is more or less divided by a transverse suture. It may bear paired lobes, the **postalar calli** between base of wing and anterior corners of scutellum.

In Cyclorrhapha but also in other groups, the chaetotaxy of scutum is of extreme taxonomic importance (see below).

sternopleuron = katepisternum

subalar knob = greater ampulla

subscutellum (= postscutellum): dorsal anterior portion of the mediotergite, posteroventrally of the scutellum. Generally concave and inapparent, it is much developed, cushion-like, in Tachinidae (Fig. 46).

transverse suture: a more or less complete suture dividing transversally the scutum. Its shape and extent is of great taxonomic importance for separating higher taxa of Diptera: acalyptrate Diptera have a medially incomplete suture while it is complete in Calyptrata (Fig. 44). In nematocerous and orthorrhaphous Diptera, the suture is variable in shape and extent (e.g., V-shaped in Tipuloidea, U-shaped in Ptychopteridae) (Fig. 43).

Chaetotaxy of thorax (Figs 42, 44). The chaetotaxy of thorax is of major taxonomic importance in Diptera, especially in Cyclorrhapha. The scutum may bear several longitudinal, more or less parallel, rows of macrotrichia: from median line the following rows or groups of macrotrichia may be recognised: **acrostichal, dorsocentral, intraalar** (all of these may be qualified **presutural** or **postsutural** according to their position in relation with the transverse suture), **posthumeral, prealar, supraalar** and **postalar** setae. Other important dorsal setae are the **postpronotal (humeral), notopleural** and **scutellar** setae. Almost all sclerites of the pleura may bear taxonomically important setae that are called after the sclerite where they are located. The most frequently used are the **propleural, anepisternal (mesopleural), katepisternal (sternopleural)** and **meral (hypopleural)** setae. Not only the location and number of macrotrichia must be considered, but also their relative size and direction (see under introduction).

Glossary (terms refer to Figs 42 and 44)

acrostichal setae: medial setae of the scutum, generally arranged into bi- to multiserial longitudinal rows. The acrostichals may often be present only as rows of setulae.

anepimeral setae (= pteropleural setae): in certain families of acalyptrate Diptera and Cyclorrhapha, the setae present on the anepimeron may be of taxonomic importance.

anepisternal setae (= mesopleural setae): in certain families of acalyptrate Diptera, the setae present on the anepisternum (generally a vertical posterior row) may be of taxonomic importance.

apical scutellar setae: a pair of setae placed at the apex of the scutellum. Their size and direction are of taxonomic importance especially in many families of Cyclorrhapha and of acalyptrate Diptera.

basal scutellar setae: 1–2 pairs of setae placed along the basal margin of the scutellum (some families of acalyptrate Diptera and Cyclorrhapha).

discal scutellar setae: setae that are sometimes present on the dorsal surface (disc) of the scutellum (some Cyclorrhapha).

dorsocentral setae: longitudinal rows of submedian macrotrichia on the scutum, laterally of the acrostichals. Their number may vary from none to less than 10. Their relative length and direction is of general taxonomic importance in Cyclorrhapha.

humeral setae = postpronotal setae

hypopleural setae = meral setae

intraalar setae: sublateral dorsal longitudinal rows of macrotrichia on the scutum, laterally of the dorsocentrals.

katepisternal setae (= sternopleural setae): macrotrichia of the upper part of the katepisternum, often forming a row or a triangle. Their number, position, size and direction are of general taxonomic importance in many Cyclorrhapha.

lateral scutellar setae: one or several pairs of setae placed along the lateral margin of the scutellum between basal scutellar and subapical scutellar setae.

meral setae (= hypopleural setae): a more or less fan-like vertical row of macrotrichia of the meron, posteroventrally of the halters, is present in some families of Cyclorrhapha (Calliphoridae, Sarcophagidae, Rhinophoridae and Tachinidae).

mesopleural setae = anepisternal setae
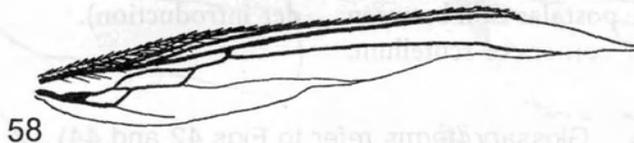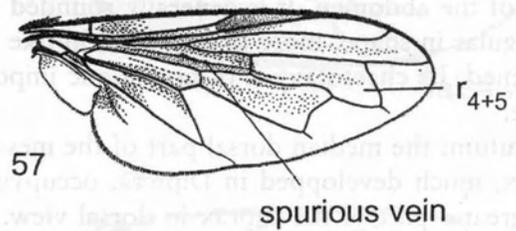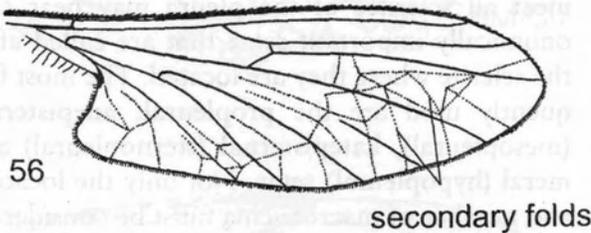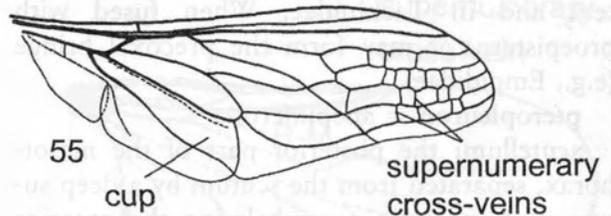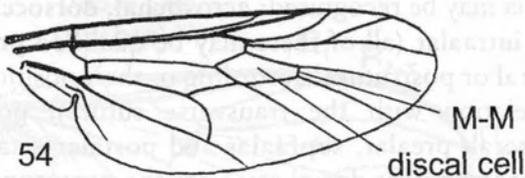
Figs 1.54–58. Wings. 54: *Beris geniculata* Curtis (Stratiomyidae). 55: *Nemestrinus obscuripennis* Portschinsky (Nemestrinidae). 56: *Blepharicera fasciata* (Westwood) (Blephariceridae). 57: *Orthonevra pulchella* (Williston) (Syrphidae). 58: *Stenepteryx hirundinis* (Linnaeus) (Hippoboscidae), falciform wing (54 after Rozkošný 1982, 55 after Richter 1997, 56 after Lindner 1930, 57 after Thompson and Rotheray 1998, 58 after Oldroyd 1966).

notopleural setae: the number and relative size of the macrotrichia of this little sunken region between the postpronotal lobe and base of wing are of frequent taxonomic importance.

postalar setae: macrotrichia of the postalar calli, on the lateroposterior corners of the scutum.

posthumeral setae: macrotrichia situated in a transverse row posteriorly of the postpronotal lobes in some Calyptrata.

postpronotal setae (= humeral setae): macrotrichia of the postpronotal lobes, whose number, direction and size are of taxonomic importance in many orthorrhaphous families and in Cyclorrhapha.

postsutural setae: this term may be used for distinguishing those of the acrostichal, dorsocen-

tral or intraalar setae placed posteriorly of the transverse suture of the scutum.

prealar setae: the anterior postsutural supraalar seta (anteromedially of the insertion of wing) whose size is often of taxonomic importance in Cyclorrhapha.

preapical scutellar setae: a pair of subapical setae on the margin of the scutellum. Their size and direction are of taxonomic importance in some families of Cyclorrhapha.

prescutellar setae: posterior postsutural pair of acrostichal setae, anteriorly of the scutellum. Their presence and size are of taxonomic importance in Cyclorrhapha.

presutural setae: this term may be used for distinguishing those of the acrostichal, dorsocen-
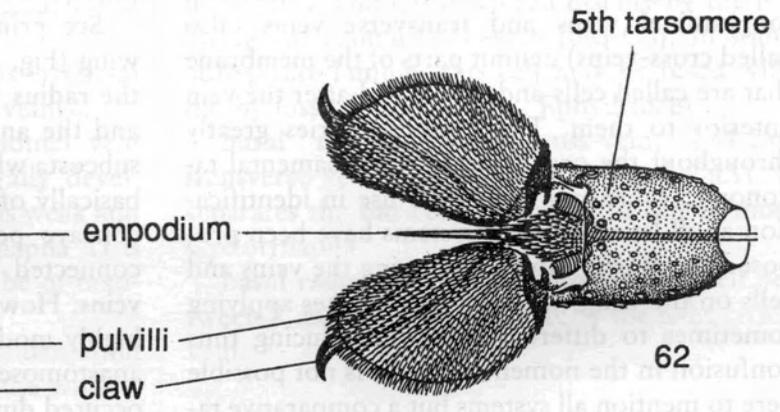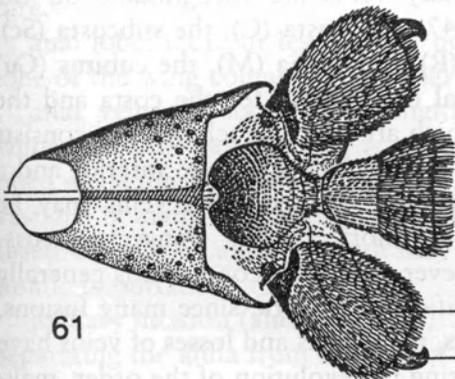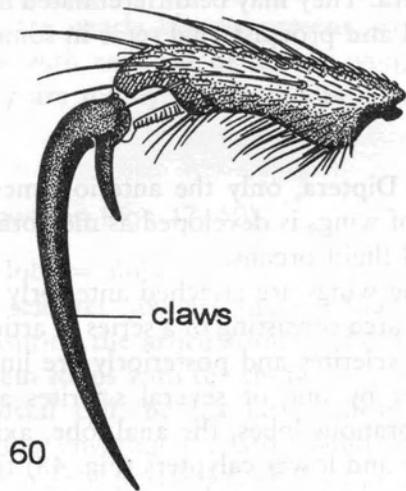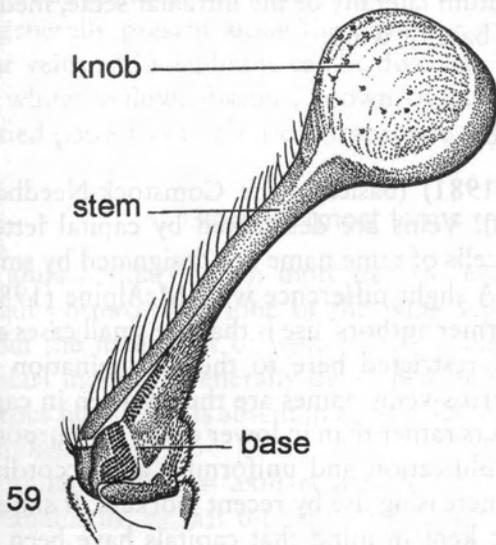
Figs 1.59–62. Halter and acropods. 59: *Bibio* sp. (Bibionidae), halter. 60: *Monohelea (Schizohelea) leucopeza* (Meigen) (Ceratopogonidae), claws of hind leg of female. 61: *Stratiomys badia* Walker (Stratiomyidae), acropod. 62: *Musca autumnalis* De Geer (Muscidae), acropod (59, 61–62 after McAlpine 1981, 60 after Downes and Wirth 1981).

tral or intraalar setae placed anteriorly of the transverse suture of the scutum. An isolated seta dorsally of the notopleural, anteriorly of scutal suture is called presutural seta in Calyptrata.

proepimeral setae (= propleural setae): the presence of setae or setulae on this propleural sclerite just above front coxa is an important taxonomic character in acalyptrate Diptera.

proepisternal setae (= propleural setae): the presence of setae or setulae on this propleural sclerite anterior to the prothoracic spiracle is an important taxonomic character in acalyptrate Diptera.

propleural setae: macrotrichia or microtrichia borne on the small sclerite anteriorly of the anterior spiracle, dorsally of the fore coxa, which are of taxonomic importance in several acalyptrate Diptera. They may be differentiated into proepimeral and proepisternal setae in some families.

pteropleural setae = anepimeral setae

scutellar setae: setae of the scutellum, whose number and position are of taxonomic importance in the families of Cyclorrhapha: see under apical, subapical, lateral, basal and discal scutellar setae.

spiracular setae: one or few setae may be present on the margin of the posterior spiracle (Sepsidae, Coelopidae).

sternopleural setae = katepisternal setae

subapical scutellar setae: a pair of setae of the margin of the scutellum, placed immediately before the tip, whose size and direction may be of taxonomic importance in some families of acalyptrate Diptera and of Calyptrata.

supraalar setae: a longitudinal row of setae of the scutum laterally of the intraalar setae, medial to the base of wing.

Wing (Figs 47–58)

In Diptera, only the anterior (mesothoracic) pair of wings is developed as membranous functional flight organs.

The wings are attached anteriorly by the **axillary area** consisting of a series of articulated **axillary sclerites** and posteriorly are linked to the thorax by one or several sclerites attached to membranous lobes, the **anal lobe, axillary lobe, upper** and **lower calypters** (Fig. 48) that may be or not present according to the taxonomic groups (best developed in Calyptrata but often practically absent in nematocerous families). The stalk of the wing contains the bases of the **veins.** The **longitudinal veins** and **transverse veins** (also called **cross-veins**) delimit parts of the **membrane** that are called **cells** and are named after the vein anterior to them. The venation varies greatly throughout the order and is of fundamental taxonomic value and of general use in identification at all levels. Several systems have been proposed for interpreting and naming the veins and cells on the wing, with the same names applying sometimes to different veins, introducing thus confusion in the nomenclature. It is not possible here to mention all systems but a comparative table may be found for example in Matile (1990). The system adopted here follows that of McAl-

pine (1981) (basically the Comstock-Needham system). Veins are designated by capital letters while cells of same name are designated by small cases. A slight difference with McAlpine (1981) and former authors' use is that the small cases are strictly restricted here to the denomination of cells: cross-veins names are thus written in capital letters rather than in lower cases, for purposes of simplification and uniformity and according to an increasing use by recent workers. It should also be kept in mind that capitals have been in use also for cells in many works prior to McAlpine (1981).

Six primary veins are recognisable on the wing (Fig. 47), the **costa (C),** the **subcosta (Sc),** the **radius (R),** the **media (M),** the **cubitus (Cu)** and the **anal (A).** Except for the costa and the subcosta which are simple, each of them consists basically of 2 branches, a convex anterior and a concave posterior. Longitudinal veins may be connected by short, usually transverse **cross-veins.** However, this basic condition is generally highly modified in Diptera, since many fusions, anastomoses, reductions and losses of veins have occured during the evolution of the order, making it sometimes difficult to homologise them. The posterior veins may be reduced or faint, in

particular in nematocerous Diptera (Fig. 51), but reduction of venation is a general trend throughout the order. This may affect practically any vein and may be encountered in numerous families (Fig. 51–53). A secondary net-like pattern of fine folds is present on the membrane of Blephariceridae and Deuterophlebiidae (Fig. 56).

The veins, particularly those on the anterior half of the wing, may be bare or covered on the dorsal, ventral or both sides with setae or spines (especially the costa), or even scales in Culicidae. The membrane may be bare (and wing is hyaline) or more or less densely microtrichiose (and wing becomes more or less dull according to the density and size of microtrichia). More rarely the membrane may bear macrotrichia (some nematocerous families). A fringe of short microtrichia is generally present along the posterior margin. The veins and membrane can be diversely tinged in white, yellow, fuscous, brown or black and varied patterns of coloured (transverse or longi-tudinal) bands and spots can be seen in several families. The pattern of wing is of taxonomic importance in several families (e.g., Tephritidae, Ulidiidae).

The wings, when functional, are usually oval, more or less elongated in shape, broadly rounded at apex, sometimes pointed (e.g., Lonchopteridae). In some cases, in relation with ectoparasitic way of life (Hippoboscidae) they may be falciform (Fig. 58). Partial or total reduction of wings may occur in genera of many families, in connexion with peculiar way of life (parasites, litter or cave dwellers, etc), or niches (high mountain, arctic, etc).

The posterior (metathoracic) pair of wings has become in Diptera the halters (Fig. 59), a paired organ of stabilisation of flight (see under Thorax), one of the basic synapomorphies of the order. These are nearly always present, even in most forms with reduced or absent wings, although they are totally absent in Braulidae for example.

Glossary (most terms refer to structures shown on Figs 47–49)

alula (axillary lobe): more or less developed small postero-basal lobe of the wing separated from the main part of wing by the axillary (or alular) incision. Generally developed in brachycerous families, it is absent in most nematocerous families.

alular incision = axillary incision

anal cells, a_1, a_2: the true anal cells are generally open and occupy the anal lobe of the wing. However the **posterior cubital cell** (cup, cu*p*) is frequently called anal cell in dipterological literature.

anal lobe: more or less distinct postero-basal lobe of the wing containing the anal vein(s).

anal vein, A: sixth (last) longitudinal vein whose anterior branch (A_1) is generally developed while the posterior branch (A_2) is weak and vestigial in many families. In Cyclorrhapha A1 is fused with CuA2 and its length may be of taxonomic importance.

axillary incision (alular incision): indentation separating the alula from the rest of the wing.

axillary lobe = alula

axillary sclerites (axillary plates): four small sclerites ensuring the articulation of the base of the main vein stems with the thorax.

basal costal cell, bc (axillary plates): four small sclerites ensuring the articulation of the base of the main vein stems with the thorax.

basal costal cell, bc: small anterior basal cell closed distally by the humeral cross-vein.

basal medial cell, bm (2nd basal): basal cell between M and CuA1, closed distally by the basal-medial cubital cross-vein (bM-Cu). In some acalyptrate families this cell may be fused with dm by loss of bM-Cu (e.g., Ephydridae).

basal medial-cubital cross-vein, bM-Cu: transverse vein joining basally M and CuA1. It separates the bm cell from the dm cell in most Cyclorrhapha.

basal radial cell, br (1st basal): basal cell between R and M, closed distally by the R-M cross-vein.

basicosta (humeral plate): articulating sclerite at the base of the costa.

branch: each of the arms of a forked longitudinal vein.

cell: surface of the wing delimited by veins (closed cell) or by veins and margin of wing (open cells). A cell is named after the vein anterior to it (abbreviations of cells are in lower case).

closed cell: see under cell

costa, C: first longitudinal vein, forming the anterior margin of the wing and reaching generally the vicinity of the apex of the wing. It may be continuous around the wing in some nematocerous and orthorrhaphous families (e.g., Tabanidae) (Fig. 48) or stop at the middle of the wing or even before (e.g., Phoridae, some nematocerous families) (Figs 51–52). The costa may be interrupted at 1 or 2 (3) places (costal breaks) that are of taxonomic importance in acalyptrate families.

costagial break: infrequently encountered break of the costa, proximal to humeral vein.

costal break: interruption of the costa in relation with special points of flexion of the wing (see under subcostal break, humeral break, costagial break) (Fig. 49). Their presence or absence is of great taxonomic importance at a family level in acalyptrate Diptera.

costal cell, c: cell of the anterior margin of the wing, distally of the humeral cross-vein, between C and Sc.

costal margin: the anterior margin of the wing, generally marked by the costa.

costal spine: a more or less thickened and long macrotrichion of the costa, at the junction of Sc. It may be present in some acalyptrate families and Calyptrata.

cross-vein: a transverse vein joining two longitudinal veins.

cubital fork: see under cubitus

cubitus or **cubital vein, Cu:** fifth longitudinal vein which is two-branched throughout the order. The anterior branch (CuA) is forked into CuA_1 and CuA_2 and is called the cubital fork. The posterior branch (CuP) is a simple and weak vein close to CuA_2. In Cyclorrhapha CuA_2 is short and transverse, joining A1 and delimiting thus a short *cup* cell (posterior cubital cell, anal cell of many authors) (Fig. 49).

discal cell, d: taxonomically important cell, occupying often a central position in the wing in the M sector (Fig. 47). It closed distally by the M-M cross-vein.

discal-medial cell, d-m (often called discal cell): taxonomically important cell often occupying a central position in wing, between M and CuA_1 (Fig. 49). It is closed proximally by bM-Cu and distally by dM-Cu cross-veins.

discal medial-cubital cross-vein, dM-Cu (= posterior cross-vein, tp): cross-vein joining M to CuA_1, closing the dm cell (discal medial cell, discal cell of many dipterists) in some nematocerous and orthorrhaphous families and in most Cyclorrhapha.

false vein: fold-like thickening of the membrane, usually associated with reduction of longitudinal veins, present in many nematocerous families, especially between M and CuA_1. The spurious vein in the medial sector of Syrphidae is a similar structure (Fig. 57).

fork: branched irapical section of a longitudinal vein (e.g., R_{2+3} and R3). If the fork is absent, the longitudinal vein will be named after the veins constituting normally the fork (e.g., R_{2+3})

humeral break: break of the costa, distal to the junction of humeral vein.

humeral vein, H: basal anterior cross-vein joining the subcosta to the costa.

humeral plate = basicosta

lower calypter (lower squama, squamula thoracica): proximal lobe of the folded membrane joining the hind margin of the wing to the thorax.

lower squama = lower calypter

media, M: third longitudinal vein, whose posterior branch reaches the wing margin in up to 3 veins (M_1, M_2, M_3), but in most Cyclorrhapha only one vein (M) is present (Fig. 49). The anterior branch of media is strongly reduced in Diptera, at most only visible as a short basal vein joining R. In some nematocerous families (e.g., Keroplatidae, Mycetobiidae), the basal part of M may be vestigial or even absent (Fig. 50), or fused with the radius for a distance.

medial cells, m_1, m_2, m_3: posterior cells of the medial sector, generally open at the wing margin. In most Cyclorrhapha, only one m cell is present.

medial cross-vein, M-M: cross-vein joining M_2 to M_3 and closing distally the true discal cell (Fig. 54).

medial-cubital cross-vein, M-Cu : transverse vein between M and CuA_1, closing distally the basal medial cell.

membrane: alar surface.

open cell: see under cell

petiole = stem

posterior cells: cells of the hind margin of the wing between the last vein of Rs and CuA_2. Their number and shape (open or closed) are of taxonomic importance in orthorrhaphous families.

posterior cross-vein = discal-medial cubital cross-vein

posterior cubital cell, cu$p$ (= "anal" of many authors): usually the last cell before the hind margin of wing. Its shape and length are of taxonomic importance: cu$p$ is long and open in nematocerous Diptera (Fig. 50), long and generally closed or nearly so in orthorrhaphous families (Fig. 55) and short and closed in most Cyclorrhapha (Fig. 49). It may be absent in some families (e.g., Hybotidae, Chloropidae) where A_1 has disappeared (Fig. 53).

pterostigma: thickened, pigmented or opaque area of the wing near the point of junction of R_1 with the costa, in the distal part of cell sc. It is frequently developed in nematocerous and brachycerous families (Fig. 54), but nearly always absent in Cyclorrhapha.

R_1 = anterior branch of the radius distal of the stem vein from which it is separated by a transverse scar or a constriction.

radial cells, r_1, r_2, r_3, r_4, r_5: cells encompassing the radial sector. Their number is reduced in many families, in relation with fusions of forks of veins. Generally open at wing margin, but r_1 may be closed in some orthorrhaphous families and Syrphidae and r_{4+5} is typically closed in Syrphidae (Fig. 57) and some Cyclorrhapha.

radial-medial cross-vein, R-M (= anterior cross-vein, ta): a transverse vein joining the media to the radius. It is an important landmark in wing, whose position and length are of great taxonomic importance. It may be horizontal in position in some nematocerous families or obliterated through fusion of these veins (e.g., Mycetophiloidea, Scatopsidae) (Fig. 51).

radial sector, Rs: posterior branch of the radius, arising from R_1. It may be furcated in up to 4 branches but more often in 2 branches (R_{2+3} and R_{4+5}) or even be simple.

radius, R: third longitudinal vein, whose anterior branch (R_1) is simple, while the posterior branch (Rs, radial sector) is primarily branched into R_2, R_3, R_4 and R_5 (only retained in families Tanyderidae and Psychodidae). In most families especially in Cyclorrhapha, the fork of R_2 and R_3 is only present as a single vein named R_{2+3} and similarly the fork of R_4 and R_5 is usually present as a single R_{4+5}. In some nematocerous families (e.g., Scatopsidae), only one vein of Rs is present.

spurious vein: see under false vein

squamula alaris = upper calypter

squamula thoracica = lower calypter

stem (= petiole): basal part of a longitudinal vein (proximal to forking).

stem vein: basal section of radius, reaching distally to level of humeral cross-vein and separated from R_1 by a transverse suture or constriction (Fig. 48).

stigma = pterostigma.

subcosta, Sc: second longitudinal vein, which is usually well-developed, but may be abbreviated in some nematocerous families (e.g., Mycetophiloidea, Scatopsidae). In acalyptrate families, the junction of Sc with costa may vary a lot: the distal part of Sc may be reduced and vestigial or fused with R_1 and the precise position of these veins and of the frequently present subcostal break are of great taxonomic importance at a family level.

subcostal break: break of the costa, proximal to where Sc joins the costa (or would join it if it were complete). Its presence or absence, position and aspect is a very important character at a family level in acalyptrate Diptera.

subcostal cell, sc: cell of the anterior margin of the wing, between C and R_1, beyond Sc. In acalyptrate families, it may be much reduced by approximation or fusion of Sc with R_1.

subcostal-radial cross-vein, Sc-R: a cross-vein joining Sc to the radius (e.g., Limoniidae), reduced or absent in most families.

supernumerary cross-vein: additional cross-vein that may be present in some families between different longitudinal veins (e.g., Scatopsidae, Bombyliidae, Nemestrinidae) (Fig. 51, 55).

tegula: articulating sclerite at the extreme base of the costa (Fig. 48).

transverse vein (= cross-vein)

upper calypter (squamula alaris, upper squama):

distal lobe of the folded membrane joining the hind margin of the wing to the thorax.

upper squama = upper calypter

vein: more or less sclerotized structures of the wing that reinforce the membrane, allowing flight movements. Longitudinal veins are generally connected by shorter transverse veins (cross-veins).

Legs (Figs 60–67)

The 3 pairs of locomotory legs of Diptera (**fore leg**, foreleg or proleg, **mid leg**, midleg or mesoleg, **hind leg**, hindleg or metaleg) consist of 5 main parts (Figs 41, 63): **coxa, trochanter, fe-**
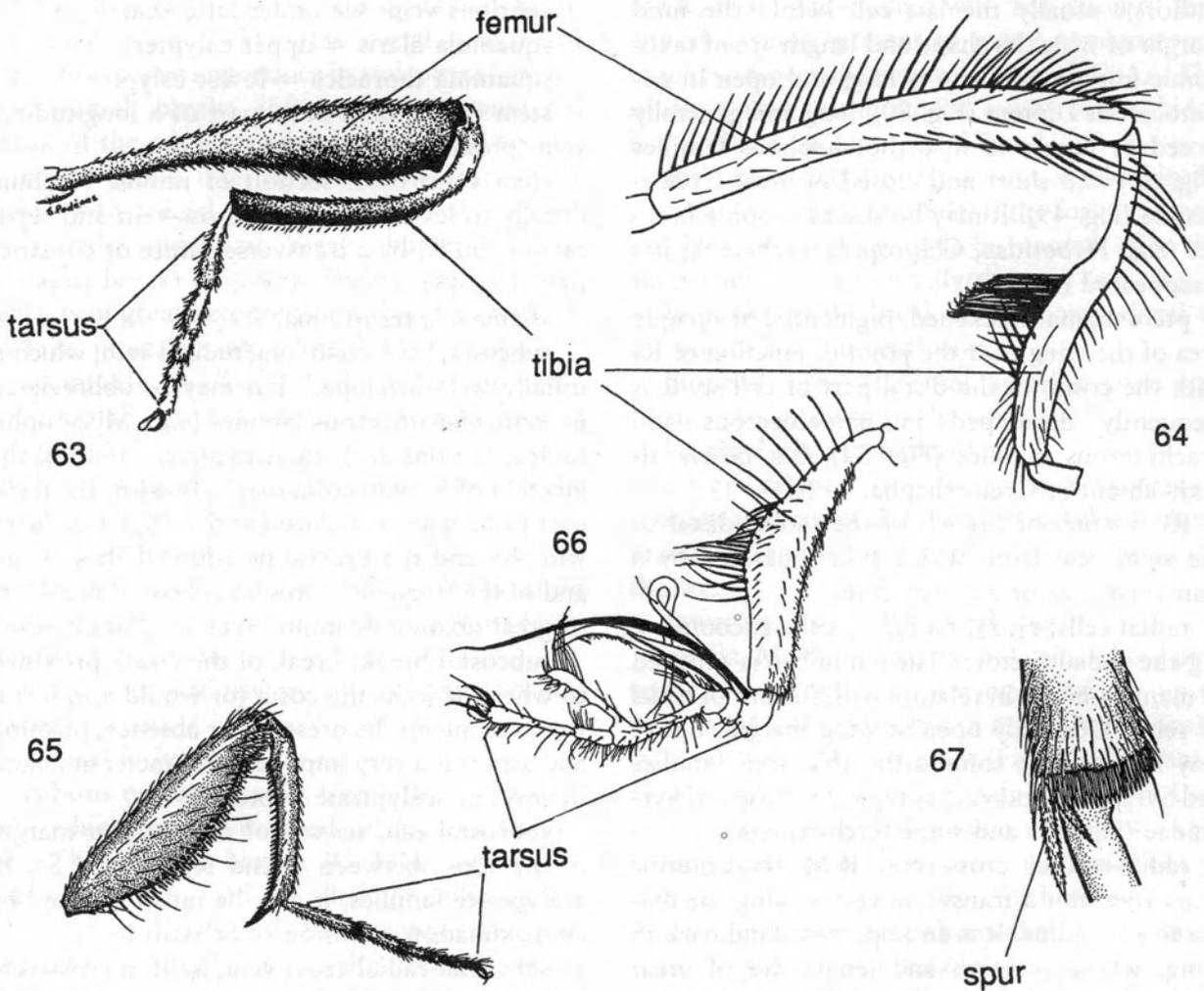
Figs 1.63–67. Legs. **63:** *Hyperoscelis eximia* (Boheman) (Canthyloscelidae), hind leg. **64:** *Hydrotaea borussica* Stein (Muscidae), male hind leg. **65:** *Platypalpus trivialis* Loew (Hybotidae), raptorial mid leg. **66:** *Campsicnemus magius* (Loew) (Dolichopodidae), male fore leg. **67:** *Sylvicola fenestralis* (Scopoli) (Anisopodidae), apex of hind tibia (63 after Haenni 1997, 64 after Hennig 1962, 65 after Steyskal and Knutson 1981, 66 after d'Assis Fonseca 1978, 67 after Peterson 1981).

mur, tibia, tarsus (itself composed of 5 tarsomeres) plus the distal acropod which is usually fused with the fifth tarsomere and bears the claws and often peculiar adhesive flap-like structures, the pulvilli and the diversely modified empodium (Fig. 61–62). Legs of Diptera are generally rather short but all parts may be more or less strikingly elongated in several groups of nematocerous Diptera (Tipuloidea, Ptychopteridae, Blephariceridae), more rarely so in some families of brachycerous Diptera (Vermileonidae, Rhagionidae, Asilidae) and acalyptrate Diptera (Micropezidae).

In a number of families throughout the order, modifications of the legs have appeared in relation with courtship behaviour and copulation, prey-catching (Fig. 65), or more rarely digging or cleaning behaviour, etc. These modifications include thickenings, swellings, indentations, torsions, elongations, etc, of peculiar segments and apparitions of various lobes or appendages or development of peculiar tufts of hairs, combs of setulae, groups or rows of thickened setae, spinules, spurs and teeth (Fig. 63–66).

Legs may bear an important vestiture of macrotrichia (setae and setulae) and microtrichia whose arrangement is of great taxonomic importance throughout the order but especially in Cyclorrhapha. Not only the number of macrotrichia is important but also their location, size, direction and even appearance. To identify their position, the leg is supposed to be extended laterally at a right angle to the body, delimiting thus anterior (a), dorsal (d), posterior (p) and ventral (v) surfaces, with intermediate surfaces called after their position anterodorsal (ad), posterodorsal (pd), posteroventral (pv) and anteroventral (av) (Figs. 3–5).

Glossary

acropod (posttarsus): a small terminal sclerite usually fused with the fifth tarsomere and bearing the claws, empodium and pulvilli when developed.

apical comb: a row of setulae or a comb of minute spinules may be present at the tip of tibia in several families (Fig. 67).

basitarsus (metatarsus, first tarsomere): proximal segment of the tarsus. It may frequently be modified in different ways (size, shape, vestiture) (Fig. 66).

claws (tarsal claws): a pair of claws is articulated on the ventral surface of the acropod. They may be diversely modified, elongated, reduced, toothed in several families (e.g., Ceratopogonidae) (Fig. 60), or present a comb-like structure in ectoparasitic forms (e.g., Hippoboscidae, Braulidae).

coxa: basal segment of the leg, articulated with the thorax (Fig. 41). The coxa is generally short, but may be elongated (especially for the anterior pair), as in several families of nematocerous Diptera (Mycetophiloidea, Scatopsidae) or swollen (e.g., Bibionidae).

ctenidium: apical comb-like row of spinules of the femur (especially fore femur).

empodium: median process of the acropod that is generally setiform (Fig. 62) but may be flap-like, similar to pulvilli, in certain families (e.g., Bibionidae, Tabanidae) (Fig. 61).

femur: subbasal segment of the leg, which is generally elongated and often robust (Fig. 63). It may be diversely provided with rows of spinules or teeth (Fig. 65), in relation with raptorial habits (Hybotidae, Ephydridae, etc) or copulation (males of Sepsidae).

metatarsus = basitarsus.

preapical seta: a dorsal seta near the apex of the tibiae. Its presence or absence is of great taxonomic importance at family level in acalyptrate Diptera.

posttarsus = acropod

pulvilli: paired membranous, flap-like process of the acropod, used as an adhesive organ for climbing smooth surfaces (Figs 61–62). Though present in most families, they may be reduced partially or absent in some groups.

spur: apical enlarged macrotrichium of the tibia (Fig. 67). May be unique or paired, fixed or articulated. The number and size of apical tibial spurs is of taxonomic importance in many orthorrhaphous families (e.g., Rhagionidae).

tarsomere (tarsal segment): each of the five parts of the tarsus. In some families all or some of the tarsomeres may be variously modified (Fig. 66) for courtship behaviour (e.g., Dolichopodidae) or for other purpose.

tarsus: distal segment of the leg, subdivided into 5 parts or tarsomeres. This number is reduced only in few Cecidomyiidae and Phoridae.

tibia: generally elongated middle segment of the leg, between femur and tarsus (Figs 63–66). It may bear rows of setae, spurs, spines, ctenidia, often in relation with raptorial habits (e.g., Hybotidae, Ephydridae) or copulation (e.g., males of Sepsidae).

trochanter: small subbasal segment of the leg between coxa and femur, generally immovably united with the latter (Fig. 41).

4. PREABDOMEN – Bernhard Merz

General remarks. The preabdomen includes all abdominal segments anterior to the modified genital segments. In nematocerous and orthorrhaphous Diptera, the number of preabdominal segments may be up to 9, in Cyclorrhapha the males usually have 5, the females 6 pregenital segments, but exceptions are known for some taxa.

pleural membrane: the pleura of abdominal segments are usually weakly sclerotized and therefore soft, allowing to expand the volume of the abdomen. In some families, the pleura contain paired glands, which secrete volatiles. The pleura bear usually the spiracular openings.

spiracle: in the ground plan of Diptera, 8 spiracular openings are present in the pleural membrane on the abdomen, but a reduction is frequent in many families, in particular in orthorrhaphous Diptera and Cyclorrhapha. In many

Calyptrata the stigmata lie in the extreme corner of the tergites.

sternite: ventral plate of each abdominal segment, usually heavily sclerotized, covered with setulae. The sternites are generally square, but may be much reduced in different ways in several families.

stigma = spiracle

syntergite: the tergites of abdominal segments 1 and 2 are united to form a syntergite 1+2 in most orthorrhaphous Diptera and Cyclorrhapha.

tergite: dorsal plate of each abdominal segment, weakly sclerotized in many nematocerous families, usually heavily sclerotized in orthorrhaphous Diptera and Cyclorrhapha. Setulae are frequently present on the surface. Strong setae may be present on the discal surface (**median discal seta**), or along the posterior margin of the tergite either laterally (**lateral marginal seta**) and/or medially (**median marginal seta**).

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1.2. Morphology and terminology of Diptera male terminalia

Bradley J. SINCLAIR

The terminal male genital segments or terminalia are also often termed the hypopygium. The following list of terms is primarily limited to external genital morphology and muscles are only included to assist in determination of homology. This list is organised under the following main subdivisions of the male genitalia: segment nine, gonopods, parameres, intromittent organ, and proctiger.

The homologies of the components of the male terminalia have received much attention since McAlpine (1981). A series of three papers by Wood (1991), Sinclair et al. (1994), Cumming et al. (1995), aided by the use of colour-coded genitalia drawings, have attempted to produce a uniform set of terms for the entire Diptera and illustrate their importance in phylogenetic analyses. Based on these three papers and several recent refinements, this chapter updates the terms of McAlpine (1981) and in particular follows the homologies of the 'revised epandrial hypothesis' of Cumming et al. (1995). An additional complimentary study of the orthorrhaphous Brachycera by Yeates (1994) provides further details. Synonymous terms are included in parentheses.

It should be noted that the ideas and homologies presented in the above papers and in the summary below, especially those concerning the Eremoneura have not been fully accepted and have spawned a series of counter papers by opponents (e.g., Griffiths 1994, 1996; Zatwarnicki 1996; see Yeates and Wiegmann 1999). The homology controversy of epandrium vs. periandrium are summarised in Cumming et al. (1995) and Wheeler (1995). In the following summary of genitalic terms, all essential aspects of the 'periandrial hypothesis' are rejected as discussed in Cumming et al. (1995). The genitalic homologies of competing theories are summarised in Table 1.

In addition to Cumming et al. (1995) which presented evidence supporting the 'revised epandrial hypothesis', several recent papers have also rejected the periandrial hypothesis (Hennig 1976; Michelsen 1988; Wheeler 1995; Shatalkin 1995). The epandrial hypothesis is based solely on morphological evidence, while the periandrial hypothesis (including the hinge hypothesis of Zatwarnicki 1996) is based on an *a priori* assumption of functional continuity in the clasping function (Griffiths 1981). Griffiths supported this view on the grounds that continuity of function is 'one of the accepted indirect criteria of homology to be applied in cases where complete transformation series are not available'. However, morphological evidence based on extensive outgroup comparisons are now available (Wood 1990, 1991; Sinclair et al. 1994; Cumming et al. 1995; Wheeler 1994, 1995). This evidence indicates that from a morphological standpoint there is no reason to presuppose continuity of horizontal clasping function throughout the Diptera (Wheeler 1995; Cumming et al. 1995). In fact, clasping function is quite variable within the order. For example, the direction of gonostylar movement shifts from horizontal to oblique or dorsoventral direction numerous times, even within families (e.g., Muscomorpha – Sinclair et al. 1994; Simuliidae – Wood and Borkent 1982; Thaumaleidae – Sinclair, unpubl. data). Gonostylar action against each other has also shifted to opposition against other structures, or gonostyli are sometimes lost entirely and the clasping function is replaced by other structures of undisputed homology (e.g., epandrium – Mydidae, cerci – Empidinae) (Sinclair et al. 1994; Cumming et al. 1995). Readers are encouraged to refer to the above papers for further detailed descriptions and contrasting view points.

Table **2.1.** Terminology of homologous structures under alternative interpretations of the eremoneuran male terminalia, with a comparison to Lower Brachycera.

Lower Brachycera[1]	Revised epandrial hypothesis[1] (Cumming et al. 1995)	Epandrial hypothesis (McAlpine 1981)	Periandrial hypothesis (Griffiths 1972)	Hinge hypothesis (Zatwarnicki 1996)
epandrium	epandrium (T9)	epandrium	gonocoxite expanded dorsally	epandrium
surstylus (T9 only in *Apsilocephala* Kröber)	surstylus (T9)	surstylus (T10)	gonostylus (S9)	gonostylus (S9)
intersegmental membrane (seg. 9)	subepandrial sclerite (+ bacilliform sclerites, seg. 9)	sternite 10 (seg. 10)	interperiandrial plate, intergonopodal sclerite (seg. 9)	medandrium (S9)
hypandrium	hypandrium + gonocoxites (fused)	hypandrium (fused with base of gonopods)	hypandrium only	hypandrium
gonocoxal apodemes (attached to separate gonocoxites)	gonocoxal apodemes (present in non-rotated Empidoidea) or absent (Cyclorrhapha)	gonocoxal apodemes (Empidoidea) or absent (Cyclorrhapha)	fused dorsally forming bridge (Empidoidea) or medially forming phallapodeme (Cyclorrhapha)	transandrium
gonostylus (ventral clasper)	gonostylus lost[2]	gonostylus fused to gonocoxite (undifferentiated)	gonostylus (migrated dorsally)	gonostylus (migrated dorsally)
–	postgonite[2] (*de novo*, derived from S9)	paramere	paraphysis (= paramere)	paraphysis
–	pregonite (derived from hypandrium + gonocoxite)	gonopod (derived from gonocoxite)	paraphysis	pregonite (derived from hypandrium)
–	phallapodeme (derived from hypandrium)	aedeagal apodeme (derived from hypandrium (McAlpine 1989))	phallapodeme (derived from gonocoxal apodemes)	phallapodeme (derived from ejaculatory apodeme of Empidoidea)
parameral sheath and internal aedeagus	phallus (fusion of aedeagus and parameral sheath)	aedeagus	aedeagus	aedeagus
ejaculatory apodeme	ejaculatory apodeme (homologous to lower Diptera)	ejaculatory apodeme	ejaculatory apodeme	ejaculatory apodeme (Empidoidea) ejacapodeme (*de novo*, Cyclorrhapha)
cercus (seg. 11)	cercus (seg. 11)	cercus (seg. 11)	cercus (seg. 11)	cercus (seg. 12)
hypoproct (S10)	hypoproct (S10)	hypoproct (S11)	sternite 10	sternite 10

[1] followed in present study; [2] new interpretation (see Cumming and Sinclair 1996)
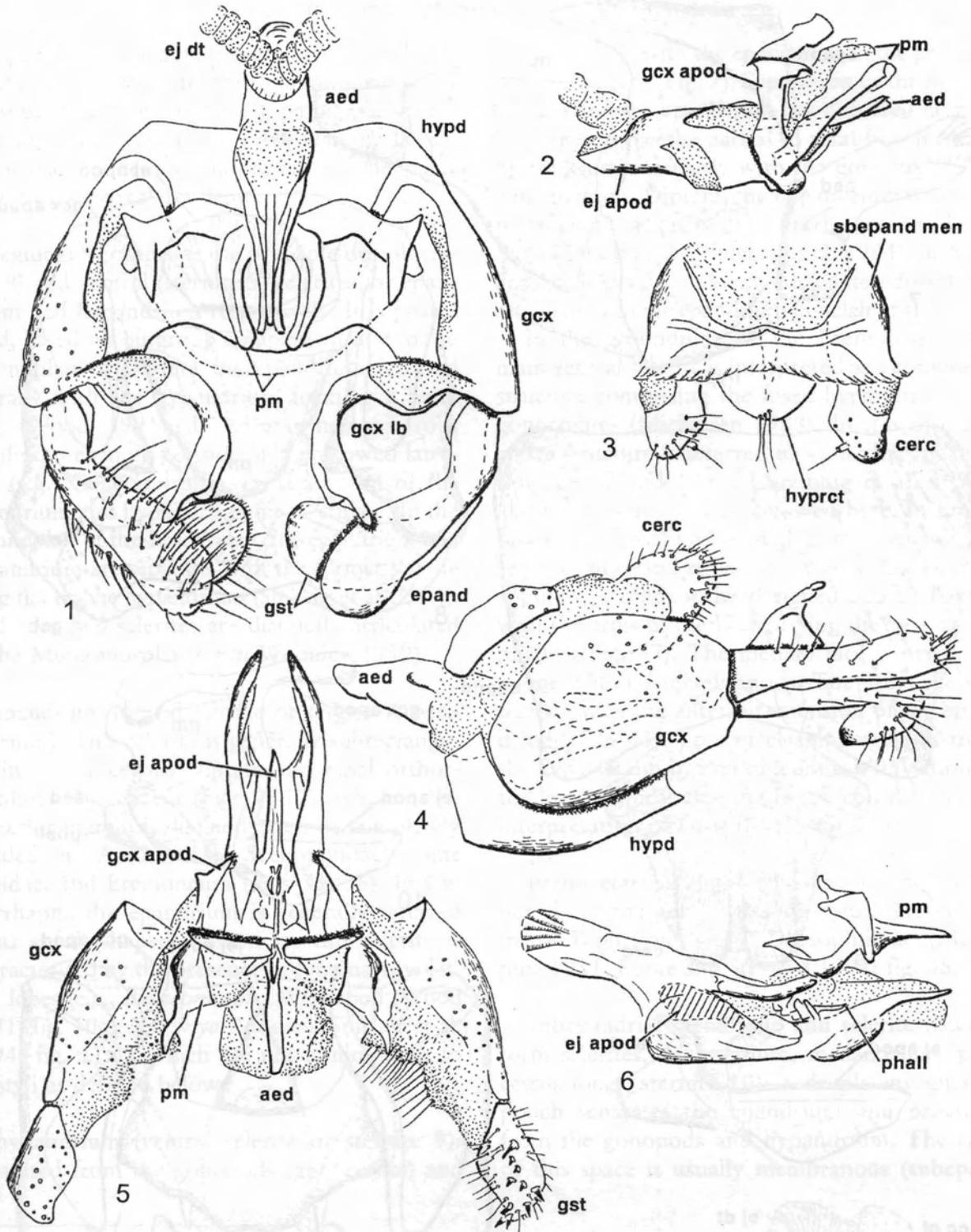
Figs 2.1–6. Blephariceromorpha and Tipulomorpha. 1–4: *Philorus vividis* Kitakami (Blephariceridae): 1: hypandrium, aedeagus, associated structures, dorsal view, 2: aedeagus, paramere, lateral view, 3: proctiger, ventral view and 4: lateral view. 5–6: *Ula* sp. (Limoniidae or Pediciidae): 5: hypandrium, aedeagus, associated structures, dorsal view, 6: aedeagus, paramere, lateral view. (abbreviations: aed: aedeagus, cerc: cercus, ej apod: ejaculatory apodeme, ej dt: ejaculatory duct, epand: epandrium, gcx: gonocoxite, gcx apod: gonocoxal apodeme, gcx lb: gonocoxal lobe, gst: gonostylus, hypd: hypandrium, hyprct: hypoproct, phall: phallotrema, pm: paramere, sbepand mem: subepandrial membrane).

7 epand gcx aed hypd gst

8 ej apod gcx apod pm gst

9 epand cerc

10 gcx apod pm ej apod aed phall

11 ej apod aed

12 acc gl ej dt sp sac ej apod

13 ej apod gcx apod pm gst
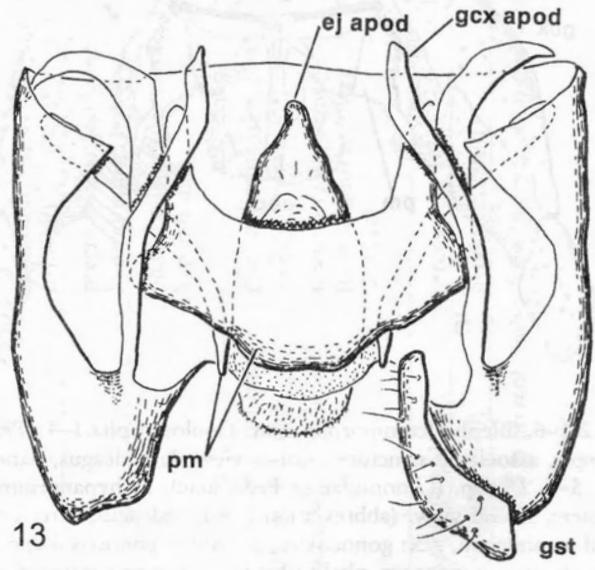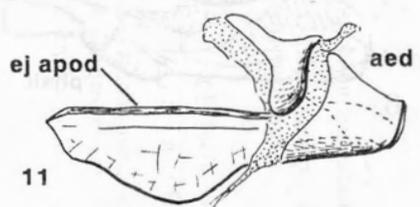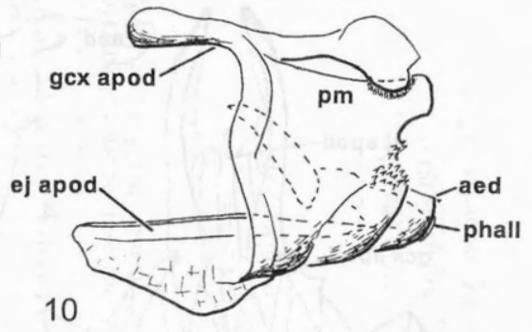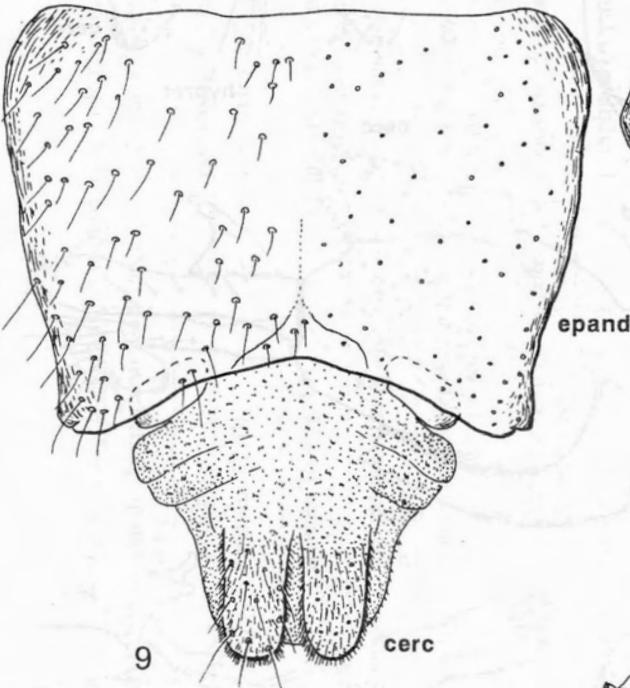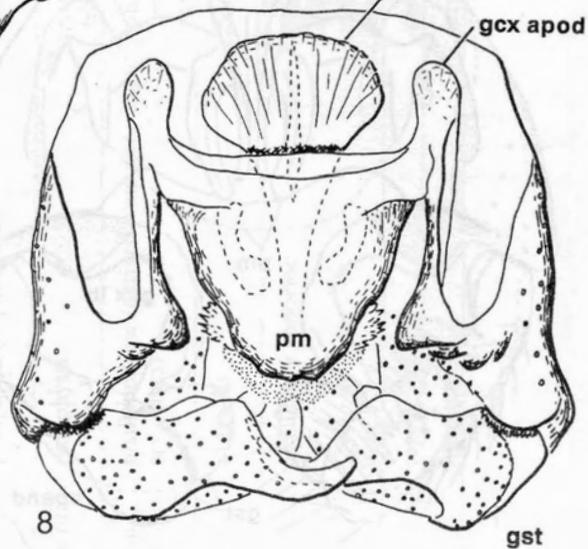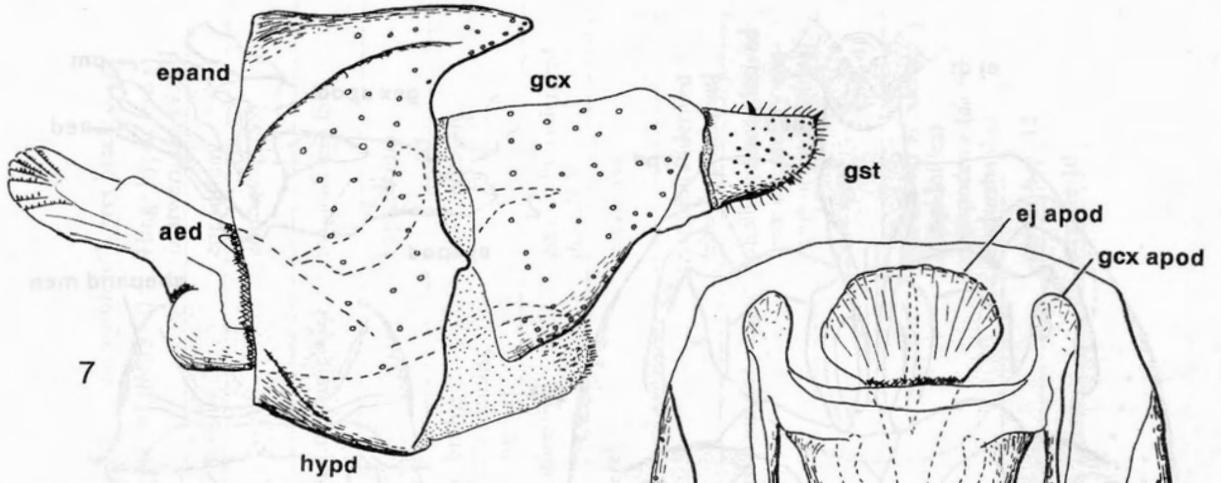
Basic components of the external male genitalia

The following landmarks are helpful in determining homologous structures: anus, junction of the subepandrial membrane + parameral sheath + gonocoxite ("point y" *sensu* Hennig 1976), gonocoxal apodemes, and fusion of the paramere to gonocoxal apodeme.

Segment 9 comprises the principle dorsal (tergite 9) and ventral (sternite 9) sclerites, or epandrium and hypandrium respectively. It is postulated, based on outgroup comparison that in the groundplan of Diptera the epandrium is fused laterally with the hypandrium forming a basal ring (Wood 1991). In several nematocerous families, the ring is considerably narrowed laterally (e.g., Culicomorpha), or separation of the epandrium and hypandrium has occurred. In the groundplan of the Brachycera, the epandrium and hypandrium are separate, with the former sclerite lying flat on the hypandrium (Sinclair et al. 1994), while the two sclerites are distinctly articulated in the Muscomorpha (*sensu* Woodley 1989).

epandrium (dorsal sclerite or tergite 9, periandrium): This sclerite is generally subrectangular in nematocerous Diptera and basal orthorrhaphous Brachycera (Figs 9, 17), whereas the posterior margin is distinctly cleft or completely divided in Apioceridae, Scenopinidae, some Asilidae, and Eremoneura (Figs 33, 36). In Cyclorrhapha the epandrium is generally referred to as saddle-shaped. Sometimes this sclerite is characterised by the presence of long narrow lateral lobes (e.g., *Bittacomorpha* Westwood (Wood 1991: fig. 10a), *Xylomya* Rondani (Sinclair et al. 1994: fig. 11a)), which are not homologous to surstyli as defined below.

hypandrium (ventral sclerite or sternite 9): separated from the gonopods (gonocoxite) and

fused laterally with the epandrium in the groundplan of Diptera (Fig. 7). Separation of the hypandrium from the epandrium has occurred numerous times as has the partial to total fusion of the hypandrium anteriorly with the gonocoxites. In nematocerous Diptera, the hypandrium is largely rectangular, whereas it is subtriangular in basal Brachycera (Fig. 24; Sinclair et al. 1994). In Asilidae, the hypandrium is extended anterodorsally to articulate with the epandrium (Sinclair et al. 1994).

In the groundplan of the Eremoneura, the main ventral sclerite is interpreted as a composite structure comprising the fused hypandrium and gonocoxites (Michelsen 1988). In this case this entire structure is referred to as the hypandrium (Fig. 29; Wood 1991; Cumming et al. 1995), and this terminology is followed here. In Empidoidea and basal Cyclorrhapha, the hypandrium remains large and rounded, whereas in the Schizophora, it tends to be flattened and U-shaped, with the arms of the U encircling the base of the phallus (Fig. 37). The median face is often unpigmented and membranous. The arms also articulate with the anterior extension of the epandrium (Fig. 43). Loss of clasping muscles from the hypandrium in Eremoneura is a reflection of the loss of apical clasping lobes, contrary to the interpretation of Griffiths (1996: 119).

prensisetae: strong, teeth-like setae on the inner distal margin of the surstylus. Present in many Tephritoidea and Drosophilidae (McAlpine 1981; Foote and Steyskal 1987: fig. 66.41).

subepandrial membrane and sclerite (bacilliform sclerites, decasternum, medandrium, processus longi, sternite 10): a deeply invaginated pouch separates the epandrium and proctiger from the gonopods and hypandrium. The roof of this space is usually membranous (**subepan-**

Figs 2.7–13. Tipulomorpha and Bibionomorpha. 7: *Ula* sp., genitalia, lateral view; 8–11: *Hesperinus brevifrons* Walker (Hesperinidae): 8: hypandrium, aedeagus, associated structures, dorsal view, 9: epandrium, proctiger, dorsal view, 10: aedeagus, paramere, lateral view, 11: aedeagus, lateral view. 12–13: *Bibio flavihalter* Hardy et Takahashi (Bibionidae): 12: ejaculatory apodeme, lateral view, 13: hypandrium, aedeagus, associated structures, dorsal view (abbreviations: acc gl: accessory gland, aed: aedeagus, cerc: cercus, ej apod: ejaculatory apodeme, ej dt: ejaculatory duct, epand: epandrium, gcx: gonocoxite, gcx apod: gonocoxal apodeme, gst: gonostylus, hypd: hypandrium, phall: phallotrema, pm: paramere, sp sac: sperm sac).
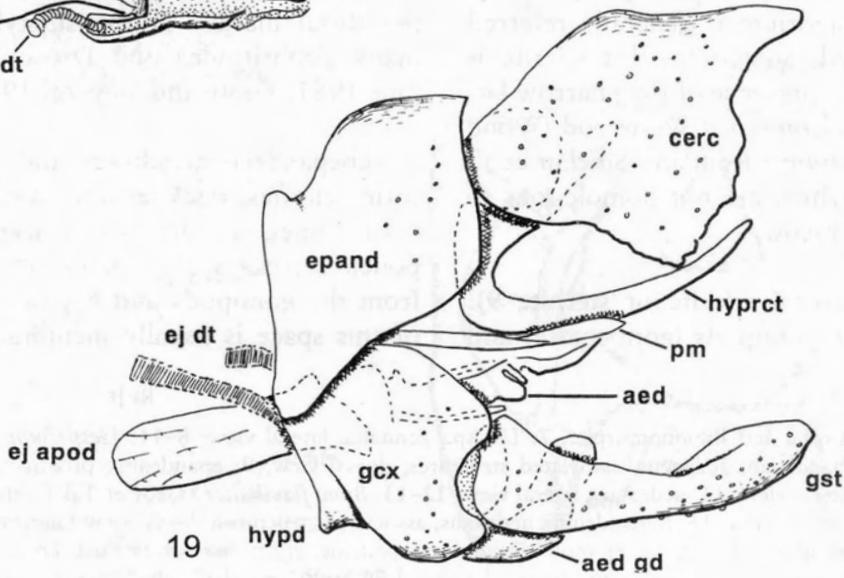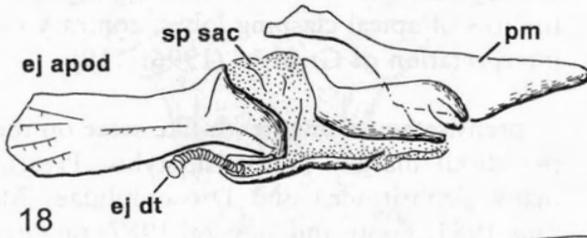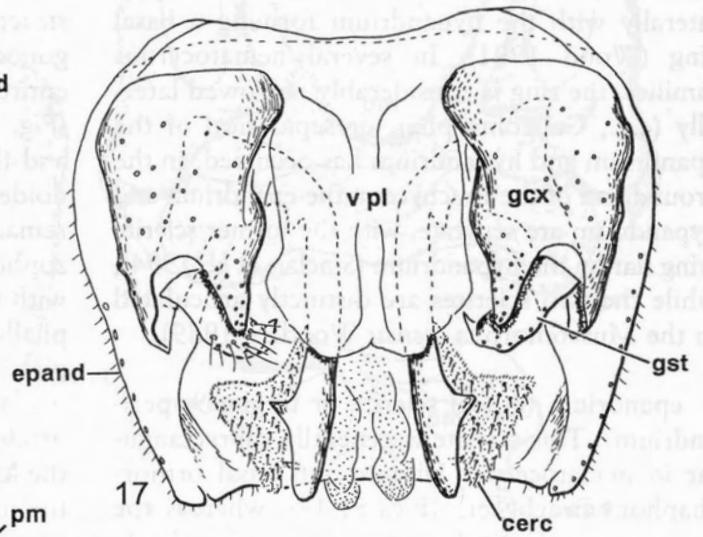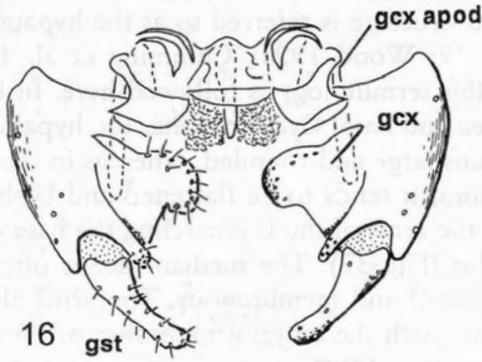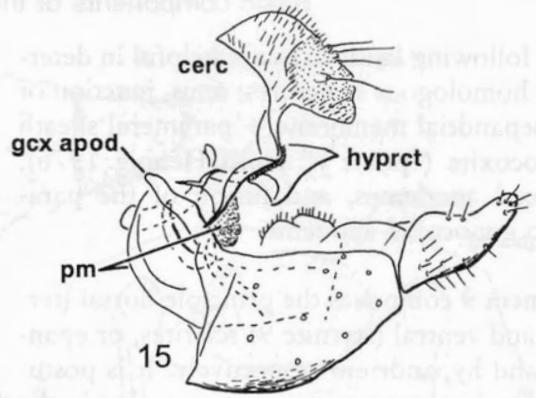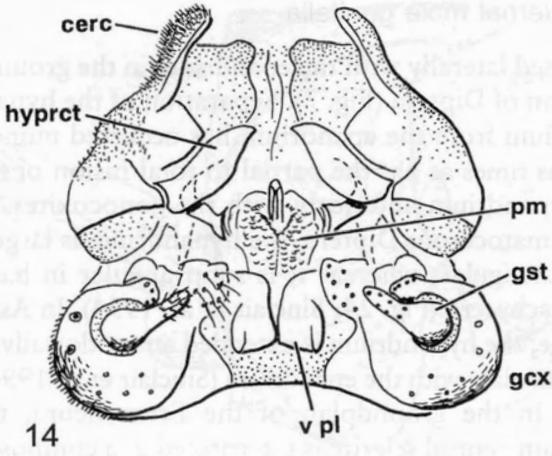
drial membrane) and extends to the anterodorsal surface of the paramere (= Dorsal-Brücke *sensu* Hennig 1976). The dorsal surface of the parameral sheath represents the floor of this space. An extensive sclerite (**subepandrial sclerite**) develops in the subepandrial membrane in numerous families of the lower Brachycera (Bonhag 1951: fig. 22; Sinclair et al. 1994). In Eremoneura, the subepandrial membrane is completely sclerotized along its length (including pair of rod-like extensions or **bacilliform sclerites** to the posterolateral corner of the epandrium or base of the surstylus) and articulates with the anterodorsal surface of the phallus (Fig. 30; see phallic plate) (Cumming et al. 1995). The subepandrial sclerite is reduced in many Schizophora and largely replaced by the bacilliform sclerites which articulate with the hypandrial arms (gonocoxal arms) (Figs 38, 40, 43).

surstylus (außerer Forcep, gonostylus, inferior forcep, paralobe, valvula lateralis): specialised apical clasping lobe that originates as a lateral outgrowth of the epandrium (tergite 9) and not segment 10 (Figs 31, 33–34, 36, 41, 43, 45; Cumming et. al. 1995). The outer surface is formed by the epandrium, whereas the inner surface is formed partially by the bacilliform sclerite. This strict definition clearly distinguishes true surstyli from apical subdivisions of the epandrium (e.g., pseudocerci or ventral epandrial lobes *sensu* Wheeler 1995), which lack bacilliform sclerites. The surstylus is abducted by the lever-like action of the bacilliform sclerites and adducted by rigidity of the epandrium assisted by a single muscle (Wood 1990). The surstylus is not always clearly distinguishable in basal Empidoidea, and is often merely a short, weakly articulated lobe (Figs 31, 33). Surstyli are clearly articulated lobes in the groundplan of the Cyclorrhapha (Fig. 34; Cumming et al. 1995).

Gonopods are paired forceps or claspers, and comprise two segments: gonocoxite and gonostylus. See Wood (1991) for review of the homologies of the gonopods with other insect orders.

gonocoxite (basistyle): basal component of the clasping organ, generally separate ventrally from each other in related orders except Mecoptera (Wood 1991), and assumed to be also separate in the Diptera groundplan. Griffiths (1996) has questioned this polarity due to the distinct fusion of gonocoxites in Mecoptera. As described under Segment 9 above, the gonocoxites may be either fused (Figs 8, 19) or separate from the hypandrium in lower Diptera (Figs 4, 7, 17). Among nematocerous Diptera, separate gonocoxites are found in Hexatomini, Culicomorpha, and some Pachyneuridae (Wood 1991). Gonocoxites fused midventrally (often with the hypandrium) have occurred independently in all infraorders.

gonocoxal apodemes (basal piece (Culicidae), basimeral apodeme, dorso-inner anterior process): pair of conspicuous, anteriorly projecting, internal processes, most readily viewed dorsally with the epandrium removed (Figs 8). Usually widely separated, but in Chironomidae they are fused apically or greatly reduced or absent in most Bombyliidae, except Mythicomyiinae (Fig. 27) and *Heterotropus* Loew (Sinclair et al. 1994; Yeates 1994). Gonocoxal apodemes are very useful landmarks for establishing the homology of internal structures. In Eremoneura, their presence clearly demonstrates that the ventral sclerite is hypandrium + gonocoxites (Figs 28, 30; Cumming et al. 1995). Gonocoxal apodemes are absent in the groundplan of the Cyclorrhapha and also in Empidoidea with permanent male genitalic rotation (Figs 31, 32, 35; Cumming et al. 1995).

Figs 2.14–19. Culicomorpha and Psychodomorpha. 14–16: *Dixa yamatoma* Takahashi (Dixidae): 14: posterior view, 15: lateral view, epandrium and hypandrium removed, 16: gonocoxite, aedeagus, associated structures, dorsal view. 17: *Androprosopa hyrcanica* (Schmid) (Thaumaleidae), hypandrium, aedeagus, associated structures, dorsal view. 18–19: *Trichomyia capitanea* Duckhouse (Psychodidae): 18: aedeagus, paramere, lateral view, 19: lateral view (abbreviations: aed: aedeagus, aed gd: aedeagal guide, cerc: cercus, ej apod: ejaculatory apodeme, ej dt: ejaculatory duct, epand: epandrium, gcx: gonocoxite, gcx apod: gonocoxal apodeme, gst: gonostylus, hypd: hypandrium, hyprct: hypoproct, pm: paramere, sp sac: sperm sac, v pl: ventral plate).
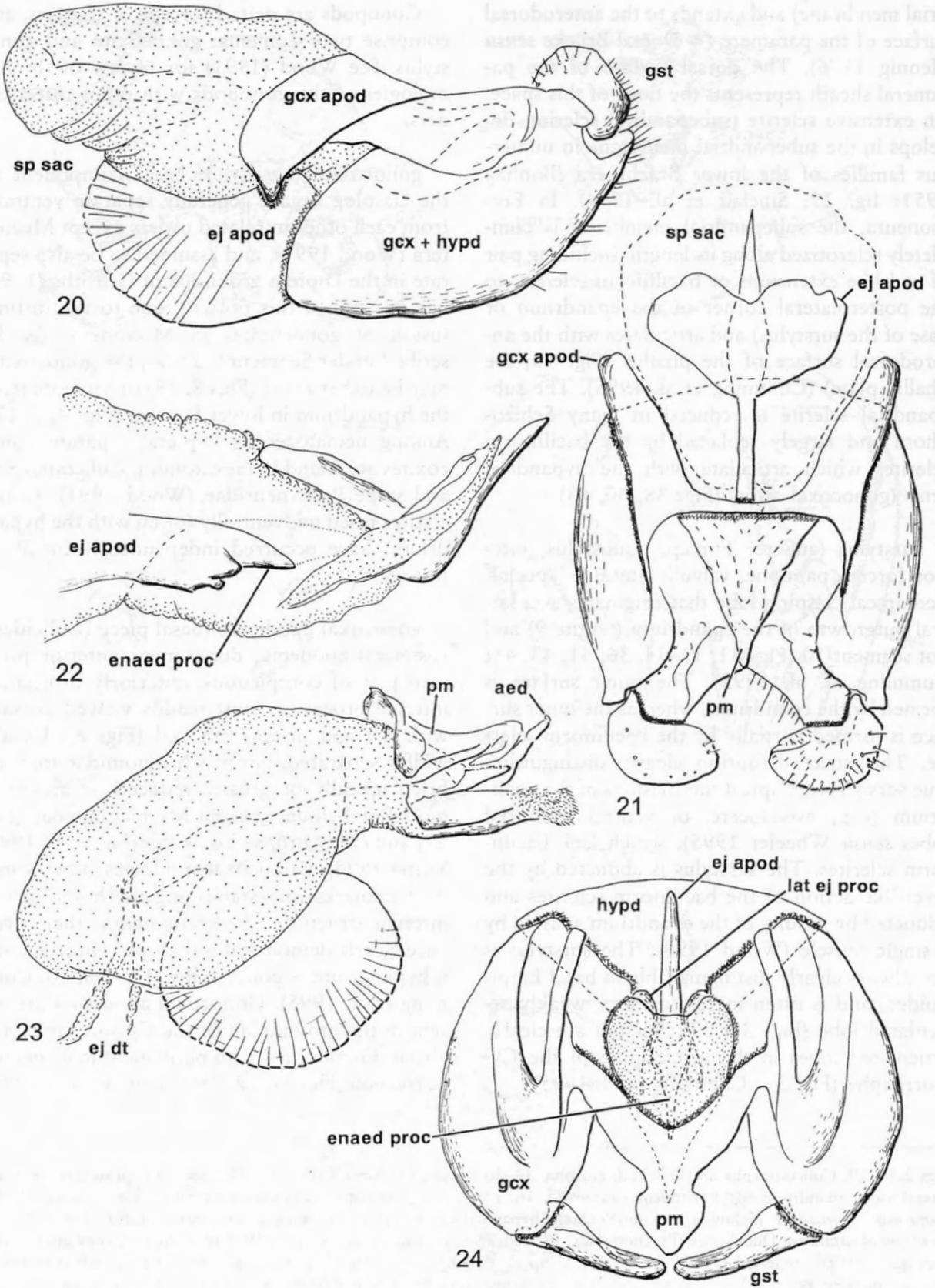
Long, slender gonocoxal apodemes with the paramere attached at mid-length are present in Bibionomorpha (Figs 8, 13), Culicomorpha, lower Brachycera, and Empidoidea (Figs 21, 24). In many other nematocerous families, the gonocoxal apodemes are inconspicuous, with the paramere attached anteroapically (Figs 2, 5).

gonostylus (clasper, dististyle): articulated lobe, normally at the posterior margin of the gonocoxite. Each often bears sensory setae and spines along the inner apical margin, occasionally subdivided into inner and outer lobes (Figs 1, 4). Gonostyli are articulated horizontally to nearly vertically. Horizontal articulation or clasping direction is assumed plesiomorphic in both nematocerous Diptera and Brachycera (Figs 8, 13, 21, 24). Among the Muscomorpha (*sensu* Woodley 1989), including Nemestrinidae (see Yeates (1994) and Griffiths (1996) for opposing interpretation), the gonostyli articulate obliquely or nearly vertically against the epandrium rather than against each other (Fig. 25; Sinclair et al. 1994; Richter and Ovtshinnikova 1996). Oblique articulation is also found in the Anisopodidae, Xylomyidae, and within numerous other families (e.g., Simuliidae and Thaumaleidae, Fig. 17). Gonostyli are absent in Eremoneura (Figs 30, 32, 35).

hypandrial arms (gonocoxal arms): arise from the posterior part of the hypandrial-gonopod complex, appearing as an extension or prolongation of the hypandrium to articulate with the base of the bacilliform sclerite in Schizophora (Figs 38, 43).

phallapodeme (aedeagal apodeme of Cyclorrhapha): novel structure of the Cyclorrhapha (exclusive of Opetiidae), derived from the hypandrium + gonopod complex (or simply hypandrium) (Michelsen 1988; McAlpine 1989: 1406; Cumming et al. 1995). The phallapodeme arose

initially as a longitudinal invagination of the hypandrium, surrounding the base of the phallus (Fig. 34). It is considered to be lever-like in the groundplan of the Syrphoidea + Schizophora (Cumming et al. 1995), assisting in the movement of the phallus and postgonites (Figs 35, 43).

The phallapodeme is normally a large, rod-shaped, median sclerite articulating with the base of the phallus and projecting anteriorly to or beyond the hypandrium (Fig. 41). Occasionally the anterior portion of the phallapodeme is expanded ventrolaterally and is secondarily fused to the U-shaped hypandrium (Piophilidae, Diopsidae), or is membranously connected ventrally to the posterior margin of the hypandrium (Psilidae, Fig. 37).

phallic or aedeagal guide: ventromedial process projecting posteriorly from fused gonocoxites (Fig. 19). This term is commonly coined for any apical ventromedial gonocoxal lobe (see McAlpine 1981). The phallic guide is quite distinct in Stratiomyidae and appears as a bilobed posteroventral prolongation of the gonocoxite (Rozkošný 1982).

In the Cyclorrhapha, the phallic guide (or intermedium) is quite different in form. It is derived from the gonocoxites and connects the phallapodeme with the lateral region of the hypandrium (Wheeler 1994). It often appears simply as an external extension of the phallapodeme (Figs 42, 44) (Michelsen 1988).

postgonite (gonopod, gonostylus, opisthoparamer, paramere, paraphysis, telomere): interpretation of this pair of lobes is extraordinarily complex and contradictory. In the recent literature, Cumming et al. (1995) suggested that the paired processes located near the phallus in Cyclorrhapha were remnants of gonostyli or possibly simply postgonites of unknown homology. Cumming and Sinclair (1996) re-evaluated these lobes and interpret them as *de novo* structures

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Figs 2.20–24. Xylophagomorpha and Tabanomorpha. 20–23: *Xylophagus matsumarai* Miyatake (Xylophagidae): 20: hypandrium, aedeagus, associated structures, lateral view, 21: hypandrium, aedeagus, associated structures, dorsal view, 22: apex of aedeagus, lateral view, 23: aedeagus, paramere, lateral view. 24: *Rhagio scolopaceus* (Linnaeus) (Rhagionidae), hypandrium, aedeagus, associated structures, dorsal view (abbreviations: aed: aedeagus, ej apod: ejaculatory apodeme, ej dt: ejaculatory duct, enaed proc: endoaedeagal process, gcx: gonocoxite, gcx apod: gonocoxal apodeme, gst: gonostylus, hypd: hypandrium, lat ej proc: lateral ejaculatory process, pm: paramere, sp sac: sperm sac).

ej apod

gcx apod

hypd

lat ej proc

sbepand mem

hyprct

ej apod

gcx apod

lat ej proc

sp dt

gcx

gcx

gst

26

25

gst

27

hyprct

cerc

epand

ph

gcx apod

ej apod

hypd

28

pgt

ph

ej apod

hypd

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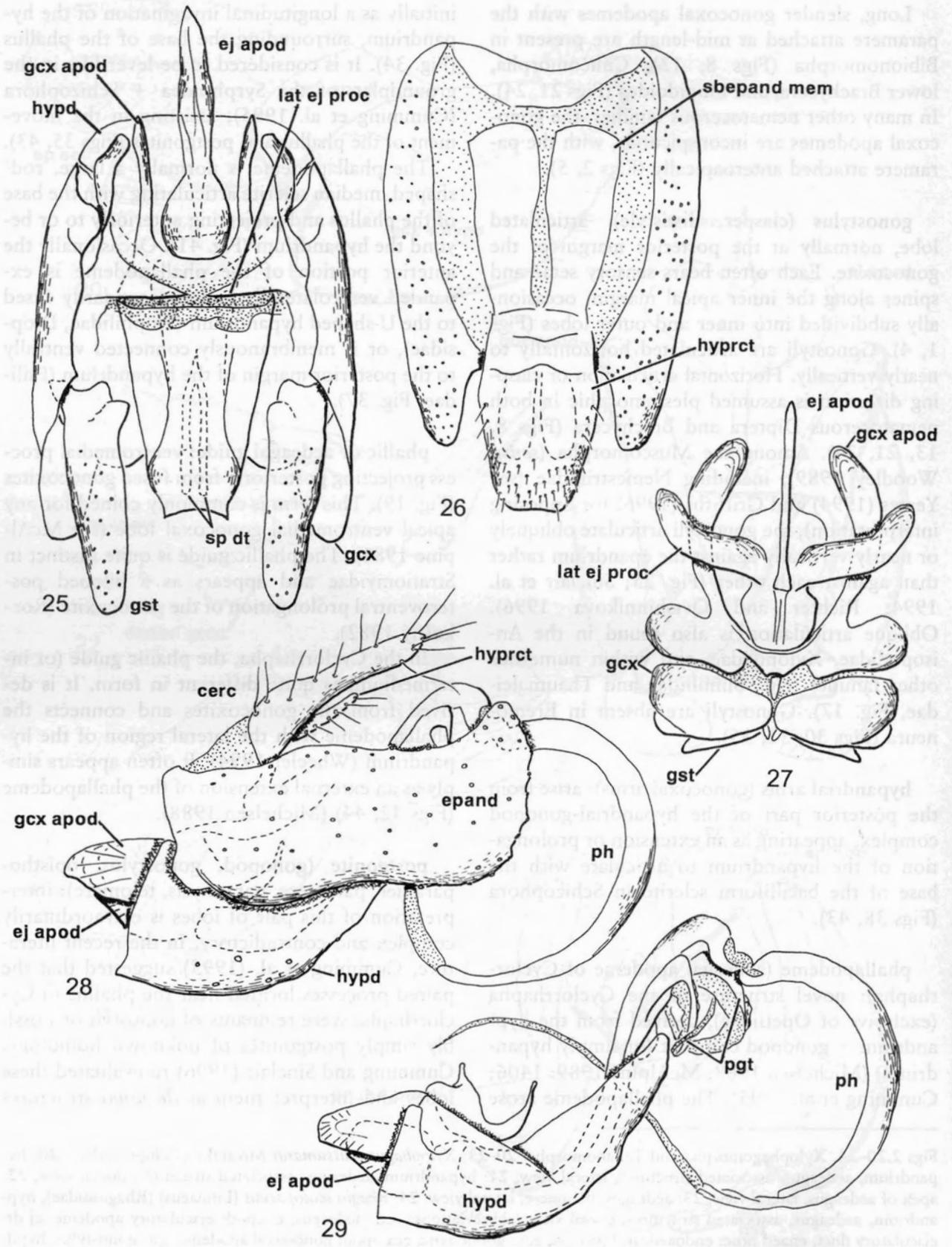
derived from the gonocoxal portion of the hypandrium in the groundplan of the Eremoneura and this interpretation is followed here.

The term postgonite has been commonly used for homologous structures in the Cyclorrhapha, especially in calyptrates. The possible groundplan condition is best illustrated in *Hormopeza* Zetterstedt (Fig. 30) and *Opetia* Meigen (Cumming et al. 1995: fig. 16), and described as a pair of lobes extending along the upper margin of the hypandrium from the base of the phallus to beyond the posterior margin of the hypandrium, often partially encircling the phallus (Fig. 29). These lobes are likely sensory in function and always are closely associated with the phallus. In most Cyclorrhapha, the postgonites are distinctly articulated (Figs 34, 35, 41, 44), moved by a single abductor muscle and adducted by action of the phallapodeme, thus turning outward as the phallus is swung into copulatory position. The ontogenetic origin of these processes was reevaluated by Cumming et al. (1995: 126–127) and a brief review of their terminology provided by Hennig (1973).

postgonal apodeme (basal piece, Gelenkfortsatz, gonostylar apodeme): small sclerite at the base of the postgonite in most tachinoid calyptrates (Salzer 1968; Rognes 1991; Pape 1992). Most easily viewed on the inner margin of the postgonite and appears to be derived from the postgonite through a subbasal weakening (Fig. 44).

pregonite (gonopod, proparamer, suspensory sclerite): pair of lobes arising from the hypandrium, anterior to the phallus, observed sporadically in the Schizophora (Figs 37–38, 44). These lobes are firmly attached to the hypandrial + gonopod complex or hypandrium.

ventral plate (aedeagus – Ceratopogonidae; claspettes, prosophallus – Dixidae; ventral appendages or gonocoxal plate – Thaumaleidae): appears to arise from the inner medial surface of the gonocoxites in the Culicomorpha, rather than ventromedially. This structure has been given various names in a number of families (see list above) and was first homologised by Wood and Borkent (1982). This structure is clearly derived from the gonocoxites as illustrated in plesiomorphic taxa (Figs 14, 17). Movement of the ventral plate helps to enlarge the genital chamber to receive the spermatophore, by lifting the anal lobes of the female (Wood 1978). The ventral plate is clearly articulated in the Chironomoidea, exclusive of Thaumaleidae. In some Dixidae, the ventral plate is greatly lengthened anteriorly into a long filament (Wood 1991: fig. 11), or lost in most Chironomidae (Wood 1978). The aedeagal guide of the tipulid *Dolichopeza obscura* (Johnson) (Wood 1991: fig. 5) is not homologous.

The **parameres** (dorsal plate, paraphyses) are posteriorly directed rods or processes attached to the gonocoxal apodeme, and in many lineages are united medially to form a single sclerotized plate, dorsal to and usually arching over the aedeagus (Wood 1991). Parameres as separate paired structures associated with the base of the aedeagus and gonocoxal apodemes are considered the groundplan condition of Diptera (Fig. 5) (Wood 1991). The lateral attachment of the gonocoxal apodemes is a very important morphological landmark. Because of the diversity of structure found in the parameres, they have been referred to by a great variety of terms; for example, tegmen (Zwick 1977 – Blephariceridae), dorsal sclerite (= Dorsalsklerit *sensu* Blaschke-Berthold 1994 – Bibionidae), penis valves (Chaoboridae), and phallus (*sensu* Belkin 1968 – Dixidae).

In nematocerous Diptera, the lateral parameres are sometimes connected dorsally by an unpigmented membrane forming a dorsal hood.

Figs 2.25–29. Asiloidea, Bombyliidae, and Empidoidea. 25–26: *Henicomyia hubbardii* Coquillett (Therevidae): 25: hypandrium, phallus, associated structures, dorsal view, 26: epandrium, proctiger, ventral view. 27: *Mythicomyia* sp. (Bombyliidae or Mythicomyiidae), hypandrium, aedeagus, associated structures, dorsal view. 28–29: *Iteaphila nitidula* Zetterstedt (Empidoidea): 28: lateral view, 29: hypandrium, phallus, associated structures, lateral view (abbreviations: cerc: cercus, ej apod: ejaculatory apodeme, epand: epandrium, gcx: gonocoxite, gcx apod: gonocoxal apodeme, gst: gonostylus, hypd: hypandrium, hyprct: hypoproct, lat ej proc: lateral ejaculatory process, pgt: postgonite, ph: phallus, sbepand mem: subepandrial membrane, sp dt: sperm duct).
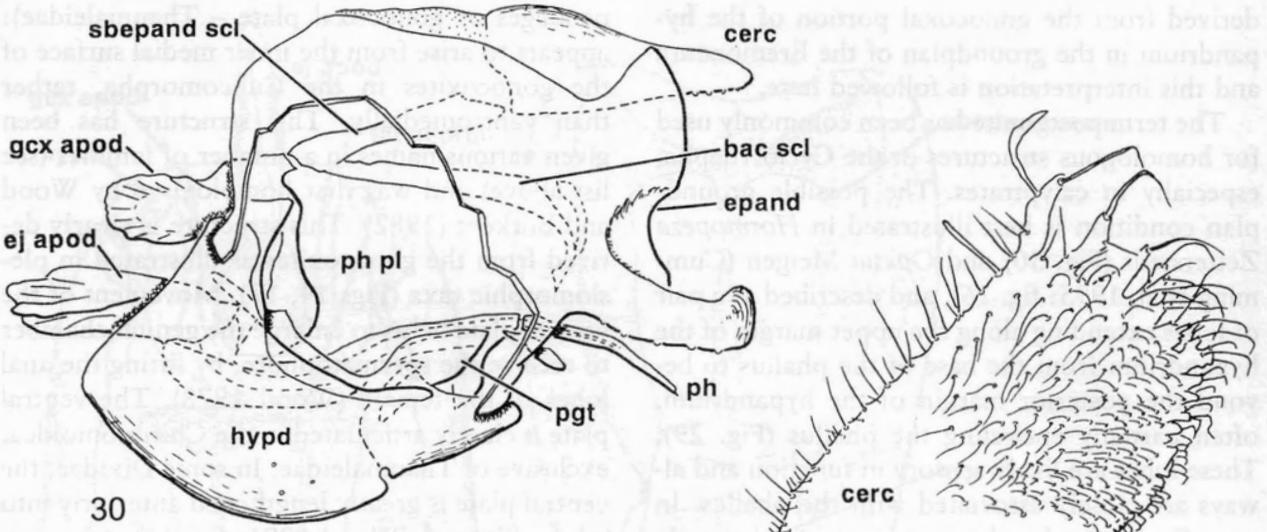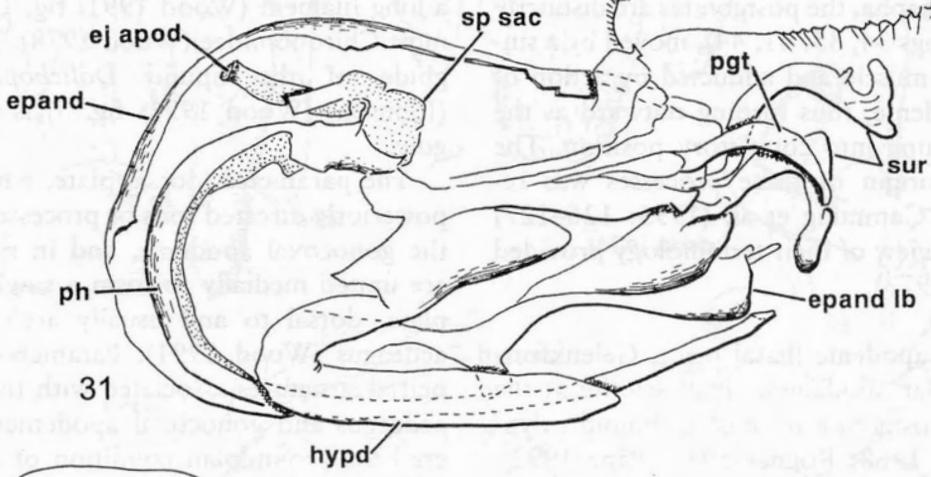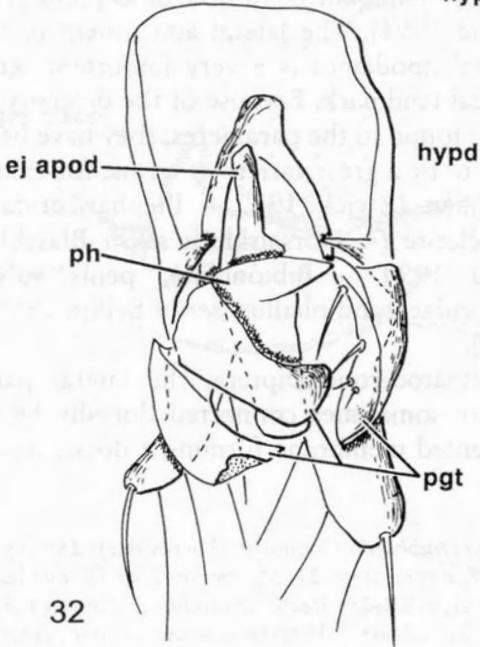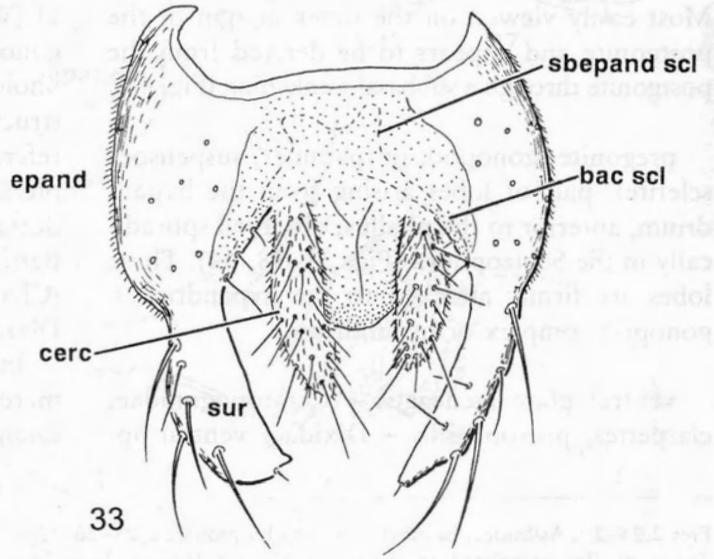
No additional lobes are present near the base of the aedeagus as suggested by Griffiths (1994, 1996). The questionable structures in orthorrhaphous Brachycera presented in Nagatomi (1984) are either the internal sclerotization of the apex of the aedeagus or ventrolateral extensions of the paramere which arch laterally around the inner aedeagus (see below). In plesiomorphic Stratiomyidae (*Chiromyza* Wiedemann and *Parahadrestia* James (see Woodley 1986)) and Xylomyidae, lateral lobes to the aedeagus are absent. The free lateral lobes in *Xylomya* (McAlpine 1981: fig. 2.122) are actually dorsally directed gonostyli (Sinclair et al. 1994: fig. 11a). Consequently, the lateral lobes or tripartite condition of many Stratiomyidae are secondarily derived lobes of the phallus (lateral phallic lobes) and not true parameres as often stated.

As stated above, the parameres are fused medially in many lineages (e.g., Blephariceromorpha (Fig. 1), Axymyiomorpha, Psychodomorpha, Bibionomorpha (Figs 8, 13), and Brachycera (Figs 21, 24) (Wood 1991; Sinclair et al. 1994)), and form a bridge connecting the gonocoxites dorsally via the gonocoxal apodemes. Occasionally the parameral sheath is displaced ventrally and a stout, sclerotized bridge extends between the gonocoxites (Yeates 1994).

In the groundplan of Brachycera, the parameres encircle the apex of the aedeagus, incompletely closed ventromedially (Hennig 1976; Sinclair et al. 1994). They remain laterally connected to the gonocoxal apodemes and are referred to as the parameral sheath (Wood 1990) (= Phallushülle *sensu* Hennig 1976, aedeagal sheath *sensu* Yeates 1994). The parameral sheath is fused indistinguishably to the aedeagus in Stratiomyomorpha + Muscomorpha (*sensu* Woodley 1989) and consequently free parameres are absent in these lineages (Wood 1990; Sinclair et al. 1994) (see phallus below).

The **copulatory or intromittent organ** has been given numerous names in different dipteran groups, and most of these names are only of purely descriptive importance. The intromittent organ is primitively a simple tube with a small, basal ejaculatory apodeme. Extensive elaboration and fusion with surrounding structures or even complete loss of a sclerotized tube occurs in Diptera.

acrophallus: represents a division of the distiphallus, bearing the phallotrema or genital opening, and sometimes clothed in small denticles (Fig. 43). This term is used primarily in calyptrates. In some Calliphoridae, external lateral grooves or ducts are present on the acrophallus, with the distal opening near the phallotrema. They conduct accessory secretions from the phallotrema to the paraphallus or dorsolateral process (Rognes 1991).

aedeagal tines (endophallic tines): elongate, slender, sickle-shaped filaments within the sperm sac, arising from the base of the endoaedeagal process and arching towards the functional gonopore. Tines are found in the Tabanidae, Athericidae, and *Bolbomyia* Loew with possible precursors found in *Rhagio* Fabricius (Sinclair et al. 1994). Contraction of the muscles of the ejaculatory apodeme pushes these filaments out beyond the parameral sheath in association with the endoaedeagal process.

aedeagus (penis, phallosome): slender, tubular aedeagus with a single external opening or phallotrema is considered the groundplan condition of the Diptera (Wood 1991). A tripartite aedeagus is present in several families (see phallotrema below).

A tubular aedeagus is considered absent in the groundplan of the Culicomorpha (Sinclair et al. 1998), enabling the passage of a preformed spermatophore. In this infraorder, the aedeagus is reduced to a membranous sac, which is easily expanded (Fig. 17). A long, filamentous "aedeagus"

Figs 2.30–33. Empidoidea. 30: *Hormopeza copulifera* Melander, lateral cutaway view. 31: *Dolichopus brevipennis* Meigen (Dolichopodidae), lateral cutaway view. 32–33: *Acarterus bicolor* Loew (Hybotidae): 32: hypandrium, phallus, associated structures, dorsal view, 33: epandrium, surstylus, proctiger, dorsal view (abbreviations: bac scl: bacilliform sclerite, cerc: cercus, ej apod: ejaculatory apodeme, epand: epandrium, epand lb: epandrial lobe, gcx apod: gonocoxal apodeme, hypd: hypandrium, pgt: postgonite, ph: phallus, sbepand scl: subepandrial sclerite, sp sac: sperm sac, sur: surstylus).
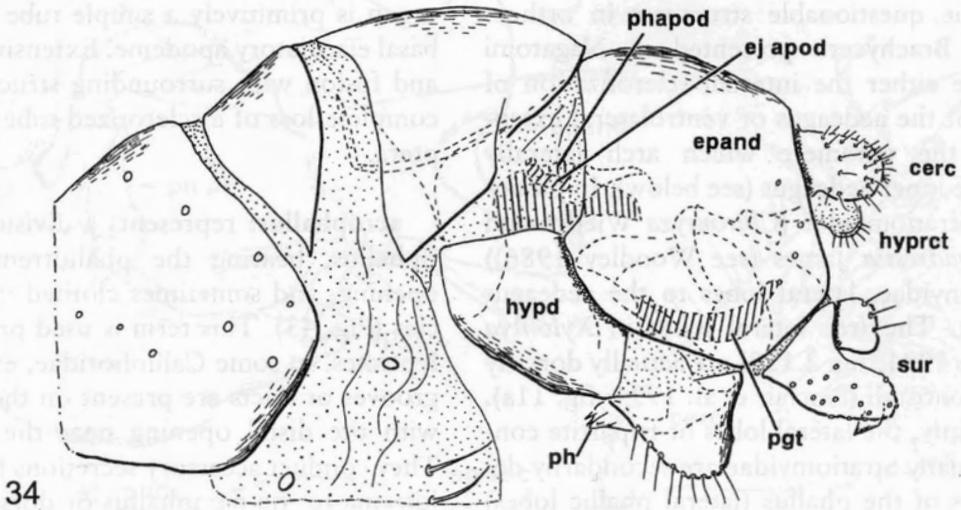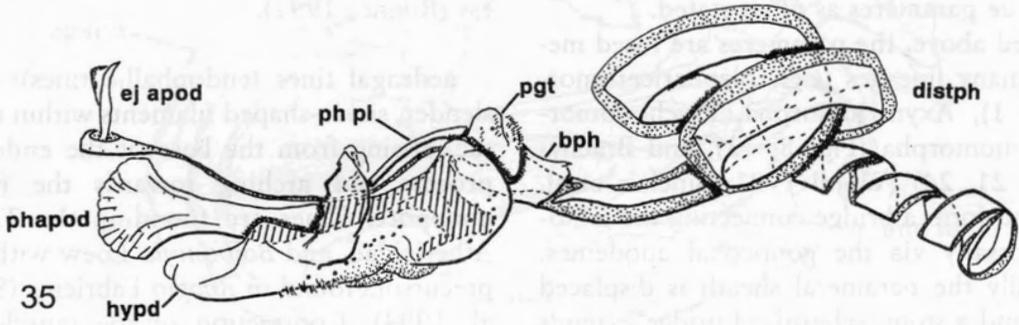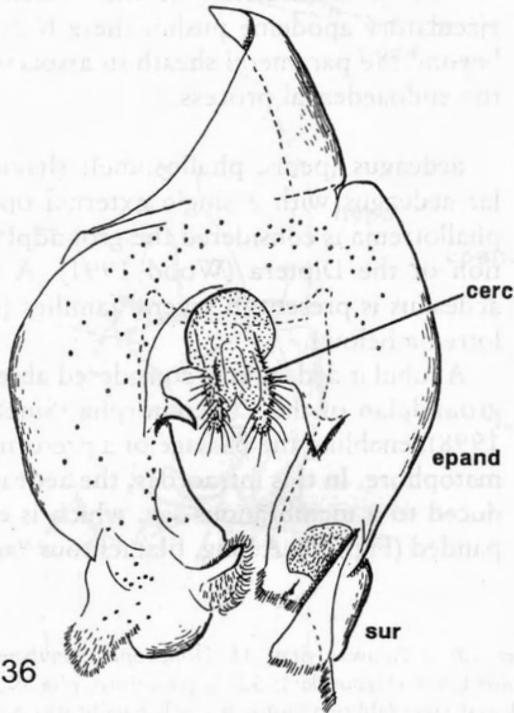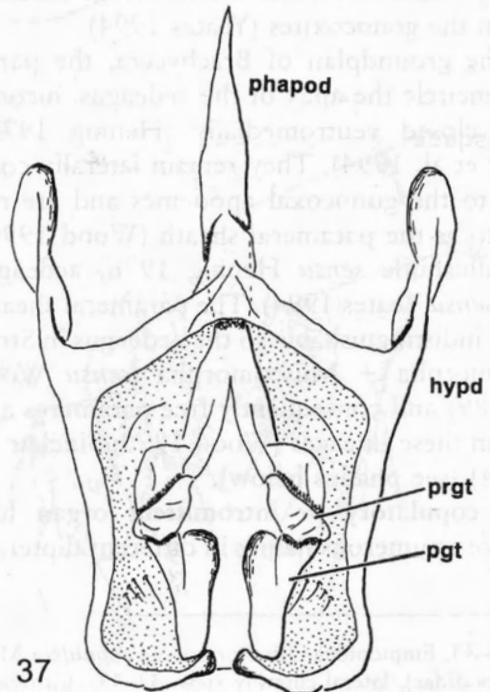
found in *Dixella californica* (Johannsen) (see Wood 1991: fig. 11) is not tubular, but merely a slender plate that possibly functions as an aedeagal guide. As suggested by Belkin (1968), the "aedeagus" of Dixidae (Figs 14, 16) and Culicidae is probably a secondary subdivision of the paramere (phallus *sensu* Belkin 1968), and hence a sclerotized aedeagus is probably absent in all Culicomorpha. This interpretation of the "aedeagus" is supported by the unique configuration of the paramere in Culicoidea, which projects anteriorly, converging to support a concave "aedeagal" plate (Wood 1991: figs 12–14). In all other nematocerous Diptera the paramere projects posteriorly from the gonocoxal apodemes.

In the groundplan of Brachycera, the aedeagus is largely membranous, encircled by a conical parameral sheath (Sinclair et al. 1994). Only the apex of the aedeagus encircling the phallotrema or external gonopore remains sclerotized (Figs 22–23) (Sinclair et al. 1994: fig. 4; Rozkošný and Nagatomi 1997: Figs 2.26.9–10). A similar condition is also found in Hesperinidae (*H. brevifrons* Walker; Figs 10–11) and Bibionidae (Fig. 13). In the Stratiomyomorpha and Muscomorpha (*sensu* Woodley 1989), the apex of the aedeagus is completely fused and indistinguishable from the parameral sheath (see phallus below).

basiphallus (phallobase): proximal portion or base of the phallus, articulated basally with the phallapodeme (Fig. 35). Continuous apically with the distiphallus and often with a distinct dorsal lobe, referred to as the epiphallus.

distiphallus: distal portion of the phallus beyond the epiphallus, a term normally used in Schizophora (Figs 39, 41). The ventral surface is often clothed in sclerotized denticles directed anteriorly in the Tachinidae family-group (Fig. 43) (Rognes 1991; Pape 1992). These denticles are often on a distinct subdivision of the distiphallus referred to as the ventrolateral process (hypophallic lobe).

Dorsolateral phallic processes (pa-raphallus) are often present, and appear as sickle-shaped rods, functioning as external canals, conducting accessory secretions into lateral sacs of the female uterus (Lewis and Pollock 1975; Rognes 1991).

ejaculatory apodeme (aedeagal apodeme of lower Diptera, ejacapodeme, endophallus apodeme): unpaired apodeme inserted at the base of the intromittent organ (Figs 2, 5, 8, 19–20, 24–25, 30, 34, 43). The ejaculatory apodeme is a component of the sperm pump and supports muscles that force the ejaculatory apodeme into the base of the sperm sac, compressing the pump. This apodeme normally bears two to three muscles in nematocerous Diptera, three muscles in lower Brachycera, and a single muscle in Cyclorrhapha (Ovtshinnikova 1989).

In nematocerous Diptera, the ejaculatory apodeme is often connected to the base of the aedeagus by a stout membrane and is not able to move freely as in some lower Brachycera (Figs 2, 6, 18). It also appears to move somewhat lever-like or rotates by compression. The ejaculatory apodeme of Mecoptera is also lever-like, articulated at a single point and thus rotates to compress the sperm sac (Willmann 1981). The sperm pump is separated from the base of the aedeagus in Siphonaptera (Günther 1961: fig. 26). Although the outgroup is ambiguous, it is assumed that an articulated and lever-like motion of the ejaculatory apodeme is likely the groundplan condition of Diptera. In the groundplan of the Brachycera, the ejaculatory apodeme moves piston-like, pulled posteriorly into the base of the aedeagus to compress the sperm sac (Figs 23–24) (Bonhag 1951; Sinclair et al. 1994). The ejaculatory apodeme is lever-like in *Iteaphila* Zetterstedt (Fig. 29), *Oreogeton* Schiner, *Hormopeza* Zetterstedt (Fig. 30), Empidinae, Hemerodromiinae, basal Clinocerinae, Microphorinae, and Dolichopodidae (Fig. 31) of the Empidoidea (Sinclair and Cumming 1994; Cumming et al.

Figs 2.34–37. Cyclorrhapha. 34: *Microsania* sp. (Platypezidae), lateral view. 35–36: *Niphrocerus daeckei* Johnson (Pipunculidae): 35: hypandrium, phallus, associated structures, lateral view, 36: epandrium, surstylus, proctiger, dorsal view. 37: *Chyliza flavifrons* Iwasa (Psilidae), hypandrium, associated structures, ventral view (phallus removed) (abbreviations: bph: basiphallus, cerc: cercus, distph: distiphallus, ej apod: ejaculatory apodeme, epand: epandrium, hypd: hypandrium, hyprct: hypoproct, pgt: postgonite, ph: phallus, phapod: phallapodeme, ph pl: phallic plate, prgt: pregonite, sur: surstylus).

ej apod · epand · bac scl · cerc · sur · phapod · ph pl · hypd · prgt · pgt · ph

38

ej apod

epand

cerc

bac scl

sur

40

phapod · epiph · distph · pgt · prgt · epand · ej apod · phapod · hypd · distph

39

epand · cerc · sur · ej apod · phapod · hypd · pgt · prgt · distph
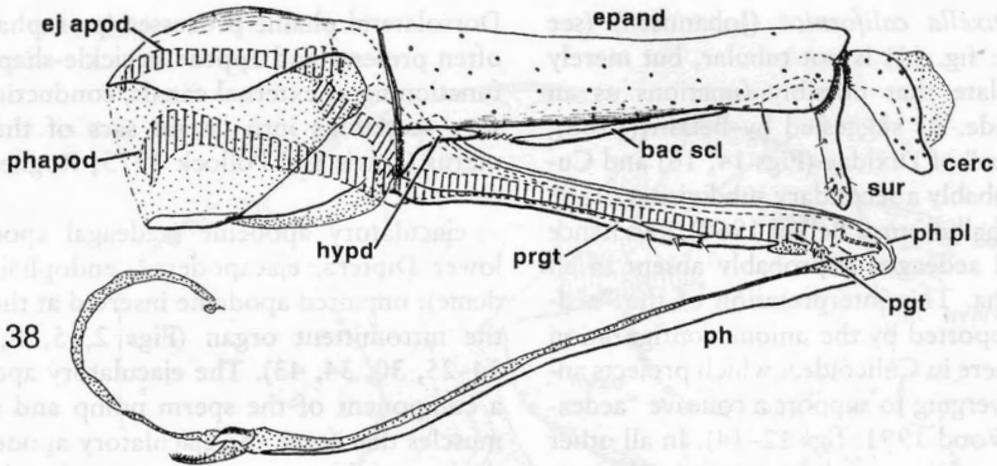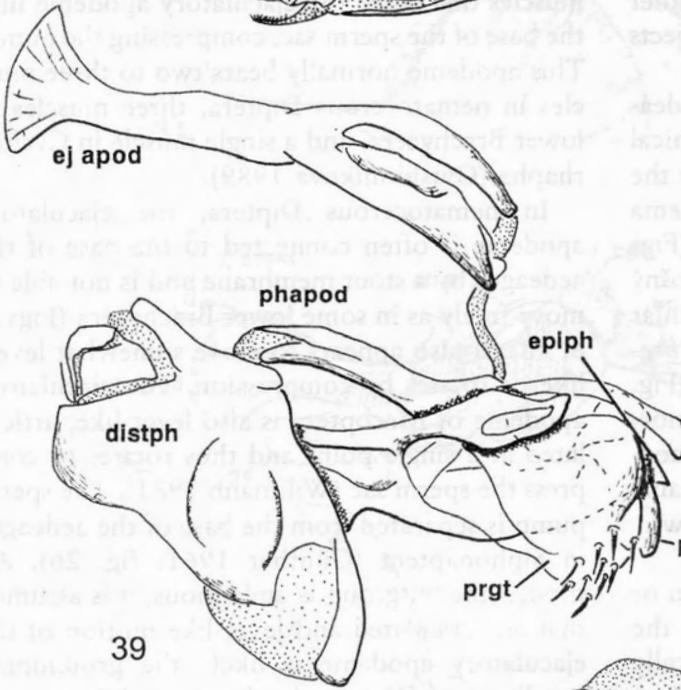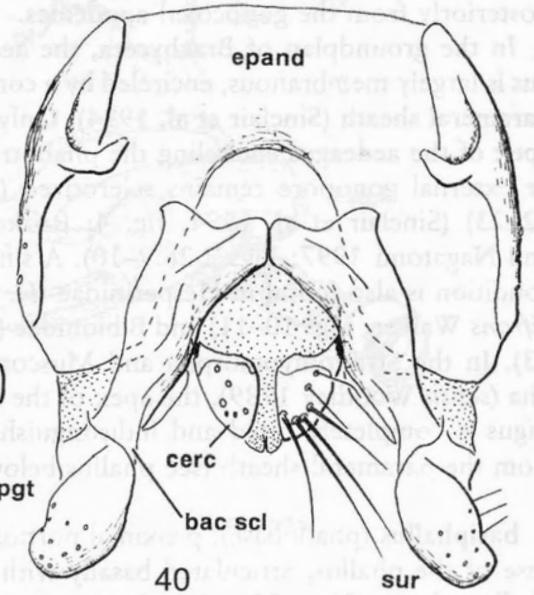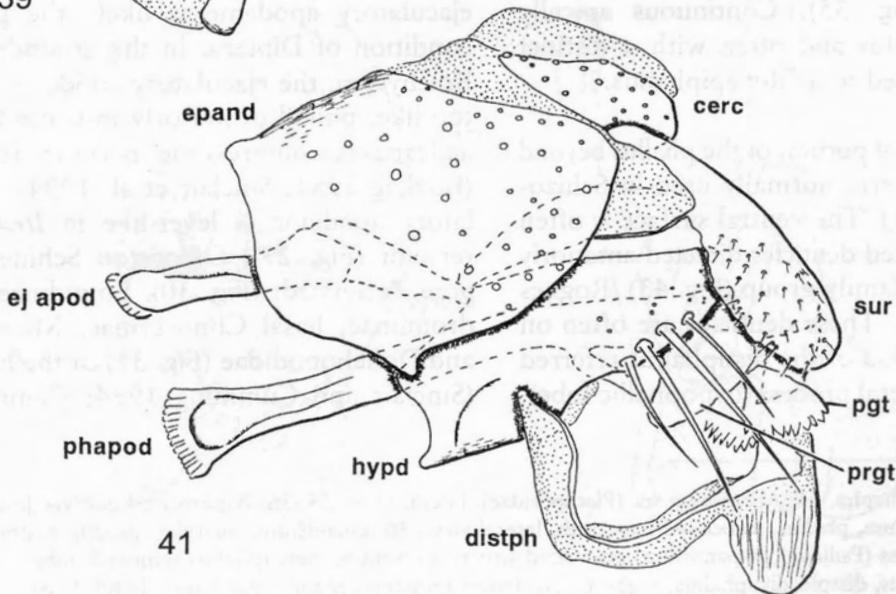
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1995). In Cyclorrhapha, the ejaculatory apodeme and sperm pump are separated from the base of phallus by a long ejaculatory duct (Figs 34–35, 39, 41–43) (see sperm pump).

The ejaculatory apodeme is present in Bibionomorpha, despite production of spermatophores, and appears as a slender, concave plate which cradles the endophallus (Fig. 12) (Blaschke-Berthold 1994). This interpretation is supported on the basis of two sets of opposing muscles homologous to the retractor and protractor muscles of Brachycera (Blaschke-Berthold 1994: M3, M5; Ovtshinnikova 1989: fig. 207, M30 and M31). The spermatophore is retained by the male and simply extended to the female (Blaschke-Berthold 1994) (see sperm pump below). In the Culicomorpha where spermatophores are also known, the ejaculatory apodeme is absent (Figs 16–17), correlated with the passage and presentation of this preformed, two-chambered capsule (Wood 1991).

endoaedeagal process (endoaedeagus, endophallus, posterior part of aedeagus): slender sclerotized lobe or extension arising from the apex of the ejaculatory apodeme. This process is found in most Xylophagomorpha (Fig. 22), Tabanomorpha (Fig. 24), and some Nemestrinidae, Asilidae (Stichopogonini), and possibly in Bombyliidae (Sinclair et al. 1994). Although interpreted as a groundplan synapomorphy of the Brachycera (Sinclair et al. 1994), the restricted distribution of this process in the latter lineages may be interpreted as independently derived and possibly not homologous with the endoaedeagal process of Tabanomorpha and Xylophagomorpha (Griffiths 1996). This process is reduced in Athericidae and absent in Stratiomyomorpha and most Muscomorpha (*sensu* Woodley 1989).

endoaedeagal tube (Ductusrohr, endoaedeagus): slender, unpigmented, membranous tube within the sperm sac, arising from the posterior margin of the ejaculatory apodeme (Reichardt 1929; Theodor 1976; Sinclair et al. 1994). This tube is perforated with pores and often clothed with posteriorly directed spinules, granules or platelets. It is thought to be an extension of the ejaculatory duct. The endoaedeagal tube is present in many Asiloidea, but has not been fully investigated in the Therevidae (Theodor 1976; Sinclair et al. 1994). It is also present in Anthracinae Bombyliidae (Theodor 1983). The sclerotized, apical process described in *Lomatia* Meigen (Lomatiinae) (Theodor 1983: fig. 508), may actually be homologous to the endoaedeagal process.

endophallus: seminal duct within the aedea-gus or phallus, and appears as a tubular extension of the sperm sac.

epiphallus: spine-like, external process arising from the posteromedial surface of the basiphallus (Figs 39, 43). Most common in the Brachycera, especially the Schizophora.

glans: swollen structure at the end of a long coiled phallus in Tephritoidea (McAlpine 1981; Foote and Steyskal 1987: fig. 66.41).

lateral ejaculatory process (aedeagal dorso-anterior sclerite, external ejaculatory sclerite, lateral aedeagal apodeme): pair of sclerites enclosing the anterodorsal wall of the sperm sac (Figs 24–25, 27), bearing one of three muscles (M32, Ovtshinnikova 1989) originating on the ejaculatory apodeme. Contraction of this muscle pulls the ejaculatory apodeme and flexes the lateral ejaculatory processes, thereby compressing the sperm sac. These processes are widely present in the lower Brachycera and interpreted as a component of the groundplan of Brachycera (Sinclair et al. 1994). Homologous structures in the nematocerous Diptera have not been confirmed and are absent in the Stratiomyomorpha and Eremoneura (Sinclair et al. 1994; Griffiths 1994; Cumming et al. 1995).

Figs 2.38–41. Cyclorrhapha. 38: *Glyphidops flavifrons* (Bigot) (Neriidae), lateral view. 39: *Teratomyza* sp. (Teratomyzidae), hypandrium, phallus, associated structures, lateral view. 40–41: *Coelopa nebularum* Aldrich (Coelopidae): 40: epandrium, surstylus, proctiger, ventral view, 41: lateral view (abbreviations: cerc: bac scl: bacilliform sclerite, cercus, distph: distiphallus, ej apod: ejaculatory apodeme, epand: epandrium, epiph: epiphallus, hypd: hypandrium, pgt: postgonite, ph: phallus, phapod: phallapodeme, ph pl: phallic plate, prgt: pregonite, sur: surstylus).
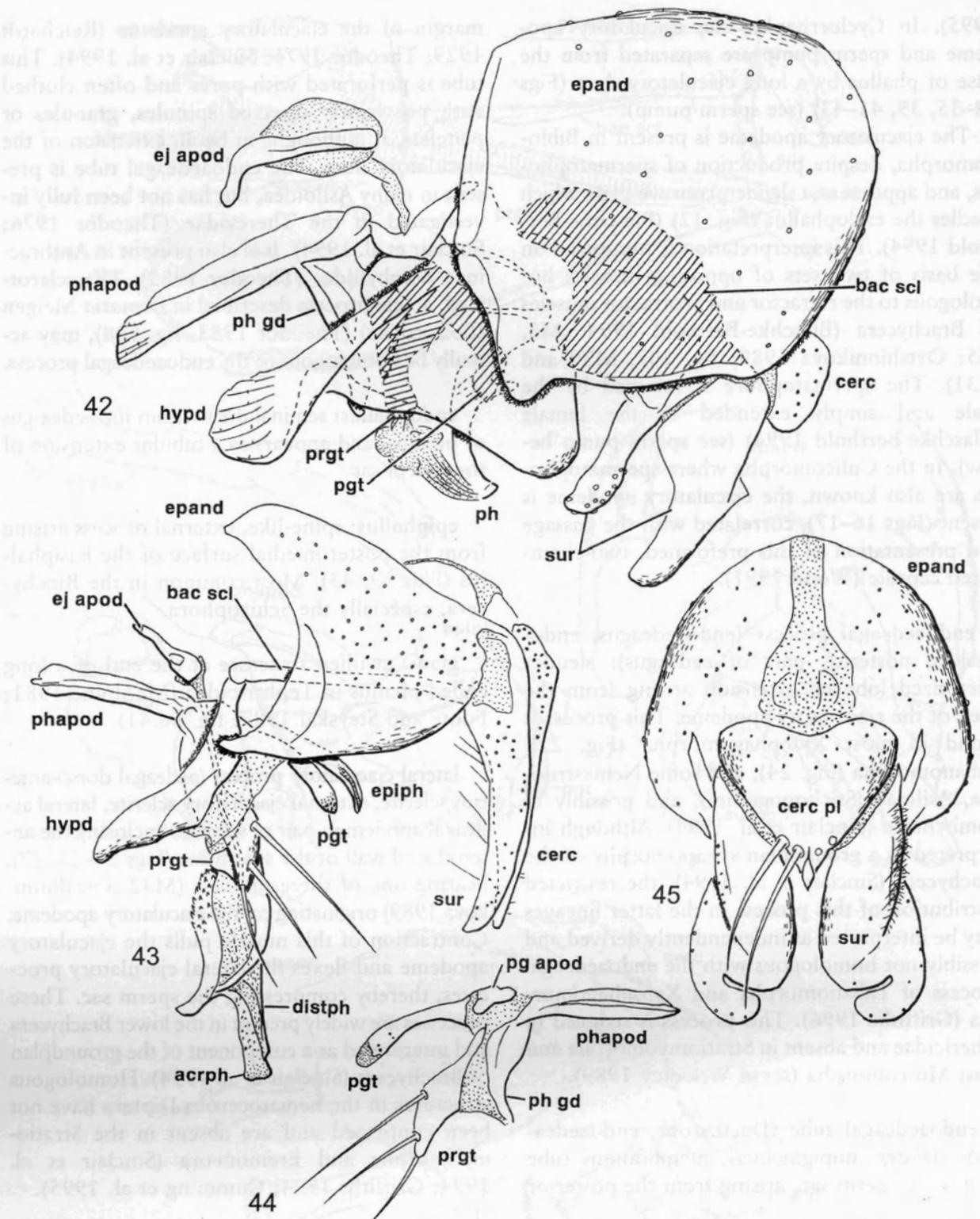
Figs 2.42–45. Cyclorrhapha. 42: *Diastata vagans* Loew (Diastatidae), lateral view. 43–44: *Calliphora nigribarbis* Vollenhoven (Calliphoridae): 43: lateral view, 44: postgonite and associated structures. 45: *Strobilomyia neanthracina* Michelsen (Anthomyiidae), epandrium, proctiger, posterior view (abbreviations: acrph: acrophallus, bac scl: bacilliform sclerite, cerc: cercus, cerc pl: cercal plate, distph: distiphallus, ej apod: ejaculatory apodeme, epand: epandrium, epiph: epiphallus, hypd: hypandrium, pg apod: postgonal apodeme, pgt: postgonite, ph: phallus, phapod: phallapodeme, ph gd: phallic guide, prgt: pregonite, sur: surstylus).

Structures somewhat similar to lateral ejaculatory processes are found in some *Hesperinus*, but could be interpreted as a subdivision of the aedeagal sheath and do not appear able to compress the sperm sac (Figs 8, 10–11). Although three sets of muscles are present at the base of the aedeagus in *Trichocera* Meigen (Neumann 1958; Ovtshinnikova 1989), no external lateral ejaculatory sclerites are found. Consequently these processes are not likely a component of the Diptera groundplan (Sinclair et al. 1994).

The paired lateral sclerites described by Wood (1991) as part of the groundplan condition are not homologous to lateral ejaculatory sclerites (see Sinclair et al. 1994). These sclerites or rods are either anterior, non-articulated extensions of the aedeagus (Fig. 5) (Tipulidae, Axymyidae – Wood 1991: figs 2–5, 9), or extensions of the paramere (Trichoceridae, Wood 1991: fig. 6). Muscles from the ejaculatory apodeme are inserted onto these sclerites (Ovtshinnikova 1989).

median sclerite: flat, Y-shaped sclerite forming the distal portion of the floor of the aedeagus of Simuliidae. Possibly a secondary sclerotization of the aedeagal membranous sac.

phallic plate (aedeagal dorsal sclerite, ventral proctiger sclerite, "y" sclerite): short to long plate or rod in Eremoneura, extending from the base of the phallus to the base of the bacilliform sclerite (or subepandrial sclerite) and arms of the hypandrium (Figs 30, 35). Hennig (1976) referred to this point of junction as "point y" and represents an important reference point or landmark in determination of homologies. In basal Brachycera, the phallus or parameral sheath is membranously connected to the subepandrial membrane. The basal phallic sclerite is extremely long and slender in Micropezidae and Neriidae (Fig. 38), where the base of the phallus is greatly extended posteriorly.

phallotrema: secondary gonopore at the apex of the aedeagus, as opposed to the primary or true gonopore which lies at the opening of the ejaculatory duct into the sperm pump (Figs 6, 10) (Hennig 1973; Ulrich 1974). There is a single opening in the groundplan of Diptera (Wood 1991). However, a tripartite condition is present in many families; e.g., Cylindrotomiinae (Tipulidae), Blephariceridae (Fig. 1), Tanyderidae, Asilinae, but is assumed to be derived independently numerous times (Wood 1991).

phallus (aedeagus): parameres are fused and form a sheath (phallushülle) that encircles the aedeagus in the groundplan of the Brachycera (Figs 21, 24) (Sinclair et al. 1994). Only the apex of the aedeagus remains recognisable (Figs 22–23) (see aedeagus above). In the Stratiomyomorpha and Muscomorpha (*sensu* Woodley 1989), the apex of the aedeagus is completely fused and indistinguishable from the parameral sheath. This composite structure is termed the phallus (Wood 1990) and is viewed as a tube within a tube (Figs 25, 29) (see Cumming et al. 1995: 126). A similar configuration is found in the Bibionomorpha (Fig. 8) (Blaschke-Berthold 1994: fig. 61). The phallus is often quite complex in higher flies and discreet subdivisions are often recognised; e.g., basiphallus, epiphallus and distiphallus (Figs 39, 41, 43).

sperm pump (genital vesica): found at the junction of the endophallus and the ejaculatory duct, represented by an ejaculatory apodeme, and is a component of the Diptera groundplan. In Cyclorrhapha, the sperm pump is separated from the base of the phallus by a long ejaculatory duct and represents an apomorphic feature of the Cyclorrhapha, including Opetiidae (Figs 34, 42–43) (Hennig 1976; Cumming et al. 1995). Similar trends have developed independently in the Psychodidae, Anisopodidae, Scatopsidae, and some Stratiomyomorpha.

The sperm pump is lost in all Culicomorpha and is correlated with the passage of a preformed spermatophore (Figs 15, 17) (Wood 1991; Sinclair et al. 1998). The Bibionomorpha are also known to produce a spermatophore, reported in at least two genera of Bibionidae (Blaschke-Berthold 1994). Based on the configuration of the male internal reproductive system, most Bibionomorpha are also predicted to produce spermatophores of some kind, including Hesperini-

dae and Pachyneuridae (Sinclair, Borkent and Wood, in prep). However, the sperm pump is not absent in this lineage, but simply modified with the ejaculatory apodeme no longer functioning as a piston (see ejaculatory apodeme above). The ejaculatory apodeme is modified in the form of a plate (Figs 8, 10–13) and is drawn posteriorly by muscle contraction beyond the apex of the paramere, possibly related to drawing the spermatophore out and into the female's vagina (Blaschke-Berthold 1994).

sperm sac (endophallus *sensu* Bonhag 1951): membranous sac that encloses the base of the aedeagus at the entrance of the ejaculatory duct(s) (Figs 12, 18, 23–24). This enclosure is a component of the sperm pump.

All structures posterior to segment nine in male Diptera are collectively referred to as the **proctiger** (Wood 1991). It is the anus bearing segment, often small and tucked beneath the posterior margin of the epandrium in much of the nematocerous Diptera and Brachyceran groundplan.

cercus (forcep, superior forcep, valvula medialis): one-segmented, pad-like lobe, often weakly developed or indistinguishable from other components of the proctiger. The anus is always positioned between the cerci and can be a useful landmark for determining homology. The cerci are apparently absent in Tipulomorpha (Fig. 7) and Trichoceridae (Hennig 1973), and are probably incorporated with the hypoproct (McAlpine 1981). In Psychodidae, the cercus (often termed surstylus (see Quate and Vockeroth 1981: fig. 17)) is clasper-like (Fig. 19), often bearing stiff,

flattened setae called tenacula (retinacula) on the inner apical portion. It is enlarged and clasper-like in many calyptrates, and certain Empididae (Cumming et al. 1995). In some Dolichopodidae, the cerci are broad, pale, flattened, ornamented lobes used as signally devices (Fig. 31). In some calyptrates, the strongly sclerotized cerci are often fused basally and articulate with the surstylus (Fig. 45).

Often a pair of weakly sclerotized plates are found on either side of the anal opening (Fig. 43). These plates are dorsal to the cerci and may be interpreted simply as sclerotization of the anal membrane dorsal to the cercus, surrounding the anus. These plates are distributed sporadically in the Eremoneura, particularly Sphaeroceridae (Wheeler 1995), Calliphoridae, and Empidoidea.

epiproct (tergite 10): mid-dorsal, shield-shaped lobe between lateral cerci. Lost in all Heterodactyla (Bombyliidae, Asiloidea and Eremoneura) (Sinclair et al. 1994) and Acroceridae (Yeates 1994).

hypoproct (opisthophallus, paraproct, sternite 10): midventral, oval or triangular sclerite between lateral cerci, and continuous with the subepandrial membrance anteriorly (Figs 3, 26). Often elaborated in Dixidae (Figs 14–15), Culicidae, some Psychodidae (Fig. 19), and Xylomyidae (Sinclair et al. 1995: fig. 11b) and may assist in clasping in some taxa.

The reader is directed to the following two references for more information on **flexion** and **rotation**: McAlpine (1981) summarised the occurrence throughout Diptera, while Cumming et al. (1995) reviewed the condition in Eremoneura.

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1.3. Morphology and terminology of the female postabdomen

Marion KOTRBA

In the dipteran ground plan the female abdomen consists of 10 segments plus a terminal portion bearing the anus and paired cerci. Each segment comprises a dorsal tergum, a ventral sternum, and a more or less extensive membranous area in between. The abdominal spiracles, originally 8 pairs, but commonly reduced to 7 or less, are positioned in the pleural membranes or in the lateral portions of the tergites. Helpful landmarks on the postabdomen are the positions of cerci and anus, as well as the position of the genital opening posterior of sternum 8.

Tergites and sternites 9 and 10 are present in the dipteran ground plan.* Within the order there is a tendency towards reduction and/or fusion of these sclerites. Thus, in most Cyclorrhapha only one dorsal and one ventral sclerite (supra-anal and subanal plate, Figs 4, 6) are present in the region between segment 8 and the cerci. The supra-anal plate is considered homologous with either tergite 10 or a fused product of tergites 9+10. The subanal plate is probably homologous with sternite 10. Sternite 9 in many nematocerous and orthorrhaphous Diptera forms a genital fork and is shifted anteriorly into the dorsal wall of the genital chamber (Figs 2, 5, see below). In the Cyclorrhapha sternite 9 is either deeply internalised or, most commonly, completely reduced.

In some lower Brachycera and most Cyclorrhapha the postabdominal segments are more or less tapered (Figs 3–4, 6) and retracted into the preceding segments, forming a telescoped ovipositor. The sclerites of these retractile segments are often subdivided, reduced, or absent, while the membranous areas are enlarged, so that the ovipositor is flexible and predominantly membranous (Fig. 4). On the other hand, several clades independently evolved other types of ovipositors, sometimes strongly sclerotized and adapted for piercing, rasping, or digging (Fig. 3). Because these structures are not homologous with the orthopteroid ovipositor, some authors prefer alternative terms, such as oviscapt or ovicauda.

The internal organs of the female postabdomen belong to the alimentary and reproductive tracts (Figs 7–8). In dissections they are easily discerned by tracing their origins either to the ventrally positioned genital chamber or vagina, or to the dorsally positioned rectum.

In the dipteran ground plan the female reproductive tract comprises paired ovaries and lateral oviducts, a common oviduct, 3 spermathecae and their ducts, as well as paired accessory glands. In some nematocerous Diptera the common oviduct extends caudad through segment 8. Spermathecal ducts and accessory glands open on sternum 9, posterior of the orifice of the common oviduct (primary gonopore). Within the order, however, there is a tendency to shift the primary gonopore, spermathecal openings, accessory glands, and sternite 9, deeper into the body cavity (compare Figs 7–8). Progressively a genital chamber and then a tubular vagina evolved to connect between the common oviduct and the vulva (secondary gonopore). This in turn provided for further developments (Fig. 8). In the Schizophora, and possibly also some other Brachycera, a fertilisation chamber or ventral receptacle arises from the anteroventral portion of the vagina, opposite of the spermathecal ducts. The openings of the spermathecal ducts themselves are enclosed by cuticular folds constituting the genital papilla, which commonly establishes close contact with the entrance of the fertilisation chamber. In addition to this, the vagina of higher Diptera can feature a variety of additional char-

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* In this chapter sternites 8-10 are named in concordance with the terminology adopted by most dipterists. However, detailed studies on the origin of these sclerites have resulted in different hypotheses regarding their homology (e.g., Matsuda 1976, Sæther 1977, Deuve 1988, Blaschke-Berthold 1994).
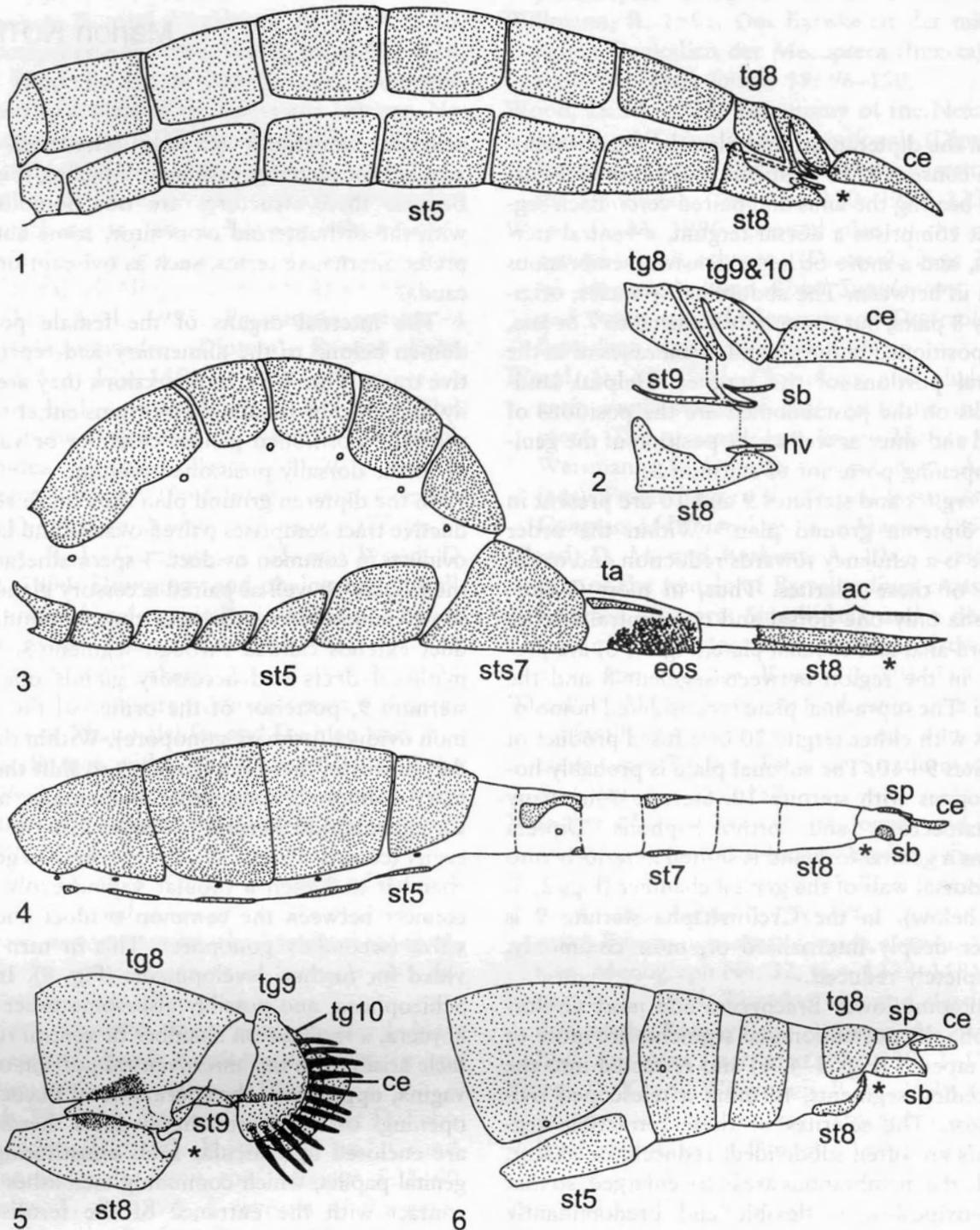
Figs 3.1–6. Female (post-) abdomen; lateral view from the left. 1–2: *Trichocera columbiana* Alexander (Trichoceridae; modified from McAlpine 1981); 3: *Rhagoletis pomonella* (Walsh) (Tephritidae; ovipositor partially everted; modified from Foote and Steyskal 1987); 4: *Camilla glabra* (Fallén) (Camillidae; ovipositor everted; modified from McAlpine 1987a); 5: *Apiocera haruspex* Osten Sacken (Apioceridae; modified from Peterson 1981); 6: *Diastata vagans* Loew (Diastatidae; modified from McAlpine 1987 b) (abbreviations: acu: aculeus, ce: cerci, eos: eversible ovipositor sheath, hv: hypogynial valves, sb: subanal plate, sp: supra-anal plate, st: sternum, sts7: syntergosternite 7, ta: taeniae, tg: tergum; the asterisk indicates the genital opening).

acters such as enlargements, pouches, valves, or sclerotizations, whose potential significance for phylogenetic analysis is only now being recognized and evaluated.

As becomes apparent from the glossary below, the terminology used by different authors is often inconsistent. If the same term has been applied to different structures, these are enumerated. If different terms have been applied to the same structure, then "=" refers from synonymous terms to the term preferred by the author. "q. v." refers to additional information under other terms in the glossary.

GLOSSARY

acanthophorites: paired spine-bearing hemitergites derived from tergite 10 in some many orthorrhaphous Diptera (Fig. 5).

accessory glands: internal glandular organs belonging to the female reproductive tract (Figs 7–8); derived from segment 9; paired in basic pattern, but secondarily unpaired in a few taxa; almost always entirely membranous. Gland lumen oval to tubular, rarely ramified, surrounded by epithelial gland cells with more or less con-

spicuous end apparatus (q. v.). Ducts muscular, often with a subapical pump; opening posterior or posterolateral of the spermathecal ducts, either externally on sternum 9 or into the dorsal wall of the genital chamber or vagina. In Bombyliidae an additional pair of tubular accessory glands is present (e.g., Mühlenberg 1971).

accessory copulatory vesicles: paired vaginal pouches in some Calyptratae (e.g., Muscidae and Calliphoridae), which receive the sperm and/or
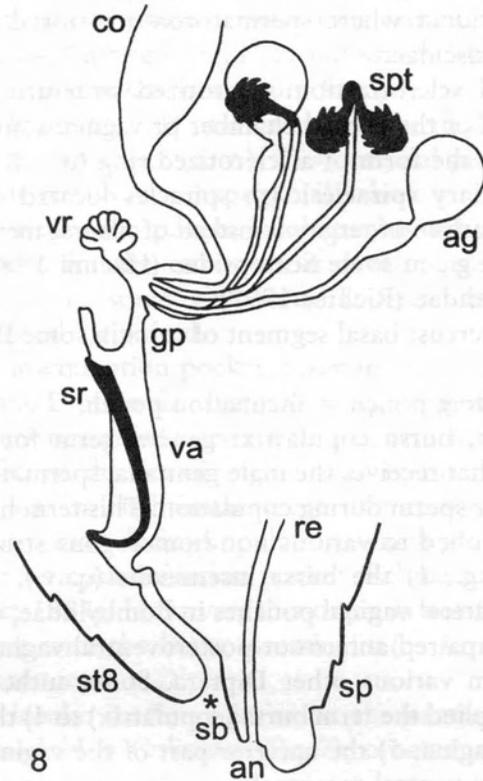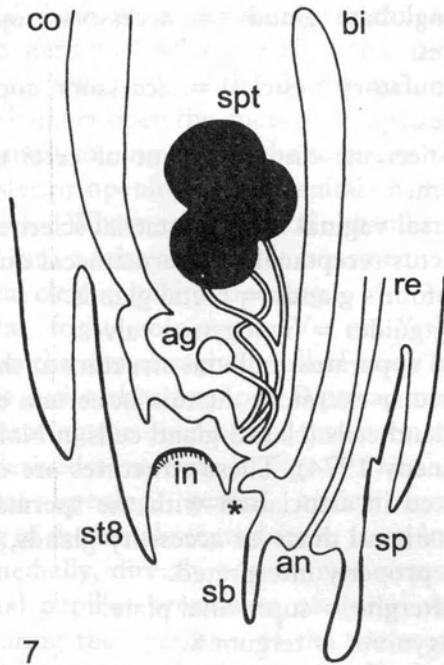
Figs 3.7–8. Internal female reproductive tract; schematic lateral view from the left; ovaries and lateral oviducts omitted. 7: *Aedes aegypti* (L.) (Culicidae); 8: *Cyrtodiopsis whitei* Curran (Diopsidae) (abbreviations: ag: accessory gland, an: anus, bi: bursa inseminalis, ce: cerci, co: common oviduct, gp: genital papilla, in: insula, re: rectum, sb: subanal plate, sp: supra-anal plate, spt: spermatheca, sr: sclerotized ring, st8: sternum 8, tg8: tergum 8, va: vagina, vr: ventral receptacle; the asterisk indicates the genital opening; modified from Harbach and Knight 1980).

male accessory secretions during copulation; inserting dorsolaterally, posterior of the genital papilla.

aculeus: highly sclerotized, pointed apical portion of ovipositor. In Tephritidae the aculeus includes the sclerites of segment 8, the postgenital segments, and the cerci (Fig. 3).

adanal plates: two small sclerites in Nycteribiidae, ventrolateral of the cerci and sometimes fused with them, possibly representing remnants of the subanal plate.

anal papillae = cerci in some Drosophilidae.

anal sclerite: small sclerite in Nycteribiidae, medioventral of the cerci, possibly representing the subanal plate.

anal opening = anus.

anal segment = proctiger.

anterior chamber = fertilisation chamber.

anus: posterior external opening of the alimentary canal.

appendicular glands = accessory glands.

atrium: 1) genital chamber; 2) region of common oviduct where spermatozoa are stored in Hippoboscidae.

atrial sclerotization: sclerotized structure in the wall of the genital chamber or vagina, sometimes in the form of a sclerotized ring (q. v.).

auxiliary spiracles: 8th spiracles located on dorsal surface of tergite 8 instead of pleural membrane, e.g., in some Scatopsidae (Haenni 1997) and Mydidae (Richter 1997).

basicercus: basal segment of cerci in some Diptera.

breeding pouch = incubation pouch.

bursa, bursa copulatrix: general term for a pouch that receives the male genitalia, spermatophore or sperm during copulation. This term has been applied to various non-homologous structures, e.g., 1) the bursa inseminalis (q. v.), 2) paired lateral vaginal pouches in Bombyliidae, or 3) an unpaired antero- or posteroventral vaginal pouch in various other Diptera. Some authors have applied the term bursa (copulatrix) to 4) the entire vagina, 5) the anterior part of the vagina, or 6) the ventral receptacle.

bursa inseminalis: pouch arising from the posterodorsal wall of the genital chamber in vari-

ous nematocerous Diptera (Fig. 7); it receives the sperm during copulation; derived of segment 9.

cerci: paired terminal appendages at either side of the anus; derived from segment 11; two-segmented in basic pattern of Diptera, but independently reduced to one segment in most nematocerous and orthorrhaphous Diptera and in all Eremoneura. In some taxa the cerci are reduced or fused.

choriothete: glandular epithelial cushion in the ventral vaginal wall for the support of the developing larva in Glossinidae (Roberts 1971).

cloaca: in Tephritidae the vagina and the terminal portion of the rectum unite to form a cloaca.

cloacal opening: single opening of the joined vagina and rectum in Tephritidae.

collateral glands, colleterial glands = accessory glands.

common oviduct: unpaired duct, which receives the lateral oviducts anteriorly, and whose posterior orifice constitutes the primary gonopore (q. v.); derived from segment 8. The common oviduct commonly forms a dorsoventral double bend, allowing for the extension of the female terminalia for oviposition.

conglobate glands = accessory copulatory vesicles.

copulatory vesicles = accessory copulatory vesicles.

disticercus: distal segment of cerci in some Diptera.

dorsal vaginal lip = postatrial sclerite.

ductus receptaculi = spermathecal duct.

Dufour's glands = rectal glands.

egg guides = hypogynial valves.

end apparatus: bulbous structure at the tip of a cuticular excretory ductule in certain ectodermal gland cells (class 3 gland cells in Noirot and Quennedy 1974). These structures are often illustrated in association with the spermathecae, spermathecal ducts or accessory glands, but are rarely properly interpreted.

endtergite = supra-anal plate.

epigynium = tergum 8.

epiproct: 1) in a strict sense dorsal sclerite of the proctiger (q. v.); 2) supra-anal plate.

eversible glands = eversible sacs.

eversible membrane = eversible ovipositor sheath.

eversible ovipositor sheath: extensive membranous area between syntergosternite 7 (q. v.) and segment 8, which can be inverted for the telescopic retraction of the ovipositor in various acalyptrate Diptera such as Tephritidae (Fig. 3) and Agromyzidae; often ornamented with cuticular denticles.

eversible sacs, eversible tubes: eversible paired tubular appendages on the dorsal postabdomen of some female Ceratopogonidae; associated with paired rod-shaped internal apodemes projecting anteriorly from the anterior rims of the tergites. As there is no evidence for a glandular function of these organs (Borkent and Craig 1994), the term "gland rods" should be avoided.

fertilization chamber: unpaired evagination of the anteroventral part of the vagina in Schizophora where the eggs are fertilised during oviposition; evolved into a ventral receptacle (q. v.) in most acalyptrate Diptera; not yet described in any other Diptera.

furca = genital fork.

genital aperture = genital opening.

genital chamber: ectodermal invagination posterior to sternum 8 which receives the common oviduct anteriorly. Into the dorsal wall of the genital chamber open the ducts of the spermathecae and most commonly also the accessory glands. The posterior opening of the genital chamber is the vulva. Where the genital chamber has evolved into a tubular organ it is termed vagina.

genital cleft = genital opening.

genital fork: commonly V- or Y-shaped sclerite in the dorsal vaginal wall of many nematocerous and orthorrhaphous Diptera; more or less embracing the openings of the spermathecal ducts; derived of sternite 9 (Figs 2, 5).

genital opening, genital orifice: external opening of the female reproductive tract; located ventromedially, directly posterior of sternum 8.

genital papilla: protrusion of dorsal vaginal wall bearing the apertures of the spermathecal ducts and accessory glands (Fig. 8). These openings are often enclosed by cuticular folds, which may form an insemination pocket (q. v). In many

Schizophora the genital papilla achieves a close fit with the opposing fertilisation chamber or ventral receptacle.

genital plate, genital sternite = sternite 8.

genital tubercle = genital papilla.

genitalia: 1) abdominal structures involved in reproduction; 2) in the strict sense those parts of sterna 8 and 9 lying adjacent to the female genital opening.

gland rods = eversible sacs.

gluten glands = accessory glands.

gonopore: primary gonopore (q. v.) or secondary gonopore (q. v.).

gonosternum = sternum 8.

gonotrema = genital opening.

gynium: 1) = segment 8. 2) Some authors apply this term to the entire aculeus (q. v.)

hypogynial plate: median plate on sternum 8 in Blephariceridae.

hypogynal valves, hypogynial valves: paired processes of sternum 8 (Fig 2); may function as egg guides. Some authors suggest that the hypogynial valves are derived from sternum 9 (Menzel and Mohrig 1997; Dahl and Krzemińska 1997).

hypogynium = sternum 8.

hypoproct: 1) in a strict sense ventral sclerite of the proctiger (q. v.); 2) = subanal plate.

hypovalvae = hypogynial valves.

incubation pouch, incubatory pouch: vaginal pouch for the retention of developing eggs or larvae in some viviparous Diptera; unpaired, bilobed, or paired.

insemination pocket, insemination pouch: In some Diptera the ducts of the spermathecae and accessory glands open into a pouch, formed by folds of the dorsal vaginal wall (genital papilla, q. v.). In Tephritidae sperm is transferred into this pocket during copulation, which gave rise to the term insemination pocket (Solinas and Nuzzaci 1984). However, this organ is not homologous with the bursa inseminalis (q. v.) of some nematocerous Diptera.

insula: median sclerite on the ventral praeatrial fold in Culicidae (Fig 7); ornamented with spiculae and setae.

intra-anal plates: medially divided sternite 10 in Tipulidae.

introvert: basal or apical sleevelike invagination of the spermathecal capsule.

lamellae: cerci in Cecidomyiidae (Skuhravá 1997); may be 2 or 3 segmented or fused into median lobe.

lateral oviducts: paired ducts leading from the ovaries to the common oviduct; derived from segment 7.

lateral pouches, lateral sacs = accessory copulatory vesicles.

lingulae: paired anterolateral processes of the subanal plate of some Calyptratae.

lower vaginal lip = preatrial sclerite.

median oviduct = common oviduct.

milk glands: glands producing a nutrient for the developing larvae in some viviparous Diptera; derived from the accessory glands in Pupipara and from the spermathecae in Mesembrinellinae (Calliphoridae).

morula gland: multichambered ventral receptacle (q. v.).

muscular apparatus = sperm pump.

operculum: apical, thimble-shaped portion of the ventral receptacle in Ephydridae.

ovaries: composed of 1 to 1000 ovarioles in Diptera.

ovarioles: egg producing tubes; polytrophic meroistic type in Diptera; composed of terminal filament, germarium, vitellarium, and calyx.

ovicauda = ovipositor.

oviductus communis = common oviduct.

oviductus lateralis = lateral oviduct.

oviposition tube = ovipositor.

ovipositor: modification of terminalia for oviposition; may involve part of or all of terminalia. Because these structures are not homologous with the orthopteroid ovipositor, some authors prefer alternative terms, such as oviscapt or ovicauda.

ovipositor blade = aculeus.

ovipositor lobes = hypogynial valves.

ovipositor sheath = syntergosternite 7.

ovipositor valves = hypogynial valves.

ovipositubus = eversible ovipositor sheath.

oviprovector: 1) = eversible ovipositor sheath; 2) eversible scaled membrane between the oviscapt lamellae (q. v.) of Drosophilidae (Grimaldi 1987).

ovisac = uterus.

oviscape, oviscapt: 1) = syntergosternite 7 (Fig. 3); 2) = ovipositor; 3) = hypogynial plate of Blephariceridae. 4) In female Drosophilidae sternum 8 is modified into 2 broad lateral plates that are joined by an anteroventral bridge and together form the oviscapt (Grimaldi 1987).

oviscapt lamellae: lateral plates of oviscapt (q. v.) in Drosophilidae.

ovisensilla: trichoid or peglike receptors on the oviscapt (q. v.) of Drosophilidae.

ovolarvipositor: modification of terminalia for larviposition.

paraprocts: paired sclerites lateral or ventrolateral of the anus.

parovaria = accessory glands.

periatrial sclerites: preatrial sclerite and postatrial sclerite in Culicidae.

perineal plates: plates of uncertain homology between vulva and subanal plate in some Drosophilidae.

pincers: paired lateral hemicircular processes of tergum 6 in Leucostomatini (Tachinidae).

postabdomen: modified posterior portion of abdomen; in some Cyclorrhapha the postabdomen extends anteriorly to include segment 6 (Fig 4).

postatrial sclerite: sclerotized dorsal rim of vulva in Culicidae, derived from sternite 9.

postgenital lobe: process of subanal plate in Culicidae.

postgenital plate = subanal plate.

preatrial sclerite: sclerotized ventral rim of vulva in Culicidae, derived from sternite 8.

primary gonopore: posterior end of common oviduct; opening to the exterior or, most commonly, into the anterior portion of the genital chamber or vagina. In higher Diptera the position of the primary gonopore is roughly defined by the position of the spermathecal openings.

proctiger: 1) In a strict sense anus-bearing region behind segment 10, furnished with the epiproct, paraprocts and hypoproct; largely reduced in Diptera. 2) The term is often extended to include all structures behind segment 9 in higher Diptera.

pseudacanthophorites: cerci adorned with spines, e.g., in Tethinidae.

receptaculum seminis = spermatheca.

rectum: terminal portion of alimentary canal; ectodermal in origin.

rectal glands: defensive glands attached to the rectum in the vicinity of the rectal papillae in Sepsidae. Similar glands occur convergently within some other families, such as Tephritidae, Coelopidae and Diopsidae.

rectal papillae: prominent ovoid epithelial structures in the wall of the rectum; most commonly 4, but sometimes more; up to 36 in Mydidae and Apioceridae (Yeates and Irwin 1996).

ring-shaped sclerite = sclerotized ring.

sand chamber: In some Bombyliidae segment 8 forms a chamber where eggs are dusted in sand before oviposition.

sacculus: enlarged anterior portion of vagina.

satellites = end apparatus.

sclerotized ring: ring-shaped sclerite in the dorsal vaginal wall of some Phoridae and convergently in the ventral vaginal wall of a number of acalyptrate Diptera (Fig. 8). Part of the vaginal musculature may insert on this sclerite, and commonly it encircles a thick epithelial cushion. Its homology is unclear.

secondary gonopore: posterior opening of the genital chamber or vagina. The secondary gonopore is generally the vulva, except in Tephritidae, where it opens into a cloaca (q. v.).

seventh spiracle: last spiracle in most Diptera; frequently shifted toward segment 6, which thus has two spiracles.

signum: unpaired or paired sclerotized plate in the dorsal vaginal wall.

spectacles-shaped sclerite: pair of sclerotized rings in the lateral vaginal wall of Sphaeroceridae; homology unclear, but reminiscent of the sclerotized ring (q. v.) in some other taxa.

sperm pumps: specialised structures in the spermathecal ducts of many orthorrhaphous Diptera and also some Schizophora such as *Stylogaster* (Conopidae). The pumps are usually comprised of a specialised section of the spermathecal duct with a thickened cuticular end plate at one or both ends, surrounded by thick longitudinal or spiral muscles inserting at these end plates.

sperm receptacles = spermathecae.

spermathecae: internal sperm-storage organs derived from segment 8 (Figs 7–8); consisting of the spermathecal capsules (q. v.) and the spermathecal ducts (q. v.).

spermathecal capsules: 0–4, but 3 in dipteran ground plan (Hennig 1973); most often spherical or cylindrical, and usually heavily sclerotized; surface smooth or ornamented with papillae, spines, or ridges; surrounded by epithelial gland cells with more or less conspicuous end apparatus (q. v.). Tubular forms occur as well and may be extremely long, especially in some orthorrhaphous Diptera. In some taxa the spermathecal capsules are membranous and easily overlooked, in others they are almost completely reduced.

spermathecal ducts: most commonly 2, 3, or 2 with one or both ducts branching apically; opening directly posterior of the primary gonopore (q. v.), either externally on sternum 9 or into the dorsal wall of the genital chamber or vagina; sometimes extremely long and coiled. Portions of the ducts can be modified, e.g., into sperm pumps (q. v.) or into apical bulbous enlargements.

spermathecal eminence = genital papilla.

spermiducts = spermathecal ducts.

sternal apodemes: paired or single rod-shaped apodemes projecting anteriorly from the anterior rim of the postabdominal sternites along the inner surface of the ventral body wall. Such apodemes occur in various families and usually serve for muscle attachment.

sternal valves = hypogynial valves.

sternite 8: sometimes medially divided into two lateral plates or lobes, or with modifications or appendages, such as the hypogynial valves (q. v.).

sternite 9: In many nematocerous and orthorrhaphous Diptera forming a genital fork (q. v., Figs 2, 5); in most Cyclorrhapha internalised and more or less reduced.

subanal plate: sclerite in the ventral postgenital region in higher Diptera (Figs 4, 6–8). Most authors homologise the subanal plate with sternite 10.

subgenital plate = sternite 8.

supra-anal plate: sclerite in the dorsal postgenital region in higher Diptera (Figs 4, 6–8). Most authors homologise the supra-anal plate

with tergite 10 or a fused product of tergites 9 and 10.

syntergosternite 7: In various acalyptrate Diptera, such as Nerioidea, Tephritoidea, and Agromyzidae, tergite 7 and sternite 7 are fused to form a conical or tubular sheath, which may receive the retracted apical part of the ovipositor (Fig. 3).

taeniae: paired, striplike, basal sclerites of the eversible ovipositor sheath (q. v.) in Tephritidae (Fig 3).

terminalia: terminal complex of modified genital and anal segments, plus any adjacent segments that show modifications for copulation or oviposition.

theca: ventral protrusion of sternum 5 in Conopidae. Part of its surface is studded with stubby bristles and serves as counterpart for the anteroventrally directed ovipositor. Very similar modifications can be found in some Pipunculidae and Tachinidae.

upper vaginal lip = postatrial sclerite.

uterus: 1) anterior portion of the vagina, enlarged for the retention of developing eggs; 2) = incubation pouch. 3) Some authors have applied the term uterus also to the vagina or the anterior portion of the vagina of non-viviparous Diptera.

uterine pouch = incubation pouch.

vagina: The genital chamber (q. v.) is to be termed vagina, if it constitutes the tubular extension of the common oviduct (Snodgrass 1935), as is the case in most higher Diptera (Fig 8).

vaginal apodeme, vaginal plate: Some authors have applied these terms to a derivative of sternite 9 in nematocerous Diptera, homologous to the genital fork (q. v.). However, these terms do not indicate homology and could be applied to other non-homologous sclerotizations of the vaginal wall as well.

valves: 1) = hypogynial valves; 2) epithelial folds that project into the vaginal lumen; usually termed according to their position, e.g., ventral valve, posterior valve, etc.

valvulae, valvulae inferiores, ventral flaps = hypogynial valves.

ventral receptacle: unpaired organ arising from the anteroventral portion of the vagina in most acalyptrate Diptera; derived from the schizophoran fertilization chamber (q. v.), and functioning as fertilisation chamber and/or sperm reservoir (Fig. 8). Extremely diverse in shape and degree of sclerotization it ranges from a membranous pocket to a long coiled tube or a large and heavily sclerotized pouch of sometimes bizarre shape. A large, heavily sclerotized ventral receptacle is frequently combined with largely reduced spermathecae, and especially in such instances the ventral receptacle is frequently mistaken for a spermatheca. In Diopsidae, most Tephritoidea, and several other families the ventral receptacle is multichambered and thus reminiscent of a morula (Fig. 8). However, the term "morula gland" is misleading, as it implies a predominantly glandular function of this organ.

ventral ring = sclerotized ring.

ventral tuft: ventral protrusion into posterior vaginal lumen of *Aedes*, ornamented with colourless spines.

ventral vaginal lip = preatrial sclerite.

vulva = genital opening.

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1.4. Morphology and terminology of Diptera larvae*

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INTRODUCTION

The Diptera are extremely diverse in species richness, morphological variation, and ecological habits. The group's diversity is due largely to its broad range of larval structure and ecology. Overall, larval Diptera exhibit nearly every type of feeding habit and include scavengers, predators, parasites, parasitoids, and herbivores. In spite of this broad range in feeding habits, larvae typically occur in moist or wet habitats (e.g., within tissues of living plants, amid decaying organic materials, inside other animals, or in association with truly "aquatic" habitats). Invasion of these and other habitats is a reflection of adaptations in the larval stage.

Diptera larvae can be distinguished from the larvae of most other insects by the absence of jointed thoracic legs; however, in most other respects the group shows tremendous structural diversity. Morphological variation is exemplified by diversity of cranial structure. Larvae of most nematocerous Diptera are eucephalic, characterised by a complete, fully exposed, and heavily sclerotized head capsule (Figs 1–8). In contrast, cranial sclerites are greatly reduced or absent in most Brachycera. The hemicephalic head capsule of many orthorrhaphous Brachycera consists of slender tentorial arms and cephalic rods that are partly retracted into the thorax (Figs 60–79). The culmination of cranial reduction is in the acephalic head of larval Cyclorrhapha, in which the externally visible head, the pseudocephalon, is membranous, and much of the head is retracted into the thorax (Figs 102–108). The term "acephalic" for the cyclorrhaphan head is unfortunate because it implies that these larvae lack heads. Cyclorrhaphan larvae are, however, normal insects with a head consisting of six segments. The only difference between these flies and lower Diptera is that each segment is withdrawn and invaginated into the thorax and thus externally hidden. Because of the term's wide use, we reluctantly continue to use "acephalic".

Although this range of cranial structure follows a general phyletic pattern from nematocerous flies to orthorhaphous- and cyclorrhaphous Brachycera, the former two groups contain several exceptions (e.g., among nematocerous groups, many Cecidomyiidae are hemicephalic or acephalic, and the cranium of many Tipulidae is excised posteriorly and retracted into the thorax (Figs 10–13); among orthorrhaphous Brachycera, larval Stratiomyidae are nearly eucephalic).

Because of the structural diversity in larval Diptera, it is difficult to provide broad generalisations about morphology. Although we attempt the latter, we also provide data on the range of structural variation in the order. As much as possible, we present information about all larval instars, especially for groups that vary significantly between stages. However, because of relative size, development of structures, and available information in the literature, we focus on structural features of last-instar larvae. Homologies among subgroups are based on a variety of data, including general resemblance of structures, spatial relationships, landmark features, and, where possible, embryology. In large part, we follow the descriptive terminology of Teskey (1981a), as modified by Courtney (1990a, 1991), Oosterbroek and Courtney (1995) and Sinclair (1992). Terms for musculature are primarily those of Matsuda (1965).

Establishing homologies of the brachyceran mouthparts and the cyclorrhaphan cephalopharyngeal skeleton has been problematic and controversial in recent years (see later). Because of the dramatic structural transitions in cranial morphology (i.e., eucephalic to hemicephalic to acephalic) and concomitant transitions in mouthpart structure between the nematocerous Diptera, orthorrhaphous- and cyclorrhaphous Bra-

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* Dedication: To the memory of Dr. Herbert J. Teskey 1928–1998. He was a quiet and humble teacher and dedicated student of larval dipterology.

chycera, each subgroup is treated separately. Cranial morphology of major taxa are presented in a phyletic sequence, beginning with the presumed groundplan condition and variation in nematocerous Diptera. Subsequent to our discussion of the head capsule, and reflecting partly the substantive overlap of characteristics among major dipteran subgroups, we provide a more generalised discussion of postcranial larval morphology. Although we accept that the nematocerous Diptera and orthorrhaphous Brachycera represent paraphyletic taxa (Hennig 1973; Wood and

Borkent 1989; Woodley 1989; Oosterbroek and Courtney 1995), we continue to use general phyletic grades to better demonstrate major structural transformations in larval Diptera. Higher taxonomic categories for nematocerous Diptera are based largely on the classification of Oosterbroek and Courtney (1995), including use of the paraphyletic "higher Nematocera". Taxonomic categories for the Brachycera follow the classifications of Woodley (1989) and McAlpine (1989) with the modification that the "Aschiza" are considered paraphyletic (Yeates and Wiegmann 1999).

Figs 4.1–3. Cranial features of larval nematocerans. 1–2: *Bibio* sp. (Bibionidae) head capsule, with right mandible and maxillae removed: 1: dorsal and 2: ventral views. 3: *Sylvicola* sp. (Anisopodidae), head capsule, ventrolateral view, with left mandible and maxillae removed (abbreviations: ant: antenna, cly: clypeus, cly su: clypeal suture, ecdy su: ecdysial suture, econ: epicondyle, ep: epipharynx, frcly ap: frontoclypeal apotome, frcly su: "frontoclypeal" suture, gen: gena, hcon: hypocondyle, hy: hypopharynx, lmpo: postmentum, lmpr: prementum, lr: labrum, md: mandible, mx: maxilla, mxc: cardo, mxl: lacinia, mxp: maxillary palpus, phr: pharynx, pmd: premandible, pca: postoccipital carina, poc: postocciput, tm: torma, taa: anterior tentorial arm, tap: posterior tentorial arm, tpp: posterior tentorial pit) (after Teskey 1981a).

HEAD CAPSULE

Nematocerous Diptera

Cranium – The larvae of most nematocerous groups are eucephalic, which is considered the groundplan condition for Diptera. This arrangement is characterised by a well-developed external cranium comprising three major sclerites: a middorsal **frontoclypeal** (cephalic) **apotome** and a pair of lateral sclerites, the **genae** (Figs 1, 7, 10). Among Diptera, Bibionidae (Teskey 1981a) and late-instar Blephariceridae (Anthon and Lyneborg 1968) possess a frontoclypeal apotome (frons) delimited anteriorly by a "frontoclypeal" suture. This suture is probably not homologous to the frontoclypeal suture of other insects, nor is it part of the Diptera groundplan (Hennig 1973). For these and other reasons (Teskey 1981a), we refer to the dorsomedial cranial sclerite as the "frontoclypeal apotome." In first-instar larvae of most nematocerous Diptera, the frontoclypeal apotome bears an **egg burster** (Figs 14–15). This tooth- or ridgelike structure permits the larva to pierce the egg and, thereby, hatch. An egg burster is part of the Diptera groundplan and one of the synapomorphies of the Antliophora [= Mecoptera + (Diptera + Siphonaptera)] (Wood and Borkent 1989).

In most eucephalic larvae, the largest and most prominent cranial sclerites are the genae. These sclerites are often contiguous dorsally and ventrally, and, thus, enclose much of the head. In most groups, the genae and frontoclypeal apotome are separated by distinct regions of thin cuticle, the **ecdysial lines**, which permit the cranium to split during molting. The typical sequence of ecdysis includes initial rupture of the thoracic cuticle and progressive splitting to the head, where the rupture continues at the ecdysial lines. The general appearance of the ecdysial lines is in some Bibionomorpha similar to an inverted Y (Fig. 1) or, in most groups, lacks a stem line and resembles a V or (some Culicomorpha) U (Fig. 7). In late-instar larvae of the Deuterophlebiidae, the ecdysial lines have disappeared and the cranial sclerites remain fused (Courtney 1990a). These changes result in a highly modified ecdysial process in which the cranium is shed

intact, and the functional ecdysial line is between the pro- and mesothorax.

The anterior and posterior margins of the genae are usually somewhat thickened and strengthened. Anteriorly, the subgenal margin provides support for the articulation of mouthparts. Posteriorly, the genae comprise all or much of the cranial margin and, thus, border most of the occipital foramen. This margin typically is heavily sclerotized to form a **postoccipital carina** (Fig. 2), which frequently accommodates the insertions of muscles that move the head. The carina can be further subdivided anteriorly by a slight groove, the **postoccipital sulcus** (Fig. 2). Ventrolaterally, the region frequently bears posterior tentorial pits (see later).

The cranial structure of some larval nematocerans is highly modified and approaches a hemicephalic condition. In the Tipulidae, the head capsule is often fully retracted into the thorax and the posterior cranial margin bears small-to-extensive longitudinal incisions (Figs 10–13). This condition is present to a lesser degree in the Axymyiidae, Cecidomyiidae, and Tanyderidae. In these groups retraction of the cranium is permanent and reflects a shift of certain muscle insertions to near the mouthparts (Teskey 1981a). Excisions in the posterior cranial margin are also present in some larval Blephariceridae (i.e., many Blepharicerinae); however, the blepharicerid head is modified through formation of a cephalothorax (fused head, thorax and first abdominal segment). In blepharicerids and some other groups (Deuterophlebiidae, Tanyderidae and Tipulidae) there appears to be a correlation between the extent of cranial excision and the presence of intermolt cuticle deposition (Courtney 1991).

Tentorium – The tentorium is the internal skeleton of the larval head and provides support for the cranium and attachment surfaces for cranial and mouthpart muscles. The presence of a tentorium is part of the Diptera groundplan; however, the specific ancestral state is less certain. Some authors (Anthon 1943a; Hennig
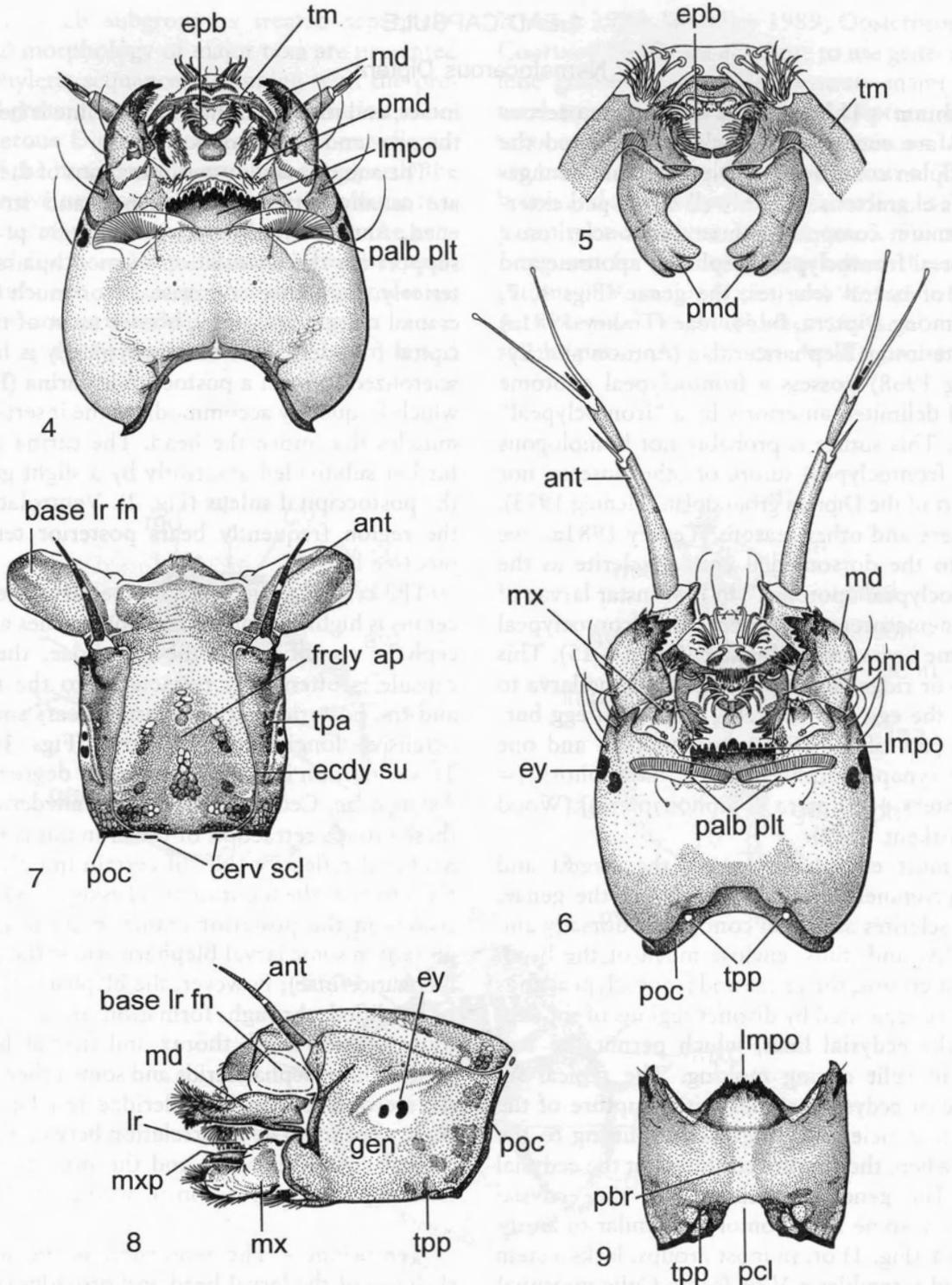
Figs 4.4–9. Cranial features of larval nematocerans. 4: *Chironomus* sp. (Chironomidae – Chironominae) head capsule, ventral view. 5: *Paracluneo* sp. (Chironomidae – Telmatogetoninae) labrum, ventral view. 6–8: head capsule: 6: *Micropsectra* sp. (Chironomidae – Chironominae), ventral view; 7: *Simulium* sp. (Simuliidae), dorsal view; 8: *Simulium* sp., lateral view, with labral fan removed. 9: *Simulium* sp., ventral cranium (abbreviations: ant: antenna, base lr fn: base of labral fan, cerv scl: cervical sclerite, ecdy su: ecdysial suture, epb: epipharyngeal bar, ey: stemmata, frcly ap: frontoclypeal apotome, gen: gena, lmpo: postmentum, lr: labrum, md: mandible, mx: maxilla, mxp: maxillary palpus, palb plt: paralabial plate, pbr: postgenal bridge, pcl: postgenal cleft, pmd: premandible, poc: postocciput, tm: torma, tpa: anterior tentorial pit, tpp: posterior tentorial pit) (4–6 after Oliver 1981, 7–9 after Peterson 1981).

1973) have postulated that primitively the tentorium comprises anterior and posterior pits, well-developed anterior and posterior arms, and a posterior bridge. However, relatively few, mostly "derived" groups (e.g., Anisopodidae, Bibionidae, Perissommatidae) have this condition (Fig. 3). In a typical nematoceran, the tentorium is somewhat reduced, especially posteriorly. Larvae of several families (e.g., Ptychopteridae, Tanyderidae, Dixidae, Culicidae, Blephariceridae, Deuterophlebiidae, Trichoceridae) have well-developed anterior and posterior tentorial arms, but lack a posterior bridge. In other groups (e.g., Nymphomyiidae, Psychodidae, Tipulidae, and most Chironomoidea) the tentorium is vestigial and represented primarily by posterior tentorial pits (Figs 6–8). Among Sciaroidea, anterior arms are distinct in some Mycetophilidae (Matile 1990) and almost all Cecidomyiidae (Mamaev and Krivosheina 1993). Although largely vestigial in later instars, a complete tentorium is present in first-stage larva of the Psychodinae (Vaillant 1971). With few exceptions (e.g., Deuterophlebiidae, Sciaroidea, Perissommatidae, Tipulidae), reduction of the tentorium is coincident with expansion of the postmentum and ventral closure of the head capsule, often through fusion of the postgenae. This arrangement presumably compensates for tentorial reduction by increasing cranial rigidity and surface area for muscle attachment (Anthon 1943a; Hennig 1973; Teskey 1981a; Wood and Borkent 1989; Courtney 1990a). Tentorial structure is variable within certain groups (Bibionomorpha, higher Nematocera) and reduction has apparently occurred independently in several unrelated clades. For these reasons, tentorial structure provides few compelling insights into relationships among nematocerous flies (Oosterbroek and Courtney 1995). It is possible that embryological studies of tentorial development will permit meaningful phylogenetic conclusions about relationships among nematocerans and brachycerans (see later).

Ventral cranium – Homologies of the ventral cranium and associated mouthparts are controversial, with most debate pertaining to the origin of the ventral bridge and "hypostoma". The basic question is whether or not these structures are derived from the postgenal (maxillary) segment (Anthon 1943a; Snodgrass 1959; Matsuda 1965), labial segment (Cook 1949; Gouin 1968), or a combination of these segments (Bengtsson 1897; Oosterbroek and Theowald 1991). Courtney (1990a, 1991) expounded on the latter hypothesis, which predicts that the hypostoma is of labial (postmental) origin and the ventral bridge of postgenal origin. Although the subject is far from resolved and variation between groups is possible, we accept the interpretation that the hypostoma is of postmental origin and the ventral bridge of postgenal origin.

As discussed by Oosterbroek and Courtney (1995), structural transformations of the ventral cranium and associated mouthparts may include one or more of the following steps: (1) postmentum shifts anteriorly as the prementum migrates inward to a preoral space; (2) postmentum becomes dentate anteriorly, acquiring the form of a typical hypostoma; and (3) postmentum and postgenal bridge fuse. Some authors (Anthon 1943a; Hennig 1973; Teskey 1981a; Courtney 1990a) suggest that the Diptera groundplan included a simple postmentum and a prementum that was large, exposed, and on the same plane as the postmentum (i.e., the prementum had not migrated inward to the preoral cavity). However, this condition is uncommon in Diptera, confined primarily to relatively derived clades (e.g., anisopodid *Olbiogaster* Osten Sacken). Furthermore, outgroup comparisons fail to support such an interpretation, suggesting instead that the Diptera groundplan included ventromedial fusion of the postgenal lobes (i.e., as seen in the Siphonaptera, Mecoptera and Trichoptera). In most larval Diptera, the ventral cranium is modified through one or more of the above steps. Transformations involving the first two steps result in a cranium similar to that of *Protanyderus* Handlirsch (Exner and Craig 1976), whereas all three steps could lead to a condition similar to that of larval Nymphomyiidae, many Culicomorpha, and most Tanyderidae (Fig. 9).

Cranial structure in larval Tipulidae is diverse (Oosterbroek and Theowald 1991) and problematic. In many tipulids the cranium is excised ven-

tromedially to (Fig. 11) or through (Fig. 13) the postmentum, and the tentorium is greatly reduced (e.g., higher Hexatominae and Eriopterinae). This unusual structure has confounded interpretations of homologies of the postgenal bridge and hypostoma (Bengtsson 1897; Anthon 1943a; Cook 1949). Courtney (1990a) postulated that this arrangement was the result of ventromedial excision of the fused postmentum (hypostoma) and postgenal bridge.

The phylogeny of Oosterbroek and Courtney (1995) suggests that desclerotization of the ventral cranium has occurred in the Bibionomorpha

Figs 4.10–13. Cranial features of larval nematocerans, head capsules. 10: *Prionocera* sp. (Tipulidae), dorsal view; 11: *Limonia* sp. (Limoniidae), ventral view; 12: *Limnophila* sp. (Limoniidae), dorsal view; 13: *Molophilus* sp. (Limoniidae), ventral view (abbreviations: ant: antenna, frcly ap: frontoclypeal apotome, gen: gena, lmhy: prementohypopharyngeal apparatus, lmpo: postmentum, lr: labrum, md: mandible, mx: maxilla, mxp: maxillary palpus, pcl: postgenal cleft, pin: postgenal incision(s)) (after Alexander and Byers 1981).

(except most Cecidomyiidae) and many higher Nematocera (e.g., Perissommatidae, Scatopsidae, Trichoceridae, psychodid *Bruchomyia* Alexander, anisopodid *Olbiogaster*). Further modifications are apparent in the Deuterophlebiidae, Synneuridae, Anisopodidae (except *Olbiogaster*), psychodid *Trichomyia* Curtis, and most Blephariceridae and Cecidomyiidae, groups in which the ventral cranium is predominantly membranous.

Stemmata – Larval eyes, or stemmata, have been described in relatively few taxa, including some Ptychopteridae, Culicomorpha, Blephariceroidea, and Tipulidae (Brodsky 1930; Teskey 1981a; Hogue and Garcés 1990). In these groups, stemmata consist of one or more lenses on the cranial surface, beneath which are bundles of elongate visual cells shielded by black pigment granules (Teskey 1981a). Similar structures presumably occur in most larval nematocerans. The Diptera groundplan probably included as many as five stemmata (Melzer and Paulus 1989).

Antenna – Antennal structure is highly variable in larval nematocerans (Figs 6–8, 16–24), ranging from the elongate, biramous antennae of Deuterophlebiidae (Figs 22, 129), to the enlarged, prehensile antennae of the Chaoboridae (Sæther 1997: Figs 17.29–30), to the reduced, buttonlike organs of many Bibionomorpha and higher Nematocera (Figs 19–20). In most groups, the antennae are relatively short and comprised of one to three articles. A maximum of six articles is reported in certain Chironomidae (Hennig 1973). Marked reduction of the antenna occurs in larval Thaumaleidae (Fig. 18), and most Bibionomorpha (Figs 19, 26) and higher Nematocera (Figs 20, 24, 28). Among the latter groups, the antennae of certain Mycetophilidae and Cecidomyiidae, and aberrant Psychodidae (e.g., *Horaiella* Tonnoir, *Sycorax* Haliday) are relatively elongate. With few exceptions (e.g., *Antocha* Osten Sacken, Fig. 24), antennal reduction is unusual for the Tipulidae (Oosterbroek and Theowald 1991), which suggests that the Brachycera groundplan included a well-developed antenna (Oosterbroek and Courtney 1995).

The antennae of larval nematocerans usually bear a variety of sensillae, most located at the apex of the distal article (Figs 17–18, 20–21). In some taxa (e.g., Scatopsidae), an enlarged apical sensillum can give the otherwise reduced antennae an elongate appearance (Fig. 20). In certain Chironomidae and Blephariceridae, enlarged apical sensilla (e.g., Lauterborn's organ in Chironomidae) suggest a biramous antennal structure (Figs 6, 16). However, only larval Deuterophlebiidae possess truly biramous antennae (Figs 22, 129). The bifurcate distal article bears several separate and distinct sensilla, confirming its identity as a true article rather than a pair of modified apical sensilla (Courtney 1990a). Although examined in relatively few taxa, the structure and arrangement of antennal sensilla hold considerable promise for future investigations of phylogenetic relationships among Diptera families (Nicastro et al. 1998).

The groundplan for larval Diptera probably included a single antennal muscle (Hennig 1973) originating from the anterior tentorial arm and inserting on the anterior margin of the antennal socket. This condition is typical of many nematocerous groups (Cook 1949; Félix 1962; Courtney 1990a). Antennal muscles are apparently absent in the Tipulidae and certain Bibionomorpha.

Labrum – The labrum, or upper lip, is one of the major mouthparts of a larval nematoceran and, in some groups, is remarkably complex. The labrum is continuous anteriorly with the frontoclypeal apotome, from which it is often delineated by a narrow suture. In most taxa the labrum is relatively broad and dorsoventrally compressed (Figs 1, 2, 25–27, 35–37), a condition presumed to be part of the Diptera groundplan. In other nematocerous taxa (e.g., Thaumaleidae, Nymphomyiidae, Blephariceridae, Axymyiidae, Scatopsidae, Psychodidae, Trichoceridae, Anisopodidae), the labrum is laterally compressed and conical (Figs 28–32, 39–40). This arrangement frequently coincides with a shift in mandibular rotation (see later) and has been used to support certain phylogenetic groupings (e.g., Psychodomorpha *sensu* Wood and Borkent 1989). Regardless of shape, the labrum's ventral,

or epipharyngeal, surface usually bears numerous sensillae, macrotrichia, or spines that may be grouped into rows, clusters or brushes (Figs 37–38). The arrangement and complexity of these structures often reflect feeding habits (Olafsson 1992) and may provide compelling characters for phylogenetic reconstruction (Wood and Borkent 1989).

Most larvae possess several small sclerites in the membranous portion of the epipharyngeal surface. The V- or U-shaped **epipharyngeal** (palatal) **bar** is usually the most obvious of these sclerites, whereas the smaller, typically paired **tormae** are present but often fused with lateral sclerites (Figs 2–5). The presence of articulated tormae has been used to support monophyly of the Culicomorpha (Wood and Borkent 1989), Blephariceromorpha (Courtney 1991), and Tipulidae (Oosterbroek and Theowald 1991); however, this condition could be part of the Diptera groundplan (Oosterbroek and Courtney 1995). The fused tormae of the Bibionomorpha (*sensu* Oosterbroek and Courtney 1995) would, therefore, represent a derived condition. These sclerites are important for muscle attachment and, thus, critical to labral movement and function.

Another prominent labral feature in many larvae is a pair of premandibles (messors). Premandibles are well-developed in most Ptychopteromorpha – Culicomorpha and higher Nematocera (Figs 3–6), and premandible-like sclerites occur in Mycetophilidae and Sciaridae. It is unclear if these sclerites are homologous in each group (Oosterbroek and Courtney 1995). Although present in several nematocerous families, premandibles are probably not part of the Diptera groundplan. These structures are absent from Diptera outgroups, many nematocerous taxa (e.g., Corethrellidae, Chaoboridae, Blephariceromorpha, Axymyiidae, Bibionidae, Pachyneuridae), and the Brachycera. Wood and Borkent (1989) considered the presence of complex, comblike premandibles a synapomorphy of their infraoder Psychodomorpha. Few members of this group lack premandibles (e.g., the psychodid *Trichomyia*, anisopodid *Olbiogaster*, and Synneuridae). Further modification of the internal structure and muscle attachments of premandibles occurs in the Ptychopteromorpha + Culicomorpha (Wood
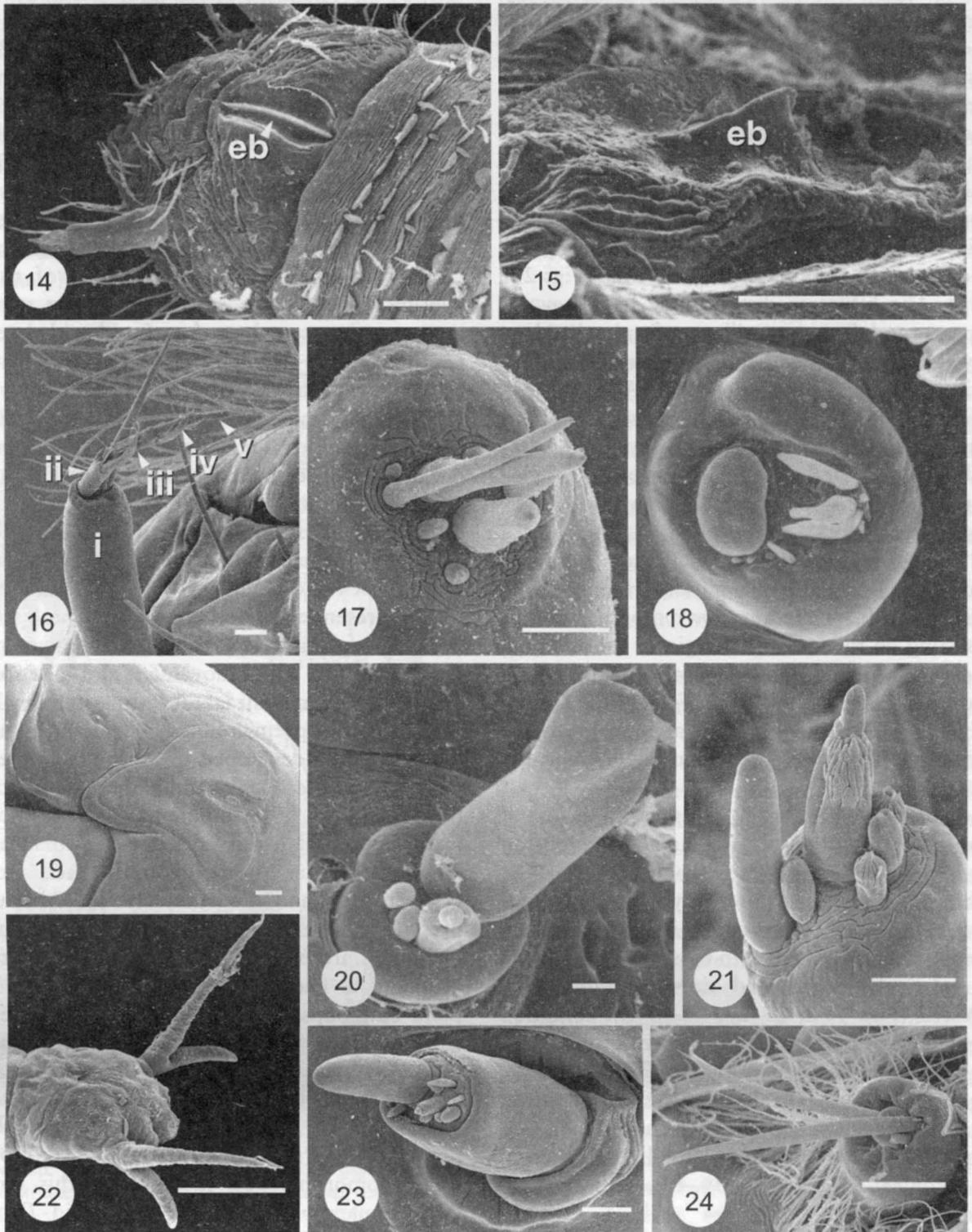
Figs 4.14–24. Scanning electron micrographs of larval nematocerans, egg bursters and antennae. 14: *Agathon* sp. (Blephariceridae), instar I head capsule, oblique-dorsal view of egg burster. 15: *Deuterophlebia* sp. (Deuterophlebiidae), instar I, dorsolateral view of egg burster (anterior = right). 16: Chironomidae (Chironominae), antenna, oblique-ventral view. 17: *Bittacomorpha* sp. (Ptychopteridae), antennal apex. 18–20: antenna: 18: *Androprosopa* sp. (Thaumaleidae), instar I; 19: Mycetophilidae sp.; 20: *Rhexoza* sp. (Scatopsidae). 21: *Blepharicera* sp. (Blephariceridae), antennal apex. 22

and Borkent 1989). These changes may be part of a transformation series, with the ultimate step an exclusively internal premandible.

Labral movement is mediated by several muscles, with their number and arrangement reflecting the complexity of associated structures. Movement of labral brushes is accomplished by muscles attached to one or more small sclerites in the epipharyngeal surface, primarily the tormae. Except in certain Tipulidae (Matsuda 1965), the paired labral compressors are inserted on the epipharyngeal bar. The labral retractor typically comprises two bundles that originate on the frontoclypeal apotome and insert on various labral scelerites (tormae, premandibles, and/or lateral margin of the epipharyngeal bar, depending on the group). A labral depressor originates on the frontoclypeal apotome and is inserted on the medial part of epipharyngeal bar.

Mandible – The larval mandibles of ancestral Diptera presumably moved in a horizontal plane and functioned as biting and chewing organs (Hennig 1973; Teskey 1981a). In many larval nematocerans, the mandibles are stout, heavily sclerotized and bear a toothed incisor lobe distally and stout molar lobe proximally (Figs 44, 49). The mandibles of other taxa, especially groups with predacious larvae, often have a slender, sickle-shaped apical lobe (Fig. 47; Olafsson 1992). In addition, the mandibles are usually adorned with rows or patches of macrotrichia, notably the **prostheca**, a cluster of modified macrotrichia on the adoral mandibular margin (Figs 44–46). In certain Tipulidae, this cluster is borne on a distinct basal lobe (Fig. 50). Although absent in a few groups (e.g., Anisopodidae), prosthecae are typical of most larval mandibles and may be homologous to the prostheca of larval Trichoptera (Anthon 1943a) and Nannochoristidae (Wood and Borkent 1989). Additional mandibular vestiture includes the "sweeping bristles" ("Fegeborsten" of Anthon 1943a) and **mandibular comb** (*sensu* Wood and Borkent 1989) of Ptychopteromorpha + Culicomorpha. In these groups, the comb consists of rows of long, curved macrotrichia (Fig. 43; Sæther 1997: Fig. 2.17.31).

The mandibles of several aquatic groups, including the Deuterophlebiidae, Nymphomyiidae, Thaumaleidae, and certain Psychodidae (e.g., *Neotelmatoscopus* Tonnoir), bear comblike apical teeth (Figs 45, 48). In early-instar larvae of many Blephariceridae, the mandibles bear apical and medial lobes that terminate in a comblike series of teeth (Fig. 30); however, the mandibular lobes of late-instar larvae typically bear only small serrations (Fig. 46). The comblike mandibles of early-instar larvae are a possible synapomorphy of the Blephariceromorpha (Courtney 1990a, 1991; Oosterbroek and Courtney 1995). Structural resemblance between the mandibles of Blephariceromorpha and other aquatic groups (e.g., Thaumaleidae, *Neotelmatoscopus*) may reflect convergent feeding habits (i.e., larvae use mandibles to scrape algae from rocks).

Subdivided ("bisegmented") mandibles occur in larval Ptychopteridae, most higher Nematocera and orthorrhaphous Brachycera (Anthon 1943a, b; Hennig 1973), and perhaps even some Blephariceroidea (Courtney 1990a). In some Tipulidae, this condition is accompanied by modification of the apical lobe into a clawlike structure. Ontogenetic changes in mandible structure suggest that the condition in Blephariceroidea is not homologous to that in Ptychopteridae and higher Nematocera. In the former, mandibular changes may reflect superposition of sclerotized layers or intermoult deposition of cuticle (Zwick 1977; Courtney 1991), rather than subdivision (*sensu* Anthon 1943a). Several authors (Anthon 1943a; Schremmer 1951; Hennig 1973; Friedrich and Tautz 1997) suggest that the presence of subdivided mandibles is plesiomorphic in Diptera. However, neither the Siphonaptera nor Mecoptera demonstrate this condition. It is more likely that subdivided mandibles is a derived feature of certain Diptera and that, in most groups, this arrangement reflects partial desclerotization (Snodgrass 1950; Gouin 1959). This theory gains further support if the subdivided brachyceran mandible is secondarily derived and unrelated to the condition in nematocerous groups (Teskey 1981a).

A presumed general trend in larval Diptera is a shift in mandibular rotation (Fig. 51) from a
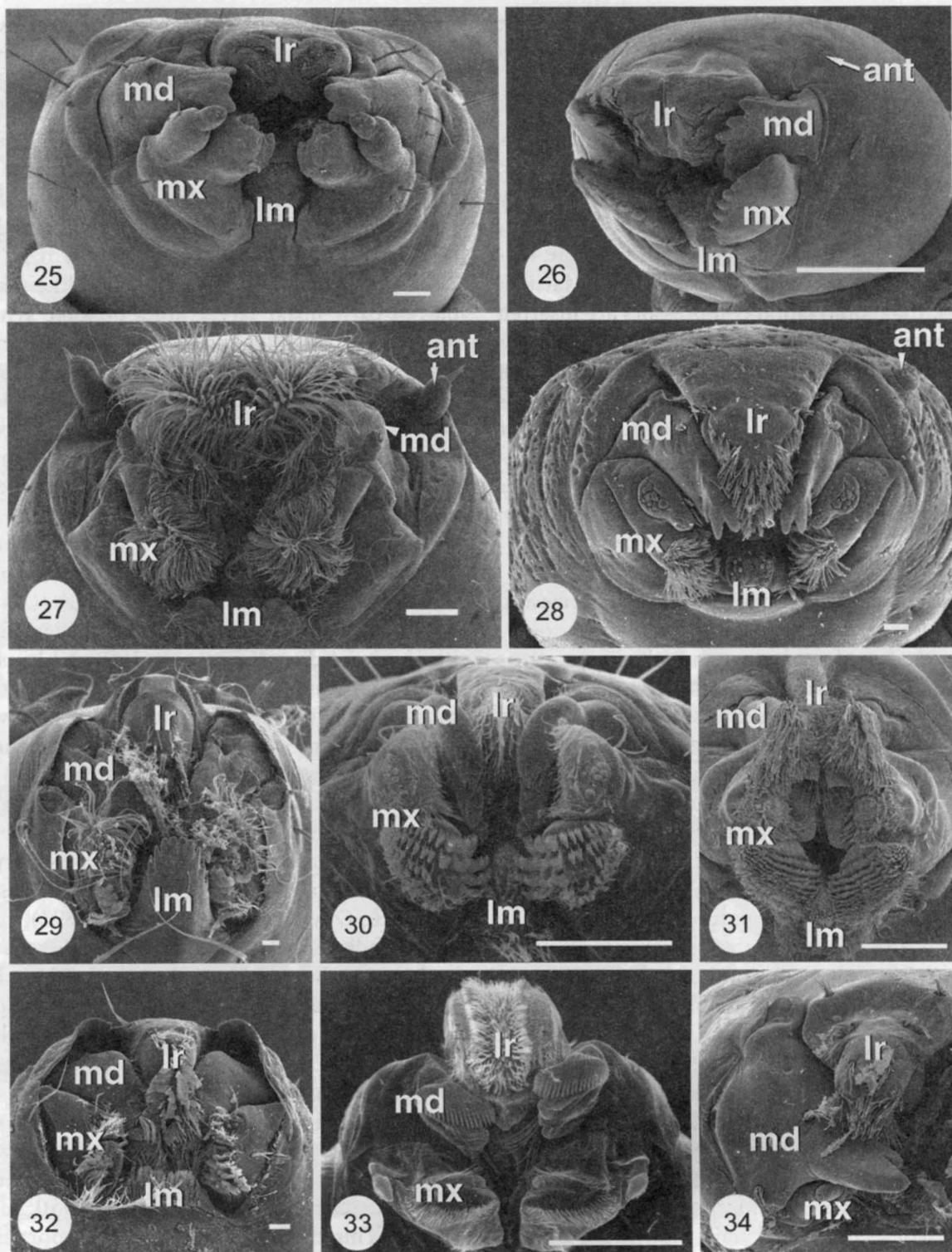
Figs 4.25–34. Scanning electron micrographs of larval nematocerans, general arrangement of mouthparts. 25: *Plecia* sp. (Bibionidae) frontal view. 26: Mycetophilidae sp., oblique-frontal view. 27: *Bittacomorpha* sp. (Ptychopteridae), oblique-ventral view. 28: *Rhexoza* sp. (Scatopsidae) frontal view. 29–33: ventral view of mouthparts: 29: *Androprosopa* sp. (Thaumaleidae); 30: *Bibiocephala* sp. (Blephariceridae), instar I; 31: *Blepharicera* sp. (Blephariceridae), instar IV; 32: *Neotelmatoscopus* sp. (Psychodidae); 33: *Deuterophlebia* sp. (Deuterophlebiidae). 34: *Axymyia* sp. (Axymyiidae), frontal view of mouthparts, with left mandible and maxillae removed (abbreviations: ant: antenna, lm: labium, lr: labrum, md: mandible, mx: maxilla; scale bars: 10μm (Figs 28–29, 32), 40μm (Fig. 30), 50μm (Fig. 33), 100μm (Figs 25–27, 31, 34)).

horizontal plane (Figs 25–26, 34) to an oblique or vertical plane (Figs 28–33). In nematocerous groups this trend is coincident with a shift in the anterior articulation (epicondyle) to a position higher on the cranium, often in association with a narrowing of the labrum and frontoclypeal apotome (Teskey 1981a). A developing tentorial phragma may further displace the epicondyle downward and inward, resulting in a nearly vertical mandibular rotation. Displacement of the epicondyle and a concomitant oblique-to-vertical shift in mandibular rotation are widespread among nematocerans, being typical of several Ptychopteromorpha, Culicomorpha, Blephariceromorpha, and higher Nematocera (Figs 27–33). Based on the distribution of this condition within nematocerous flies, several recent investigations (Oosterbroek and Courtney 1995; Friedrich and Tautz 1997) conclude that oblique mandibular rotation is plesiomorphic for Diptera. This interpretation and possible correlation between mandibular rotation and subdivision are discussed further by Friedrich and Tautz (1997).

Mandibular movement is mediated by two primary muscles, a mandibular adductor and a mandibular abductor. Both typically consist of four bundles, two each with their origin on the posterolateral cranium (genae) and dorsomedial occipital carina, and their insertion on large, flat apodemes near the mandibular fulcra.

Maxilla – The basic structure of the maxilla includes a basal **cardo**, two endites (**galea, lacinia**), and a distal **stipes** bearing a one-segmented palpus (Fig. 2). The cardo, which in many groups is predominantly membranous, usually bears two-to-several prominent setiform sensilla (Figs 52–55, 58). In some Blephariceroidea and most higher Nematocera, the cardo is entirely membranous. Although some larvae possess relatively large maxillae, few groups (e.g., Deuterophlebiidae) retain both endite lobes (Fig. 56). Most larvae have only one recognisable endite, variously identified as the lacinia (Gouin 1959) or galea-lacinia (Matsuda 1965). The shape and complexity of this endite vary tremendously across nematocerous Diptera (Figs 52–59). General reduction of the maxilla, particularly fusion of endites,

is often associated with increased development of the postmentum (hypostoma). Exceptions include Axymyiidae larvae, which have a poorly developed postmentum and greatly reduced maxillary endites (Fig. 59).

Among the more prominent features of the maxilla is the palpus. Its form is variable, being borne on a secondary lobe (palpifer) in some groups (Figs 58–59), but reduced in others (Figs 54–56). Regardless of its general shape, each palpus bears numerous sensilla. The function of specific palpal sensilla is poorly known, but most probably serve as chemoreceptors, assisting in the detection of dissolved substances or particles on the substrate (Craig 1977; Craig and Borkent 1980). The arrangement and homologies of palpal sensilla have been studied in relatively few groups (Craig and Borkent 1980); however, further investigation of these and other maxillary structures should provide valuable insights into the relationships within and between certain nematocerous groups.

In many larval nematocerans, the maxillae are predominantly membranous and play a passive role in feeding, serving mostly as a sensory organ and as the ventrolateral margin of the mouth (Teskey 1981a). Exceptions include the Blephariceridae and Sciaroidea, which use their maxillae to acquire food particles. Blepharicerid maxillae are enlarged, bear a variety of macrotrichia, and play an important role in dislodging food from the substrate and sweeping these particles to the mouth. In many sciaroid larvae, the maxillary endites are heavily sclerotized, bear serrated inner margins (Figs 26–27), and function as rasping organs (Teskey 1981a).

In most larvae, maxillary movement is accomplished by two primary muscles, a tergo-lacinial muscle (lacinial flexor) and stipito-galeal muscle (galeal flexor). The lacinial flexor originates near the posterior margin of the genae (e.g., on the occipital condyle) and, depending on reduction of the maxilla, inserts on the lacinial sclerite or stipes. The galeal flexor originates ventrolaterally on the genae and, depending on maxillary reduction, inserts on the galeal sclerite or stipes. Only one pair of maxillary muscles is present in most Tipulidae and all Brachycera.
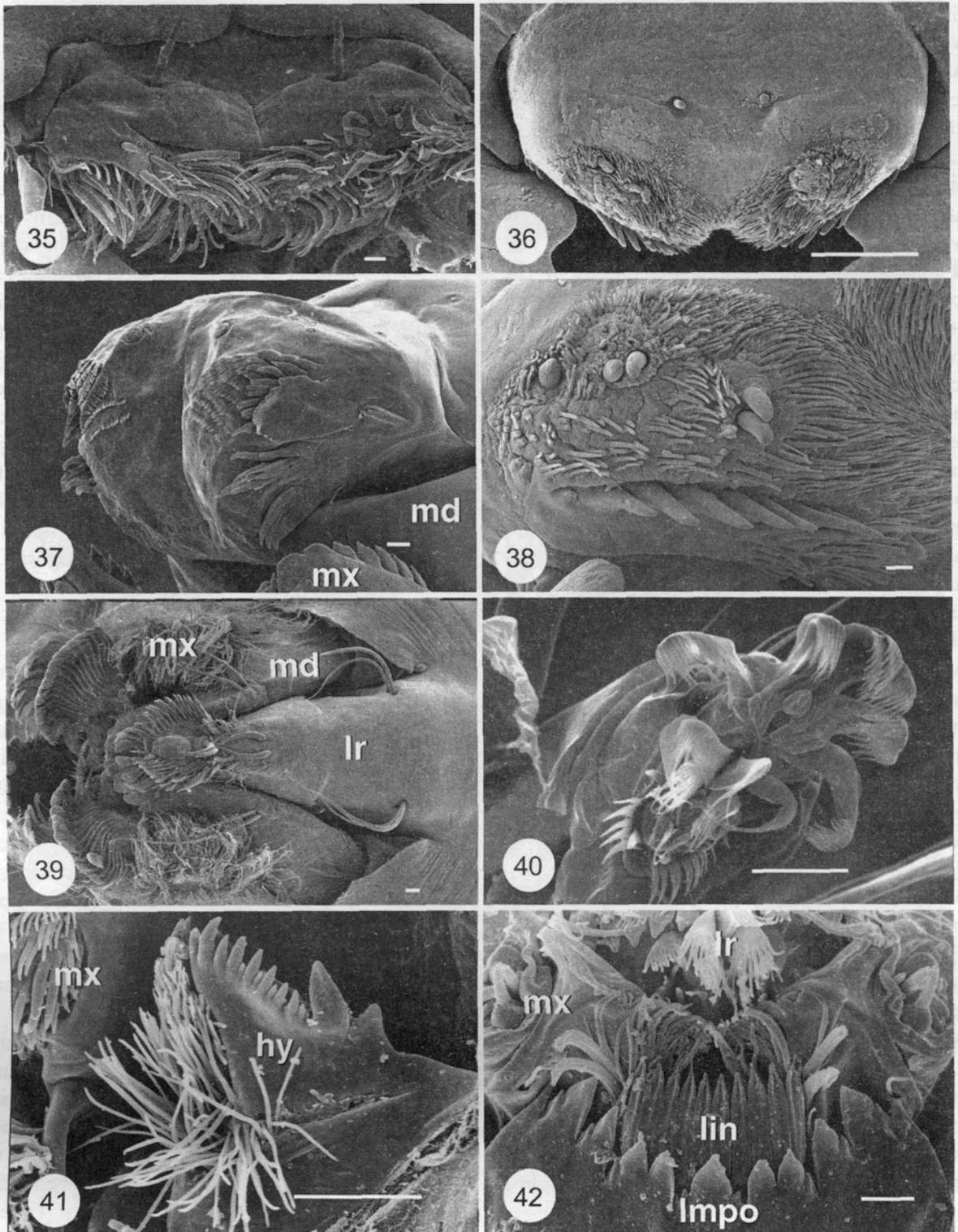
Figs 4.35–42. Scanning electron micrographs of larval nematocerans, mouthparts. 35–37: labrum: 35: *Protanyderus* sp. (Tanyderidae), dorsal view; 36: *Plecia* sp. (Bibionidae), dorsal view; 37: Mycetophilidae sp., oblique-frontal view. 38: *Plecia* sp. (Bibionidae), epipharyngeal surface, lateral view. 39: *Androprosopa* sp. (Thaumaleidae), labrum, dorsal view. 40: *Nymphomyia* sp. (Nymphomyiidae), epipharyngeal surface, ventral view. 41: *Perissomma* sp. (Perissommatidae), hypopharynx, oblique-lateral view. 42: *Nymphomyia* sp. (Nymphomyiidae), postmentum and "lingua" of prementohypopharynx ventral view (abbreviations: hy: hypopharynx, lin: "lingua" of prementohypopharynx, lmpo: postmentum, lr: labrum, md: mandible, mx: maxilla; scale bars: 4μm (Fig. 42), 10μm (Figs 35, 37–40), 20μm (Fig. 41), 100μm (Fig. 36)).

Labium and hypopharynx – Although found in few taxa (e.g., anisopodid *Olbiogaster*), the presumed primitive condition of the ventral head capsule is characterised by widely separated genae and a labium with a recognisable submentum, mentum, prementum, glossae, and labial palpi (Anthon 1943a, b). In most groups with a well-developed labium (e.g., Ptychopteromorpha, Bibionidae), the submentum and mentum are fused into what is generally referred to as the **postmentum**, and other elements are collectively called the **prementum**. In nearly all groups, even those with a highly modified labium, the **labial palpi** provide a distinctive landmark for the prementum.

In most larval nematocerans, the postmentum is either a broad sclerite that covers much of the ventral cranial surface (e.g., *Olbiogaster*: Anthon 1943b) or a small sclerite that has shifted anteriorly to the ventral margin of the preoral cavity (e.g., Nymphomyiidae: Courtney 1994). The postmentum typically forms the posteroventral margin of the mouth. The position and structure of the postmentum are perhaps correlated with ventral closure of the head capsule (see discussion of ventral cranium). In groups characterised by ventral fusion of the postmentum and postgenae (e.g., Nymphomyiidae, most Culicomorpha), the postmentum often bears a serrate anterior margin (Figs 4, 6, 9, 29, 42). As described previously and elsewhere (Courtney 1990a; Oosterbroek and Courtney 1995), the highly modified labium of many Tipulidae may reflect ventral fusion of the postgenae and postmentum, followed by ventromedial excision of the fused postgenae and postmentum (cf. Figs 11, 13). The Psychodidae are also problematic in that larvae demonstrate a range of cranial and postmental structure. Psychodid larvae typically possess a well-developed postgenal bridge and an anteriorly serrated postmentum (e.g., *Bruchomyia*, Phlebotominae, most Psychodinae). However, in other groups, the postmentum can be a simple sclerite (e.g., *Maruina* Müller) or a delicate plate (e.g., *Trichomyia*). Furthermore, the postmentum and postgenae are fused in larvae of the Psychodinae (e.g., *Pericoma* Walker) but separate in

other genera (e.g., *Bruchomyia*). The postmentum of a few groups (e.g., Blephariceroidea) is predominantly or exclusively membranous (Courtney 1990a). Other taxonomically important structures associated with the postmentum include the **paralabial plates** (Figs 4, 6) of certain Chironomidae.

In larvae of the Ptychopteromorpha and most Blephariceromorpha, Bibionomorpha, and higher Nematocera, the hypopharynx and various premental elements (e.g., labial palpi) are separate and easily recognisable. In many other groups, there is an intimate association between the prementum and hypopharynx, which often coincides with the progressive development of a postgenal bridge and concomitant displacement of the labium anteriorly and internally (Anthon 1943a). In some groups (e.g., Culicomorpha, Nymphomyiidae, Tipulidae), this association is manifest in a complex **prementohypopharyngeal apparatus**. The **ligula**, an apically toothed plate above the postmentum of certain Chironomidae and perhaps Nymphomyiidae, is apparently derived from this structure. Separating the subunits of the prementohypopharyngeal apparatus is difficult and usually dependent on locating the salivary duct. Formation of a prementohypopharyngeal apparatus is probably correlated with structural changes in the ventral cranium and postmentum (Anthon 1943a; Teskey 1981a).

In the larvae of most nematocerous groups, the labial muscles consist of two bundles, with their origin on the genae near the occipital condyle and their insertion on a premental sclerite.

In some taxa (e.g., Perissommatidae, certain Tipulidae, and first instar Deuterophlebiidae), the hypopharynx has a serrate anterior margin (Fig. 41); however, this structure is relatively simple in the larvae of most nematocerous Diptera (Fig. 3).

Pharynx and **pharyngeal filter** – Food particles are concentrated in the preoral mouth cavity, or cibarium, prior to entry into the pharynx and esophagus. All three regions are well differentiated and often highly modified in larval nematocerans. The cibarium and pharynx typically
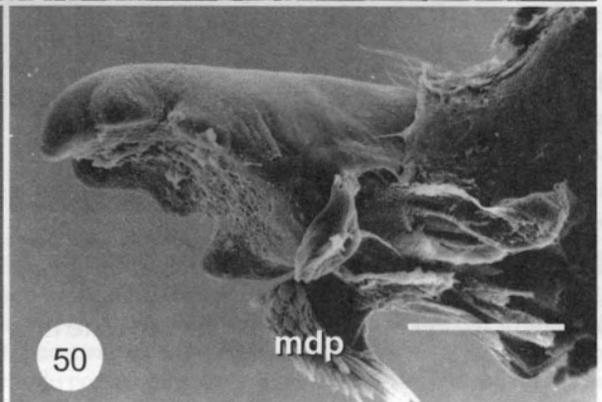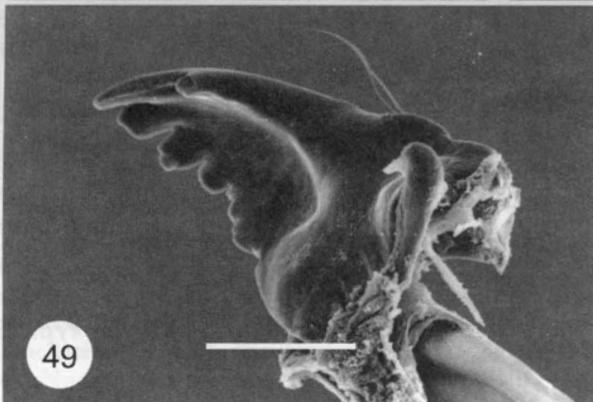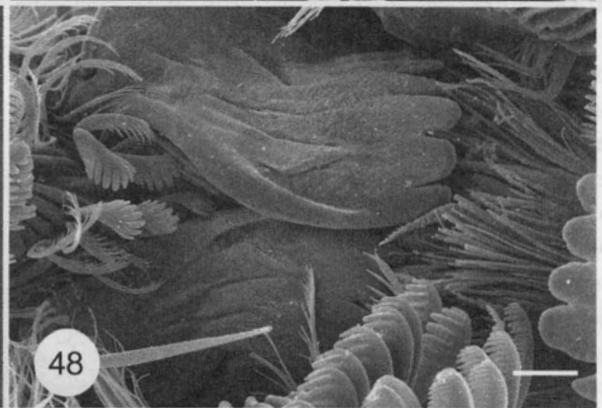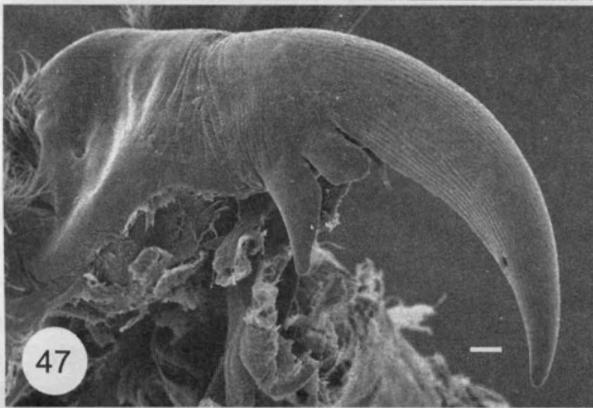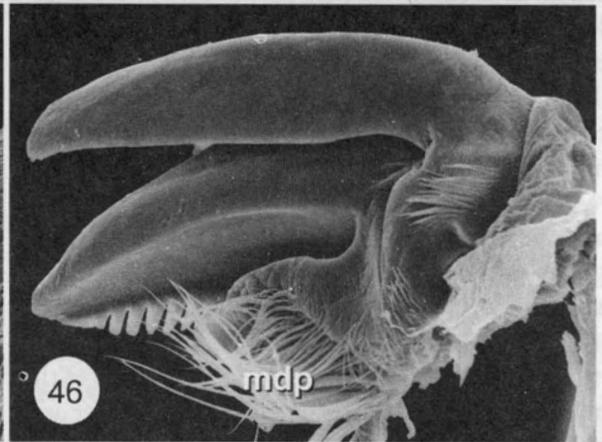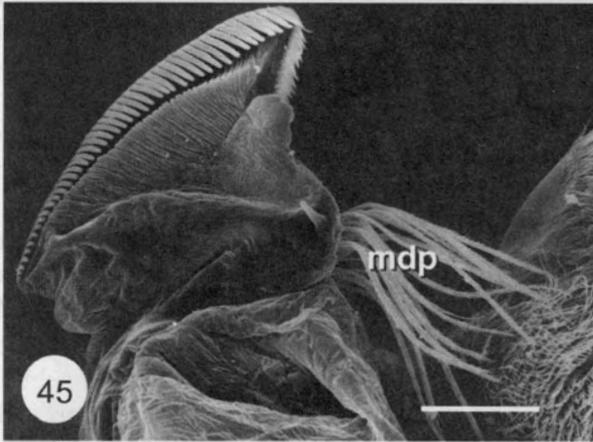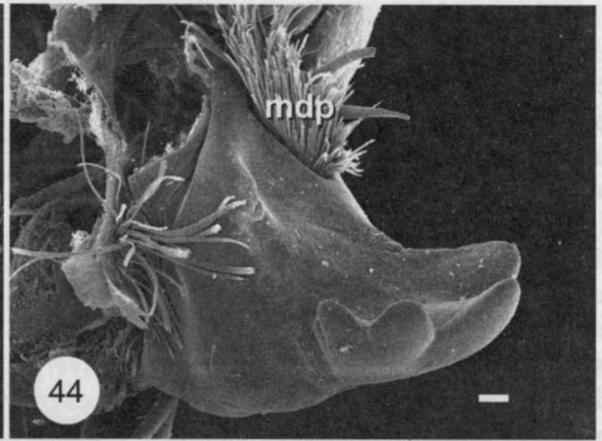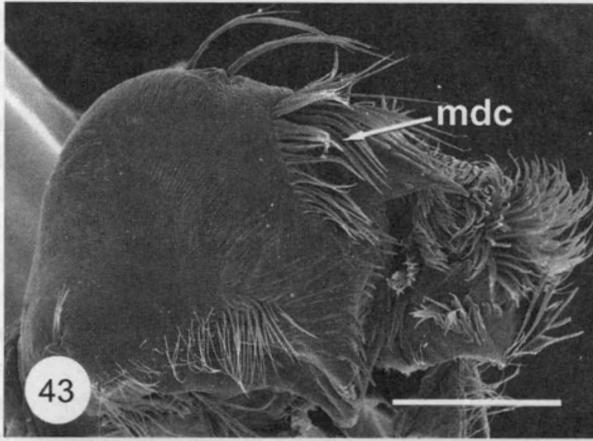
possess highly musculated walls and are responsible for the passage of food particles into the anterior digestive tract.

In the larvae of many nematocerous Diptera, the pharynx is a complex filtering structure. A **pharyngeal filter** occurs in larvae of Tanyderidae (Anthon 1988), Ptychopteridae, Thaumaleidae, Dixidae, Culicidae (Borkent et al. 1987), Blephariceridae (Anthon and Lyneborg 1968), Axymyiidae (Wood 1981), Scatopsidae, Trichoceridae, and Anisopodidae (Anthon 1943a), but it is absent in Corethrellidae, Chaoboridae, Ceratopogonidae, Simuliidae, Chironomidae (Wood and Borkent 1989), Deuterophlebiidae (Courtney 1991), Bibionomorpha (*sensu* Wood and Borkent 1989), all Psychodidae except Psychodinae (Quate and Vockeroth 1981), and all Tipulidae except *Ula* Haliday (Sinclair 1992). Although absent in outgroups, a pharyngeal filter could be part of the Diptera groundplan (Oosterbroek and Courtney 1995). If this interpretation is correct, the structure has been lost secondarily in many lineages. Although the filtering devices of larval nematocerans and brachycerans could be homologous, comparative morphology suggests that they are derived from different structures and, thus, nonhomologous. The relative position of the frontal ganglion, which demarcates the boundary between the cibarium and pharynx (Snodgrass 1935), suggests that the ne-matoceran filter is pharyngeal in origin (Cook 1944; Snodgrass 1959; Ameen 1969) whereas the brachyceran filter is cibarial (see later). Additional studies of both groups are needed to resolve this potentially informative phylogenetic character.

The structure and operation of the pharyngeal filter are similar across nematocerous groups, with the filtering mechanism described as follows "Contraction of the dilator muscles inserted on the dorsal walls of the cibarium and pharynx, together with closure of the esophagus, enlarges the pharynx, thereby creating a negative pressure that sucks in the water which contains the food particles. The opening to the pharynx is then constricted and the intrinsic muscles in the pharynx are contracted. This action creates sufficient pressure to force the water back through the constriction. During expulsion, the water passes through a filter formed by dense, comblike fimbriations that retain the very fine food particles" (Teskey 1981a: 73).

Pumping and filtration are accomplished through the action of several dilators inserted on the walls of the cibarium and pharynx. In the larvae of most nematocerous Diptera, these muscles originate on the frontoclypeal apotome. The egg burster of first-instar larvae appears to be operated by certain of these muscles (Courtney 1990a).

Brachycera

General discussion of groundplan and common features. The head capsules of larval Brachycera are reduced in sclerotization and partially invaginated into the prothorax. The posterior elements of the head capsule are elongate and form an internalised structure, with a tendency toward retraction of the entire head capsule into the thorax (Woodley 1989). These posterior elements include a single dorsal plate and elongate tentorial rods. The mouthparts are directed anteriorly and comprised of sickle-shaped mandibles moving in a vertical plane. The mandibles are subdivided into two components, with the apical hook articulated to the basal sclerite. Mandibular movement and configuration, and elongation of the head capsule posteriorly into the thorax are considered groundplan synapomorphies of the Brachycera (Woodley 1989; Sinclair 1992).

Figs 4.43–50. Scanning electron micrographs of larval nematocerans, mandibles. **43–46**: adoral view: **43**: *Bittacomorpha* sp. (Ptychopteridae); **44**: *Protanyderus* sp. (Tanyderidae); **45**: *Deuterophlebia* sp. (Deuterophlebiidae); **46**: *Bibiocephala* sp. (Blephariceridae). **47**: *Hexatoma* sp. (Tipulidae), oblique-aboral view. **48**: *Androprosopa* sp. (Thaumaleidae) apical teeth, aboral view. **49**: *Antocha* sp. (Limoniidae), adoral view. **50**: *Tipula* sp. (Tipulidae), adoral view (abbreviations: mdc: mandibular comb, mdp: prostheca; scale bars: 10μm (Figs 44, 47–48), 40μm (Figs 45–46), 100μm (Figs 43, 49–50)).

Fig. 4.51. Diagrammatic representation of the shift in mandibular rotation in larval Diptera (abbreviations: econ: epicondyle, frcly ap: frontoclypeal apotome, hcon: hypocondyle, lr: labrum, md: mandible, tph: tentorial phragma) (adapted from Teskey 1981a).

The cibarium of larval Brachycera is little differentiated from the pharynx and greatly elongated compared with the condition in nematocerous Diptera (Cook 1949; Roberts 1969a). This elongation is apparently related to the development of a cibarial pump with large cibarial muscles that attach to the frontoclypeal apotome. The long cibarial pump is thus an autapomorphy of the Brachycera. All known larvae of Xylophagomorpha, Tabanomorpha (incl. Vermileonidae), Asiloidea, and Empidoidea are predators. Larvae of these lineages lack any type of filter apparatus. Among the lower Brachycera, larvae of only the Stratiomyomorpha and the dolichopodid *Thrypticus* Gerstaecker are known to be non-predacious. Stratiomyomorpha have apparently evolved a cibarial filter independently from the Cyclorrhapha. If a pharyngeal filter is part of the groundplan of Diptera (Oosterbroek and Courtney 1995) or some higher nematoceran clade inclusive of the Brachycera, the absence of this structure in orthorrhaphous Diptera could represent a groundplan apomorphy of the Brachycera (Sinclair 1992). Resolving this hypothesis will require further investigation of nematocerous Diptera and Brachycera, particularly regarding putative nonhomology of the nematoceran pharyngeal filter and higher-brachyceran cibarial filter. Additional groundplan synapomorphies of the Brachycera include the absence of both premandibles and an anteriorly serrated postmentum (Sinclair 1992; but see Oosterbroek and Courtney (1995) for alternative interpretation of latter feature).

Despite claims to the contrary (Griffiths 1994), we continue to view the mouthhooks of Brachycera larvae as mandibular in origin. Griffiths (1994) proposed that either the mandible was lost in all Brachycera or the mandible was lost in Eremoneura. However, two morphological landmarks argue strongly in favour of the mandibular origin of brachyceran mouthhooks. First, there is a campaniform sensillum near the epicondyle on the adoral surface of the basal sclerite of the Brachycera mouthhook. This sensillum occurs in a similar position on the mandible of Nannochoristidae (Mecoptera) and many nematocerous Diptera, and led Sinclair (1992) to conclude that

this feature is a groundplan plesiomorphy of Diptera. Second, the number of apodemes arising on the mouthhooks confirms their mandibular origin. In Mecoptera, Siphonaptera, and nematocerous Diptera, the maxilla possesses at most a single apodeme (Matsuda 1965). If the mouthhooks are maxillary in origin, the three apodemes in orthorrhaphous Brachycera (Figs 62, 69–70) would require the gain of two apodemes. Furthermore, if mandibles were lost in Eremoneura, at least one additional muscular apodeme must have been gained. Based on this evidence, it is much more parsimonious to consider that both mandibles and maxillary structures are part of the Brachycera groundplan.

Orthorrhaphous Brachycera

Cranium – The larvae of lower Brachycera range from nearly eucephalic to a hemicephalic condition of articulated cephalic rods and tentorial arms. The cranium is mostly a concave plate, with the frontoclypeal apotome (Fig. 80) often weakly defined, and absent in Empidoidea (Fig. 79). The cranium is produced anterolaterally (gena) in Stratiomyidae and Xylophagidae, extending parallel to the mouthparts and labrum. In the former family, the inner anterior margin of these lateral lobes bears a comb of plumose setae (Fig. 68).

The posterior portion of the cranium is extended into the prothorax as a large shieldlike plate, normally continuous with the exposed anterior portion and with its lateral edges curved downwards (e.g., Stratiomyidae, Rhagionidae, Tabanidae, Bombyliidae s. lat. except *Glabellula* Bezzi) (Hennig 1973; Andersson 1974; Woodley 1989; Yeates and Irwin 1992). In families of the Asiloidea and Empidoidea, the posterior portion is weakly sclerotized and reduced to a pair of united **metacephalic rods** (manubrium) that are separated from the anterior portion by a distinct suture or articulation (Figs 71, 73, 76). In many taxa, the rod is more than twice the length of the exposed anterior section and extends nearly the length of the prothoracic segment. The lateral margin of the rod is thickened and darkly pigmented, giving it a paired appearance, and it often bears a posterior cleft (Sinclair et al. 1994). The rod is primitively unpaired, and secondarily divided in only some Empidoidea (Tachydromiinae, Dolichopodidae, and some Hemerodromiinae). The paired rods in Dolichopodidae are expanded apically (Fig. 79; Dyte 1967; Steyskal and Knutson 1981). In Therevidae, the apex of the metacephalic rod is spatulate, which is an autapomorphy of the family (Woodley 1989). Posterior metacephalic rods are present in Xylophagomorpha but are considered non-homologous to those in asiloids and empidoids. In many taxa, the rods are broad, triangular, and fused to the head capsule (Webb and Lisowski 1983). Slender, paired, widely separated articulated rods occur in *Xylophagus* Meigen (Fig. 60).

Tentorium – The tentorium is a prominent feature of lower Brachycera. The anterior tentorial arms are well-developed, projecting from the tentorial phragmata, and are major points of attachment of the adductor mandibular muscles in Rhagionidae and Tabanidae (Cook 1949; Roberts 1969a). The anterior arms normally arise opposite the mandibular condyle, project parallel to the cibarial plate, and are weakly fused laterally in some taxa. The posterior ends of the tentorial arms are usually not connected to the head capsule, except in some Tabanidae and Athericidae (Cook 1949). Anteriorly the rods are continuous with the tentorial phragmata (Figs 65–68) but weakly fused in some Rhagionidae (Roberts 1969a) and Pelecorhynchidae. The tentorial rods are fully articulated in Asiloidea (Figs 72, 74; exclusive of Bombyliidae, although weakly connected in *Glabellula* (Mythicomyiinae) (Andersson 1974)) and Empidoidea (Fig. 76; Teskey 1981a).

In Stratiomyidae, the tentorial arms are fused posteriorly with the cibarium, presumably to strengthen the grinding apparatus (Fig. 68). They remain free in Pantophthalmidae (Thorpe 1934). The tentorial arms are greatly shortened or absent in Apioceridae, Therevidae (Fig. 74), and

Fig. 4.51. Diagrammatic representation of the shift in mandibular rotation in larval Diptera (abbreviations: econ: epicondyle, frcly ap: frontoclypeal apotome, hcon: hypocondyle, lr: labrum, md: mandible, tph: tentorial phragma) (adapted from Teskey 1981a).

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Scenopinidae, and do not extend to the distal margin of the metacephalic rod (English 1947; Krivosheina 1980; Woodley 1989).

The **tentorial phragmata** (paraclypeal phragmata) are platelike invaginations of the dorsal sclerite formed by expansion of the anterior tentorial pits (Cook 1949). They meet anteriorly and fuse with the labrum. The tentorial phragmata are narrow and extend posteriorly as rodlike condyles, articulating with the tentorial rods in Apioceridae, Mydidae, and Therevidae (Fig. 74) (English 1947; Cook 1949; Toft and Kimsey 1982).

Ventral cranium – The lateral margins of the cranium, or genae, are widely separated by a large occipital opening, with the ventral face filled primarily by a large plate posterior to the labium (Fig. 66). This plate is often termed the submentum (Cook 1949; Teskey 1981a) or ventral sclerite (Roberts 1969a). Following the interpretation described in the Nematocera section, this plate is considered labial in origin but is termed the **ventral plate**. A narrow, toothed, ventral bridge (i.e., postmental or hypostomal bridge) is absent in Brachycera.

In Xylophagidae, the ventral cranium is continuous with the dorsal plate, forming a narrow conical head capsule and small opening for the mouthparts. The mouthparts are retracted within this uniquely shaped head capsule, which probably represents a derived condition.

Stemmata – Although larval eyes, or stemmata, often appear to be absent, light-sensitive cells probably occur in most larvae. Stemmata are described in several families of orthorrhaphous Brachycera, including Rhagionidae, Athericidae, Stratiomyidae and Therevidae (Constantineanu 1930; Roberts 1971a; Melzer and Paulus 1989). There are as many as five stemmata in the Diptera groundplan, but all are fused into a single unit in the Brachycera groundplan (Melzer and Paulus 1989). The stemmata are on the head capsule in Stratiomyomorpha, Xylophagidae, Therevidae, and *Heterotropus* Loew (Bombyliidae) (Melzer and Paulus 1989; Yeates and Irwin 1992). The convex, dome-shaped larval eyes of Stratiomyidae are on the lateral margin of the head capsule, occasionally on an anteriorly directed prominence.

The stemmata of Rhagionidae and most other brachycerans differ from Stratiomyidae, Xylophagidae, and most Nematocera in the absence of a lens or cornea (Roberts 1971a; Melzer and Paulus 1989). Furthermore, the stemmata are situated ventral to the sclerotized lateral margin of the head capsule, posterior to the tentorial phragma. Although the stemmata are deeply embedded beneath layers of cuticle, these layers are relatively translucent and permit penetration of light. The optic nerve is slender compared with that of nematocerous Diptera and presumably reflects the reduced importance of larval eyes, which apparently perceive only the direction of light. In addition, pigment grains are absent in all asiloids and Empidoidea (Melzer and Paulus 1989).

Antenna – The number and length of antennal segments are variable in the lower Brachycera, but the antennae of most groups are one-segmented, appearing as a small knob or buttonlike protuberance on the anterodorsal margin of the cranium near the outer mandibular condyle (hypocondyle) (Figs 60, 73). In Tabanidae (Figs 97–98) and Nemestrinidae, the antenna is usually three-segmented (Fuller 1938; Teskey 1969), retaining a single antennal muscle in the Tabanidae (Cook 1949). A two-segmented antenna occurs in Stratiomyidae, Pelecorhynchidae, Athericidae (Fig. 81), and certain Bombyliidae (*Heterotropus* and *Glabellula*) (Teskey 1970; Andersson 1974; Yeates and Irwin 1992; Webb 1995).

In Empidoidea, the antenna is positioned far forward, anterior to the hypocondyle (Fig. 79). The antennae of this lineage bear several apical

Figs 4.52–59. Scanning electron micrographs of larval nematocerans, maxillae. 52: *Protanyderus* sp. (Tanyderidae); 53: *Bittacomorpha* sp. (Ptychopteridae); 54: *Antocha* sp. (Limoniidae); 55: *Rhexoza* sp. (Scatopsidae); 56: *Deuterophlebia* sp. (Deuterophlebiidae); 57: Mycetophilidae sp.; 58: *Plecia* sp. (Bibionidae); 59: *Axymyia* sp. (Axymyiidae) (abbreviations: mxc: cardo, mxg: galea, mxl: lacinia, mxp: maxillary palpus; scale bars: 10μm (Figs 52, 55–57, 59), 100μm (Figs 53–54, 58)).
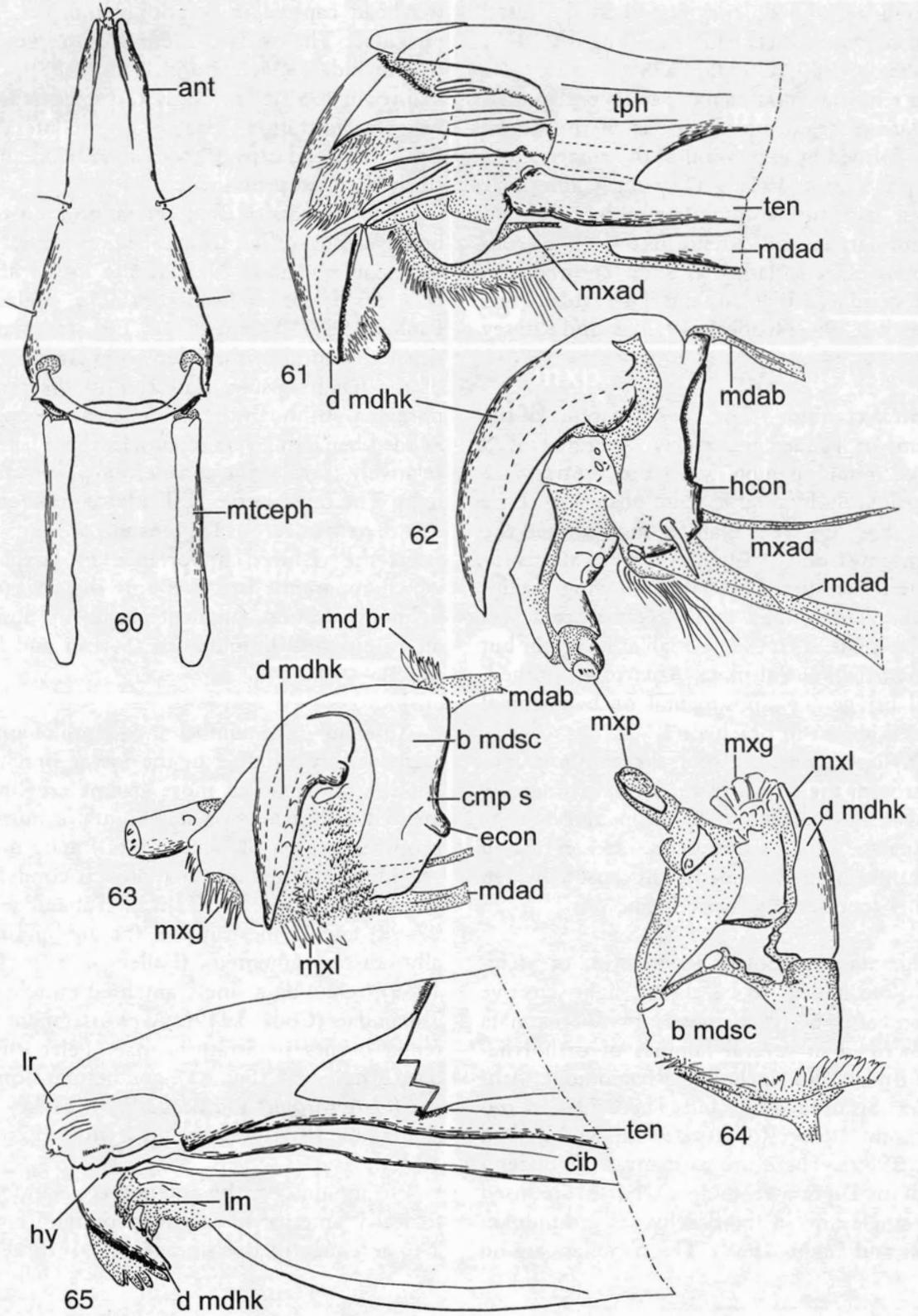
sensory pits of various length, occasionally lengthened into a pair of slender papillae (Vaillant 1952, 1953). The length of the apical segment, and position of the antenna (dorsal vs. apical) are useful characters in separating genera and subfamilies in Tabanidae and Stratiomyidae (Teskey 1969; Rozkošný 1982).

Labrum – The labrum is not clearly separated from the frontoclypeal apotome in orthorrhaphous Brachycera. It is narrow, laterally compressed, heavily sclerotized, strongly curved ventrally, and fused internally with the tentorial phragma, forming a rostrum between the mouthparts (Figs 72, 80–81, 88, 97–98). In some final-instar larval Bombyliidae, the labrum is hornlike and truncate (Berg 1940; Bohart et al. 1960), whereas in Empidoidea the labrum is upturned and pointed apically (Fig. 76; Vaillant 1952: fig. 7) . The labrum bears sclerotized teeth anteriorly in some Rhagionidae, and stout spines anterolaterally in Pelecorhynchidae (Fig. 88; Roberts 1969a; Teskey 1970; Mackerras and Fuller 1942; Krivosheina 1997a: Fig. 2.27.10). Premandibles are absent in the Brachyceran groundplan, but 'messorial' muscles are retained in some groups (e.g., Tabanidae: Cook 1949). Although appearing rigid, the labrum of some taxa can be moved, primarily through the action of compressor muscles (Cook 1949).

The posteroventral face of the labrum is sclerotized, forming an epipharyngeal plate (Figs 66–68). A shallow depression or labral channel is anterior to this plate and continuous with the cibarium. A row of ventrally directed spines, or labral comb, lines the external opening of the labral channel in some Rhagionidae (Fig. 65). This structure probably acts as a filter to remove large particles (Roberts 1969a).

First-instar larvae are poorly investigated in orthorrhaphous Brachycera; however, a few groups possess structures that could function as egg bursters. In these taxa, the putative egg burster forms a sawlike ridge near the apex of the head capsule (Irwin and Stuckenberg 1972: cranial crest). Although the orthorrhaphan egg-burster appears to be a labral structure, the fused nature of the labrum and frontoclypeal apotome does not preclude homology with the nematoceran egg-burster. Additional studies are needed on these and other structures of first-instar larvae.

Mandible – The mandible of lower Brachycera comprises two components: a pointed, heavily sclerotized **distal mandibular hook** and an inverted U-shaped **basal mandibular sclerite** with attached apodemes (Figs 62–64; Sinclair 1992). There are two points of articulation: the **epicondyle** (anterior), positioned midway on the inner vertical arm of the basal sclerite and articulating with the tentorial phragma, and the **hypocondyle** (posterior), situated at the posterolateral apex of the external arm of the basal sclerite and articulating with the cranium. The mandibles thus operate in a parallel fashion in a vertical plane.

The distal hook is articulated with the basal sclerite in the groundplan of Brachycera and rarely extends beyond the apex of the maxilla (Figs 62–63). The inner (adoral) surface of the hook is characterised by a lateral groove along its entire length (Figs 63, 75) and is termed the promuscis-type. When both hooks are juxtaposed, they form a sucking tube or food canal (Schremmer 1951). This groove is widespread in the lower Brachycera (Melin 1923; English 1947; Schremmer 1951; Ludwig et al. 1996) and possibly also in Empididae (Fig. 77). This feature

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Figs 4.60–65. Xylophagomorpha and Tabanomorpha, head capsules and mouthparts. 60–61: *Xylophagus reflectens* Walker (Xylophagidae), head capsule: 60: dorsal view, 61: longitudinal section, left mandible and maxilla removed. 62: *X. reflectens* Walker, left mandible, maxilla, aboral view. 63: *Symphoromyia* sp. (Rhagionidae), mandible, maxilla, adoral view. 64–65: *Symphoromyia* sp., head capsule: 64: anterior left side, dorsal view, 65: longitudinal section, left mandible and maxilla removed (abbreviations: ant: antenna, b mdsc: basal mandibular sclerite, cib: cibarium, cmp s: campaniform sensillum, d mdhk: distal mandibular hook, econ: epicondyle, hcon: hypocondyle, hy: hypopharynx, lm: labium, lr: labrum, mdab: apodeme for mandibular abductor, mdad: apodeme for mandibular adductor, md br: mandibular brush, mtceph: metacephalic rod, mxad: maxillary adductor apodeme, mxg: galea, mxl: lacinia, mxp: maxillary palpus, ten: tentorial arm, tph: tentorial phragma).
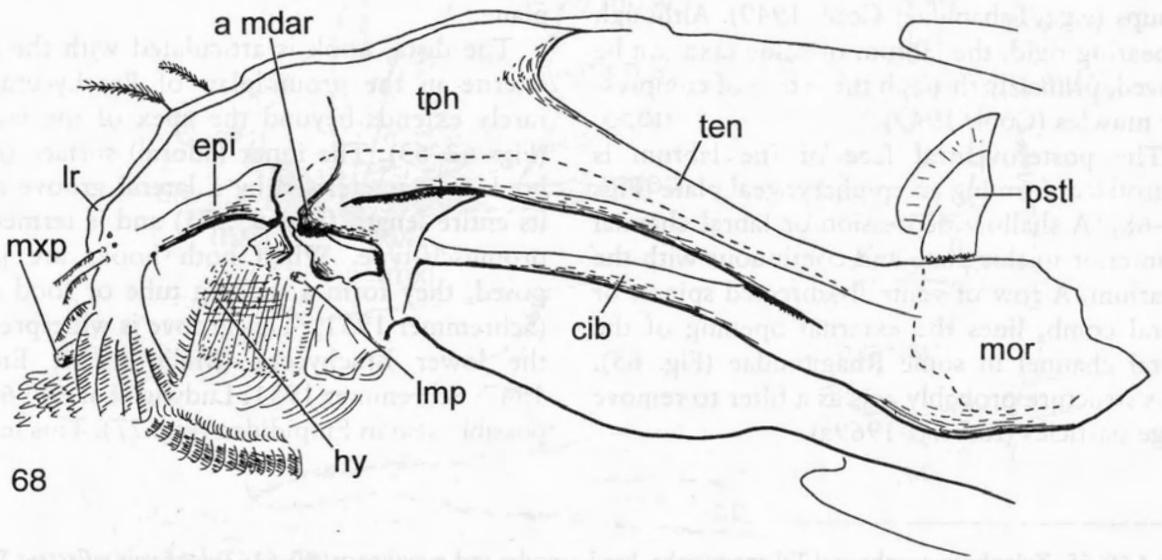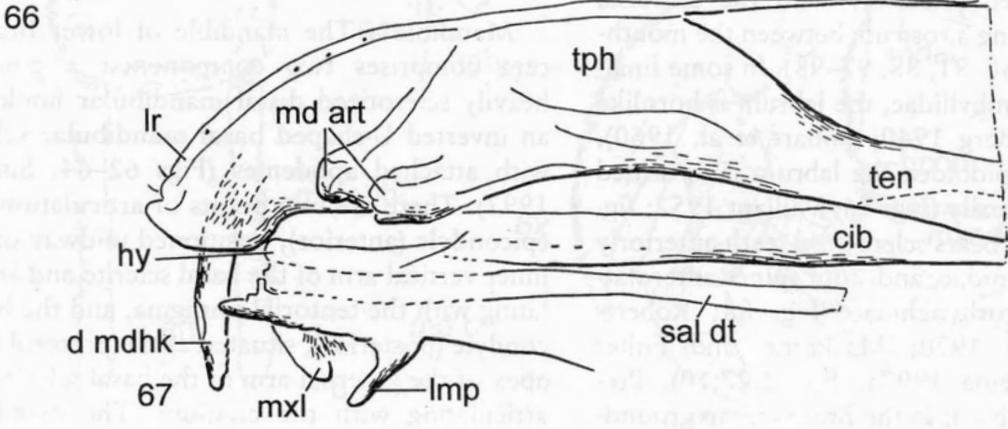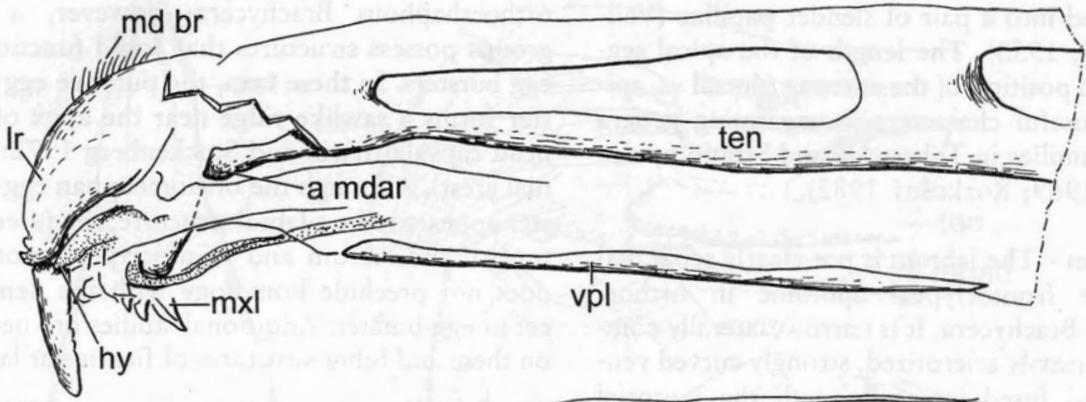
Figs 4.66–68. Mouthparts of Tabanomorpha and Stratiomyomorpha. 66: *Atherix lantha* Webb (Athericidae), longitudinal section, left mandible and maxilla removed. 67: *Hybomitra epistates* Osten Sacken (Tabanidae), longitudinal section, left mandible and maxilla removed. 68: *Euparyphus* sp. (Stratiomyidae), longitudinal section, left mandibular-maxillary apparatus removed (abbreviations: a mdar: anterior mandibular articulation, cib: cibarium, d mdhk: distal mandibular hook, epi: epipharynx, hy: hypopharynx, lmp: labial palpus, lr: labrum, md art: mandibular articulations, md br: mandibular brush, mor: mortar, mxl: lacinia, mxp: maxillary palpus, pstl: pestle, sal dt: salivary duct, ten: tentorial arm, tph: tentorial phragma, vpl: ventral plate).

probably represents the groundplan condition of the Brachycera. In addition, the distal hook often possesses a serrate posterior margin (Fig. 70), which prevents the hook from being dislodged from prey.

The inner lateral groove is absent in Tabanidae, Athericidae, and Pelecorhynchidae (Tabanomorpha), replaced by an internal **poison canal** that conveys poison from special glands (Woodley 1989; Sinclair 1992). The distal end of the mandible possesses a subapical opening (Figs 70, 83, 89, 96, 98) and upon penetration, poison is injected to immobilise the prey. The poison gland is located near the anterior margin of the salivary pump. The injected substance is believed to be paralytic (Schremmer 1951) because, upon insertion of the mandibles, the arthropod prey makes one or two violent movements before becoming quiescent within a few seconds (Teskey 1969; Thomas 1975). In small vertebrate prey, the poison appears to be slow-acting (Jackman et al. 1983).

The basal sclerite has often been misidentified and labeled as the cardo (maxilla), but its homology is readily determined by several landmarks. Mandibular apodemes are easily observed in dissected specimens and include the **abductor apodeme** inserted on the posterodorsal margin and the **adductor apodeme** inserted partially on the ventral margin of the inner arm of the basal sclerite and partially on the base of the mandibular hook (Figs 62–63, 69–70; Schremmer 1951; Sinclair 1992). The abductor and adductor muscles originate partially on the dorsal plate (cranium) or metacephalic rod and partially on the tentorial arm (Roberts 1969a). Another landmark is the presence of a **campaniform sensillum** (pore, mandibular ring, mandibular pit organ) on the adoral surface of the basal sclerite, near the epicondyle (Figs 63, 69, 75; Sinclair 1992). This sensillum, a mechanoreceptor that perceives strains in the exoskeleton, is widespread in the Brachycera and Nematocera and probably represents a groundplan feature of Diptera.

The base of the inner wall of the basal sclerite sometimes bears a brush of setae or spines along the ventral margin of the adductor apodeme (Figs 61–62). In some Rhagionidae, this region bears saw-like teeth (saw sclerite) that appear to lacerate the cuticle and tissues of the prey while the distal hook maintains its grip (Schremmer 1951; Roberts 1969a). A somewhat less stout setose or spinous margin occurs in Pelecorhynchidae (Mackerras and Fuller 1942; Teskey 1970).

The mandibles of larval Tabanomorpha possess a distinctive **mandibular brush** (Hennig 1973; Teskey 1981a; Sinclair 1992) comprised of posteriorly directed, sclerotized spines at the base of the abductor apodeme on the posterior margin of the basal sclerite (Figs 63, 70, 81–82, 88, 97–98). At rest, the spines are concealed beneath a cuticular covering. Upon adduction of the mandible, the spines are exposed and spread, thereby gripping the substrate. Following initial puncture of the prey, this brush possibly assists in further penetration of the head by clinging and maintaining its position within the body of the prey. In Rhagionidae, the mandibular brush arises from the cuticular membrane, whereas in Pelecorhynchidae, Athericidae, and Tabanidae, the brush attaches to the apex of an articulated rod (Fig. 70; Sinclair 1992). The hypocondyle also is greatly expanded laterally in Tabanidae and Athericidae.

The arms of the basal sclerite are closely approximated in Xylophagidae, with both condyles articulated to the tentorial phragma, probably due to retraction of the mouthparts within the head capsule (Fig. 60). In Acroceridae, the components of the mandible appear to be secondarily fused into a single unit (Sinclair 1992). The mandibles of Nemestrinidae also appear undivided, but this modification requires further study. Another unusual modification of the mandible occurs in the Stratiomyomorpha, in which the distal hook is lost (see discussion of Mandibular-maxillary apparatus). In most known Empidoidea larvae, including Dolichopodidae, the mandible is subdivided into four or six components, which is an autapomorphy for the superfamily (Dyte 1967; Sinclair 1992). In these groups, the mandible comprises a distal hook, two connecting sclerites, and a basal sclerite (Fig. 77). Two additional connecting sclerites are present in larval Hemerodromiiinae and Clinocerinae (Fig. 78; Sinclair 1992). Another modification in the Ere-
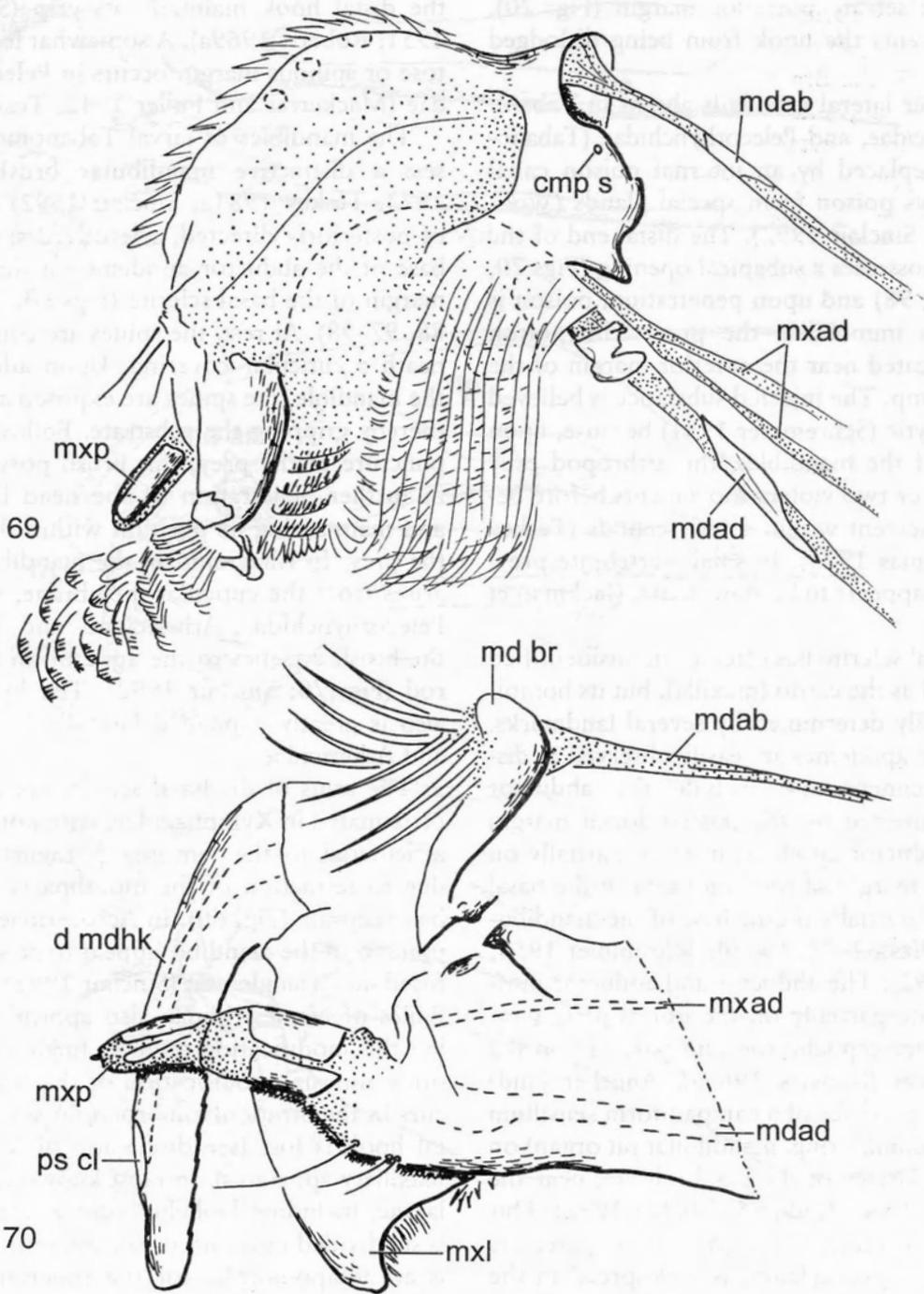
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moneuran groundplan is a shifting of the epicondyle to the ventral margin of the inner arm of the basal sclerite (Sinclair 1992).

Ontogenetic changes in mandibular structure have been reported in some families. In Nemestrinidae, the distal mandibular hook is slender and pointed in third-instar larvae, but shovel-shaped, projected divergently, and with a convex dorsal surface in final-instar larvae (Fuller 1938; Greathead 1958).

Maxilla – There is much confusion concerning homologies of the maxilla because its components are not always clearly distinguishable and what is often labelled as the cardo is actually of mandibular origin (Sinclair 1992; see discussion of Mandible). The palpus is the most prominent element laterally or apically (Figs 62, 64, 70, 72). It is variable in length, number of segments, position, and relative size, ranging from robust and three-segmented in Rhagionidae and Tabanidae to short and one-segmented in many other families. The palpus is elongate and slender in Athericidae (Fig. 81) and button-like in Empidoidea (Fig. 79). The palpi of Vermileonidae are prominent, broad, and equipped with mechanoreceptors to aid in determining the position of prey (Ludwig et al. 1996).

In Xylophagidae, Rhagionidae, and asiloid families, the lacinia forms a sheath or groove appressed against the distal mandibular hook, and often bears a notch for the apical mandibular tip. The apex of the lacinia is trimmed with setae in Rhagionidae and Xylophagidae (Fig. 63) and bears toothlike processes in Athericidae (Fig. 83; Schremmer 1951; Webb 1995). Below the groove is a pre-oral cavity lined with ridges and fine setae (Figs 61, 72, 75). External to the lacinia, the galea projects anteriorly and bears tooth-like processes in Rhagionidae (Fig. 64) but is a simple lobe in most lineages (see later). The dorsal surface of the maxilla bears a small, narrow sclerite or stipes extending to the mandibular hypocondyle. Cook (1949) labelled this sclerite the cardo in Therevidae.

The membranous surface of the maxilla is attached to the anterior surface of the external arm of the basal mandibular sclerite. Thus, both the mandible and maxilla move essentially as a unit, mediated by the mandibular muscles. In orthorrhaphous Brachycera, the maxilla is operated only by the maxillary adductor muscle (Cook 1949), which inserts on a long, slender apodeme attached to the posterior border of the lacinia (Figs 62, 70).

The apical maxillary component is strongly sclerotized and stout, somewhat scoop-shaped or toothed in Apioceridae, Asilidae (Figs 72–73), and some fourth-instar larvae of Bombyliidae (Melin 1923, erroneously labelled mandible; Berg 1940; Bohart et al. 1960; Toft and Kimsey 1982). This structure is generally considered to be the stipes but is probably homologous to the galea described in Rhagionidae (Schremmer 1951). The galea of Vermileonidae is largely membranous, bearing small, subapical mechanoreceptor(s) (Ludwig et al. 1996). Sensory pits are also present in Asilidae (Fig. 73) and Apioceridae (English 1947). These lobes might assist in movement through soil, the detection of prey, and in determining a suitable location for penetration of the mandibular hooks (Engel 1929). The maxilla is reduced to an elongate, primarily membranous lobe in Empidoidea, which is probably a synapomorphy for the Eremoneura (Sinclair 1992).

Mandibular-maxillary apparatus – The arrangement in which the mandible and maxilla of lower Brachycera is partially or entirely fused is known as the **mandibular-maxillary apparatus**. This condition is most extensive in Stratiomyomorpha, especially Pantophthalmidae (Sinclair 1992). The mandibles are not lost in this infraorder, but the distal portion (i.e., distal hook) is replaced by maxillary structures (Figs 69, 93), including the palpus. This fused apparatus is unique among Diptera. The basal sclerite possesses the same landmarks used to determine homology of the basal mandibular sclerite (Sinclair 1992). The maxillary component is fused to the outer, apical margin of the basal segment, with the maxillary apodeme passing between the basal sclerite, guided by a pulleylike structure on the mandibular base (Fig. 69; Schremmer 1951). The apparatus is set in motion by the two mandibular muscles, which move the basal seg-

ment up and down around a horizontal axis, and by the maxillary adductor, which pulls the distal segment towards the base. The distal segment is abducted by contraction of the mandibular abductor muscle. In both Stratiomyomorpha and Xylophagomorpha (most likely independently), the mandibular condyles are internal, with the hypocondyle articulating with the inner genal face.

Labium – The labium in lower Brachycera is highly reduced, consisting of a pair of small labial palpi ventral to the hypopharynx, hidden within the mouthparts (Fig. 68). Compared with most lower Brachycera, the labium of Empidoidea is highly modified and characterised by a distinctive V-shaped labial sclerite (Fig. 76; Vaillant 1952; Sinclair 1992). This sclerite is in the form of sclerotized rods with tooth-like processes on the apex of the labium. The salivary duct passes through the V-shaped rods. Reduced labial palpi are external, on the ventral membranous surface of the head region.

Table 4.1. Commonly used terms for elements of the cephaloskeleton of the Cyclorrhapha.

Terms used in text	Alternative terms
cephaloskeleton	head skeleton, cephalic skeleton, cephalopharyngeal skeleton, buccopharyngeal apparatus, cephalopharyngeal sclerites, cephalopharyngeal apparatus, buccal armature, pharyngeal skeleton, mouthparts
pseudocephalon, cephalic region	head segment, cephalic segment, pseudocephalic segment
cephalic lobes	antennomaxillary lobes
antenna	dorsal organ
maxillary palp	terminal organ
maxillary sense organ	ventral organ
labial lobe	ventral lobe
cirri	facial combs
Bolwig's organ	visual cells, stemmata, photoreceptor organ
optic depression	ocular depression
mouthhooks	oral hooks, labial sclerites, lateral hooks, mandibles, mandibular sclerites, maxilla
dental sclerite	dentate sclerite, ectostomal sclerite
intermediate sclerite, H-shaped sclerite	hypostomal sclerite, hypopharyngeal sclerite or arch, labial sclerite, labiohypopharyngeal sclerite
epistomal sclerite	epistomal plate, epipharyngeal sclerite
parastomal bars	parastomal sclerites, lateralgräten, atrial rod
basal sclerite	pharyngeal sclerite, basal piece, lateral plates, paraclypeal phragma, basal plates, lateral pharyngeal sclerite, posterior lateral plates, thecal sclerite
vertical plate	tentorial phragma
cornua	wings, processes
dorsal cornu	dorsal wing, clypeofrontal phragma
dorsal bridge	dorsal thecal arch
ventral cornu	ventral wing, cibarial phragma, ventral arm
cibarial pump	pharyngeal pump
ventral cibarial ridges, T-ribs, Y-ribs	ventral pharyngeal ridges

Hypopharynx – The hypopharynx forms the floor of the cibarium in generalised insects (Snodgrass 1935) and is greatly lengthened in the groundplan of the Brachycera (see cibarium below). A slender, anterior, articulated, hypopharyngeal sclerite often extends beyond the tentorial phragma (Figs 65–68, 72) and, in some taxa (e.g., Stratiomyidae), could act as a valve. In some Rhagionidae, the apex of the hypopharynx bears a series of recurved, dorsolateral teeth below the epipharyngeal plate and probably aids in the mastication of semiliquid food. In Tabanidae, the hypopharynx is stout and well-developed (Figs 67, 98). The salivary pump is also enlarged in this family and bears a sclerotized dorsal plate (Cook 1949; Teskey 1969).

Cibarium-Pharynx – The cibarium can be separated from the pharynx by the position of dilator muscles relative to the frontal ganglion. Muscles anterior to the frontal ganglion are cibarial and those posterior are pharyngeal (Cook 1949; Roberts 1969a). Compared to the condition in nematocerous Diptera, the cibarium is greatly lengthened and sclerotized ventrally, with a series of muscles attached dorsally to the membranous roof. Contraction of these muscles makes the cibarium function as a suction pump, drawing in semiliquid material (Cook 1949; Teskey 1981a). In many orthorrhaphous Brachycera, the floor of this structure is plate-like and supported by or fused laterally to the tentorial rods (Figs 67–68).

In orthorrhaphous Brachycera (incl. Empidoidea), a cibarial filter is present only in Stratiomyomorpha (Sinclair 1992) and is presumably not homologous to the "pharyngeal" filter of many nematocerous Diptera. The filter and posterior grinding mill occur in all families of the Stratiomyomorpha (Fig. 68; Sinclair 1992). The floor of the cibarium bears two longitudinal ridges, thereby dividing the filter into three chambers (Vaillant and Delhom 1956). The longitudinal ridges bear setae that function as a filtering comb when water is forced through into lateral draining troughs. Excess water then collects in draining canals that lead to a common ventral exhalant orifice. The grinding mill lies posterior to the frontal ganglion, and thus represents the pharynx (Roberts 1969a). The roof of the pharynx is modified into a pestle and the floor is thickened and forms a bowllike mortar.

Cyclorrhapha

The "acephalic" head of larval Cyclorrhapha is one of the most dramatically modified tagmata in all insects. How it is derived from the head of nematocerous Diptera and orthorrhaphous Brachycera is easiest to understand if data from different sources are considered. These data include (1) traditional morphological study of the soft and sclerotized parts of the cyclorrhaphan head, including musculature and neuroanatomy; (2) embryological information, including results of fate mapping studies of the embryonic cells from the different head segments; and (3) functional considerations. This approach is adopted here, but it has several obvious shortcomings. First, embryological study ends at the onset of the first-instar larva, wheras traditional morphological treatments focus on the last instar (= third instar). Sometimes it proves difficult to reconcile information from both sources. Second, there is limited information on phylogenetically interesting basal groups of Cyclorrhapha (e.g., Platypezidae). This paucity of information applies to traditional morphological study but is even more pronounced for embryology, where only derived Schizophora have been studied in detail (e.g., *Drosophila melanogaster* Meigen, *Calliphora vicina* Robineau-Desvoidy, *Bactrocera tryoni* Froggatt).

Development. It is almost impossible to understand the topology of the cyclorrhaphan head without basic knowledge of cyclorrhaphan head development. We therefore summarise the three most important movements of the head segment primordia during embryogenesis (see Jürgens et al. 1986; Jürgens and Hartenstein 1993; Younossi-Hartenstein et al. 1993). (1) Most of the ventral and lateral material from the labral, in-

tercalary, and gnathal head segments is involuted into the primary larval-mouth opening. Other material from the same segments remain external (e.g., sensory structures such as the maxillary palpus). The involution creates a new cavity anterior to the cibarium, the so-called atrium. (2) Close to the border between the thorax and head, a fold consisting of most of the acron and the dorsal material of all head segments sinks in and grows over to form an epidermal sack that comes to rest dorsally over the cibarium. This fold results in two exterior openings of the embryonic head, one leading into the dorsal pouch and another into the atrium. These openings are separated by the so-called clypeolabral lobe. (3)

The latter is now withdrawn into the embryonic head, thereby creating a connection between the opening of the dorsal pouch and the opening of the atrium and thus reducing the number of external head openings to one. Simultaneously, the non-involuted lateral regions of the head segments come to lie at the apex of the embryonic head. These movements explain the position and close proximity of the maxillary palpus to the antenna. The result of all three movements is a new interconnected system of internal epidermal folds that in sagittal section resemble the shape of the cephaloskeleton of Cyclorrhapha. These folds secrete the mouthhooks and cephaloskeleton that are so characteristic of the higher Diptera.

Table 4.2. Number and distribution of larval prolegs in various Diptera (adapted from Hinton 1955; Teskey 1981a).

	Thorax			Abdomen								
	1	2	3	1	2	3	4	5	6	7	8	„9"
Ptychopteridae	–	–	–	2	2	2	–	–	–	–	–	–
Tanyderidae	–	–	–	–	–	–	–	–	–	–	–	2
Dixidae	–	–	–	2	0–2	–	–	–	–	–	–	–
Corethrellidae[1]	2	–	–	–	–	–	–	–	–	–	–	–
Chironomidae	2	–	–	–	–	–	–	–	–	–	–	2
Ceratopogonidae	0–2	–	–	–	–	–	–	–	–	–	–	1–2
Thaumaleidae	1	–	–	–	–	–	–	–	–	–	–	1
Simuliidae	1	–	–	–	–	–	–	–	–	–	–	1
Blephariceridae[1]	–	–	–	2	2	2	2	2	2	2		
Deuterophlebiidae	–	–	–	2	2	2	2	2	2	2	–	–
Nymphomyiidae	–	–	–	2	2	2	2	2	2	2	–	2
Tipulidae (Dicranota)	–	–	–	–	–	2	2	2	2	2	–	–
Tabanidae[2]	–	–	–	6–8	6–8	6–8	6–8	6–8	(6–8)	(6–8)	–	–
Athericidae	–	–	–	2	2	2	2	2	2	2	1	–
Vermelionidae	–	–	–	1	–	–	–	–	–	–	–	–
Therevidae[3]	–	–	–	–	–	–	–	–	–	–	2	–
Scenopenidae[3]	–	–	–	–	–	–	–	–	–	–	2	–
Asilidae												
Laphriinae	–	–	–	6–8	6–8	6–8	6–8	6–8	6–8	–	–	–
Dasypogoninae	–	–	–	2	2	2	2	2	2	(2)	–	–
Empididae (several)	–	–	–	(2)	2	2	2	2	2	2	2	–
Syrphidae (Eristalinae)	2	–	–	2	2	2	2	2	2	–	–	–
Ephydridae (several)	–	–	–	2	2	2	2	2	2	2	2	–
Muscidae (Limnophora)	–	–	–	–	–	–	–	–	–	–	2	–

1 First-instar larvae of Chaoboridae (Borkent and McKeever 1990) and Blepharicerinae (Courtney 1991).
2 Usually with creeping welts, but these sometimes in the form of prolegs (see text).
3 Anal division with retractile lobes bearing pairs of long bristles.

Topology and use of terms. A few remarks are necessary to explain the use of the terms "mouth opening", "anterior/posterior", and "internal/external". Because the ventral portions of the head segments are invaginated, the order of segments is reversed in some areas of the head. For example, parts of the mandibular segment are posterior to the maxillary segment. We use the terms anterior/posterior to describe the situation after the involution. The invagination also obscures the meaning of "mouth opening" and "internal/external". The functional mouth opening of basal Diptera leads into a cibarium formed by the epipharynx dorsally and the hypopharynx ventrally (Roberts 1969a). In cyclorrhaphan larvae, the cibarium is withdrawn into the thorax,

Table 4.3. Number and retractability of anal papillae in Diptera. For taxa demonstrating more than one state, the presumed ancestral state is presented first, followed in parentheses by the hypothesized derived state(s); n.a., not applicable (modified from Courtney 1991).

Family	# A. p.	Retract.	Reference(s)
Tipulidae	4(2,6,8)	(+)	Brindle 1957; Byers 1983
Blephariceridae	4	(−)	Courtney 1991
Deuterophlebiidae	5	(−)	Courtney 1991
Nymphomyiidae	4	(+)	Courtney 1994
Psychodidae	2(0,6,8)	(+?)	Satchell 1953; Hogue 1973; Quate and Vockeroth 1981
Trichoceridae	4	(+)	Könnemann 1924; Karandikar 1931
Perissommatidae	4?	(+?)	Colless 1962
Anisopodidae	0	(n. a.)	Hennig 1973
Scatopsidae	0	(n. a.)	Hennig 1973
Synneuridae	0	(n. a.)	Hennig 1973
Tanyderidae	4	(−)	Courtney 1991
Ptychopteridae	2	(-?)	Courtney 1991
Dixidae	4	(+)	Peters 1981; Wood and Borkent 1989
Chaoboridae	4	(−)	Hennig 1973; Wood and Borkent 1989
Corethrellidae	4	(−)	Hennig 1973; Wood and Borkent 1989
Culicidae	4(2)	(−)	Hennig 1973; Wood and Borkent 1989
Thaumaleidae	4	(+)	Thienemann 1909
Simuliidae	3	(+)	Rubtsov 1969
Chironomidae	4(2,6)	(−)	Oliver 1981; Wood and Borkent 1989
Ceratopogonidae	4	(+)	Lawson 1951; Wirth and Grogan 1979
Axymyiidae	2,4	(−)	Mamaev and Krivosheina 1966; Wood 1981
Pachyneuridae	0	(n. a.)	Hennig 1973
Bibionidae	0	(n. a.)	Hennig 1973
Mycetophilidae*	0	(n. a.)	Madwar 1937; Matile 1990
Sciaridae	0	(n. a.)	Madwar 1937
Cecidomyiidae	0	(n. a.)	Hennig 1973
Brachycera**	0	(n. a.)	Various sources

* Exceptions include *Keroplatus* and *Sciophila*, both with four, retractable anal papillae (Plachter 1979; Matile 1990).
** Exceptions include the Pantophthalmidae (Thorpe 1934), certain Syrphidae (Vockeroth and Thompson 1987) and perhaps Cryptochetidae (see discussion and Fig. 152).
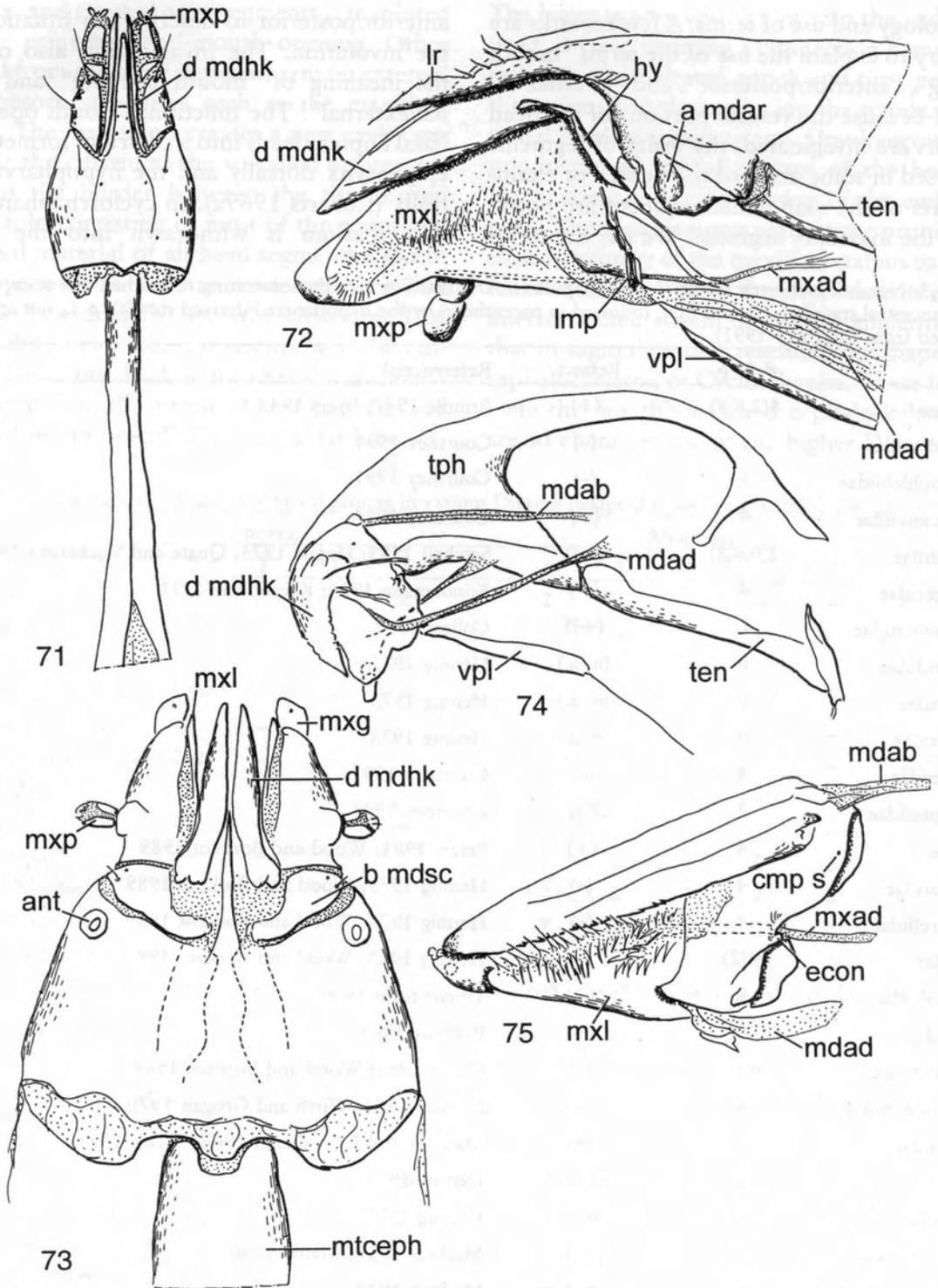
Figs 4.71–75. Mouthparts of Asiloidea. 71: *Mydas clavatus* (Drury) (Mydidae), head capsule, dorsal view. 72: *Promachus*? sp. (Asilidae), longitudinal section, left mandible and maxilla removed. 73: *Promachus*? sp., head capsule, dorsal view. 74: *Thereva furcata* Loew (Therevidae), longitudinal section, left mandible and maxilla removed, metacephalic rod not shown. 75: *Mydas clavatus* (Drury) (Mydidae), right mandible, maxilla, adoral view (abbreviations: ant: antenna, a mdar: anterior mandibular articulation, b mdsc: basal mandibular sclerite, cmp s: campaniform sensillum, d mdhk: distal mandibular hook, econ: epicondyle, hy: hypopharynx, lmp: labial palpus, lr: labrum, mdab: apodeme for mandibular abductor, mdad: apodeme for mandibular adductor, mtceph: metacephalic rod, mxad: maxillary adductor apodeme, mxg: galea, mxl: lacinia, mxp: maxillary palpus, ten: tentorial arm, tph: tentorial phragma, vpl: ventral plate).

thereby creating a new cavity anterior to the cibarium. The old mouth opening and some of the previously external head elements shift internally and a new "mouth opening" is created. We refer to the latter as the cyclorrhaphan mouth opening, and consider all parts of the functional alimentary canal posterior to this opening as being internal.

External Morphology. The Cyclorrhapha head is called **acephalic** because it lacks external sclerotizations (but see larval Lonchopteridae: de Meijere 1900). The outer, membranous part of the head is called the **pseudocephalon** (Fig. 102; Hewitt 1910; Lohs-Schardin et al. 1979) or **cephalic region** (Meier 1996). Viewed dorsally or ventrally, the pseudocephalon is bilobate anteriorly consisting of two **cephalic lobes** (Fig. 104). Each lobe carries at its tip two sense organs, the **antenna** and **maxillary palpus** (Figs 102, 104, 115–116; Bolwig 1946; Richter 1962; Kankel et al. 1980; Singh and Singh 1984; Jürgens et al. 1986). Both sensory organs are in some Syrphidae found on a single long projection (Roberts 1970). The antenna has a bilobed appearance with the distal **dome** resting on a **basal ring** (Fig. 117). Homology between the larval and adult antennae appears likely (Ludwig 1949; Stocker et al. 1995; Tissot et al. 1997), although it has been questioned (Snodgrass 1924; Kankel et al. 1980). The groove between the two lobes usually has a conspicuous lateral pore receptor (Chu and Axtell 1971) that appears to have a sense hair protruding in *Cuterebra* Clark (Baker 1986). The antennal ultrastructure is similar in *Musca* Linnaeus, *Calliphora* Robineau-Desvoidy, and *Drosophila* Fallén and includes mostly olfactory receptors but also some contact chemoreceptors and mechanoreceptors (Bolwig 1946; Richter 1962; Chu and Axtell 1971; Gasc et al. 1984; Singh and Singh 1984; Schmidt 1993; Tissot et al. 1997). The maxillary palpus is a complicated sense organ and, contrary to its name, is of mixed segmental origin. It is button-like as in the Empidoidea (Figs 79, 115) and, based on neuroanatomy and fate mapping of *Drosophila* embryos, most palpal sensillae are derived from the maxillary segment. However, there are usually two or more dorsolateral sensillae separated from the remaining (e.g., Chu and Axtell 1972; Ross and Anderson 1991; Schmidt 1993; Meier 1996). At least one is formed by the antennal segment, whereas the other is either of antennal or mandibular origin (Fig. 117; Bolwig 1946; Frederick and Denell 1982; Jürgens et al. 1986). Ultrastructure of the sensillae and cauterisation experiments suggest that the maxillary palpus is involved mostly in contact chemoreception and mechanoreception (Yamada et al. 1981; Stocker 1994).

Additional sense organs of the pseudocephalon include a pair of **ventral organs** anterior to the functional mouth opening, near the cirri (Figs 115–116; Bolwig 1946; Kankel et al. 1980; Singh and Singh 1984; Jürgens et al. 1986). These organs, which are absent in first-instar larvae of some Anthomyiidae (Yamada et al. 1981), are probably of maxillary origin (but see Hartenstein 1988) and have gustatory functions (Tissot et al. 1997). The **labial lobe** is of labial origin (Figs 102, 104, 113–115; Snodgrass 1953; Jürgens et al. 1986), forms a median fleshy cone on the posterior end of the functional mouth opening, and carries the sense organs known as **lower lip organs** (Jürgens et al. 1986; Jürgens and Hartenstein 1993), sense organ of the lip (Bolwig 1946), or **labial organ** (Fig. 115; Kankel et al. 1980; Singh and Singh 1984; Stocker 1994). These organs have been homologised with the labial palpi, which implies that the labial lobe incorporates the prementum (Roberts 1971b; Hennig 1973). The labial lobe can be moved by a muscle that Hennig (1973) homologised with the retractor muscle of the prementum. In Sepsidae, a lobe on either side of the labial lobe carries an additional sense organ whose distribution beyond the family is unknown (Fig. 115, "sense organ"; Meier 1996).

The most conspicuous structure on the ventral side of the pseudocephalon is the **facial mask** that slopes into the functional mouth opening (Figs 102, 114–115). The space before the mouth opening is called the **preoral cavity**. Most Cyclorrhapha have many **cirri** or **oral ridges** flanking the mouth anteriorly or laterally (Figs 104, 113–115). The extent and composition of the facial mask is of great diagnostic value and varies

lr

mxp

lmhy

sal dt

76

con scl

d mdhk

v mdsc

ten

77

mtceph

ten

cib

mdab

mtceph

d mdhk

mx lb

tph

mdad

78

d mdhk

lr

mxp

b mdsc

ant

mtceph

ten

a spir

79
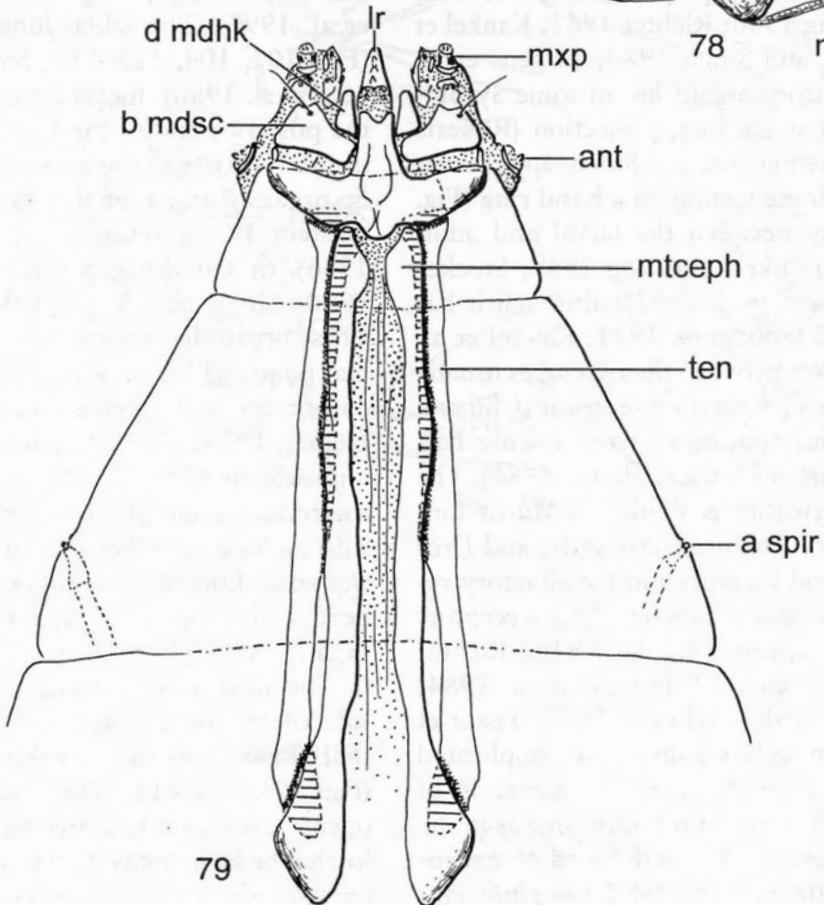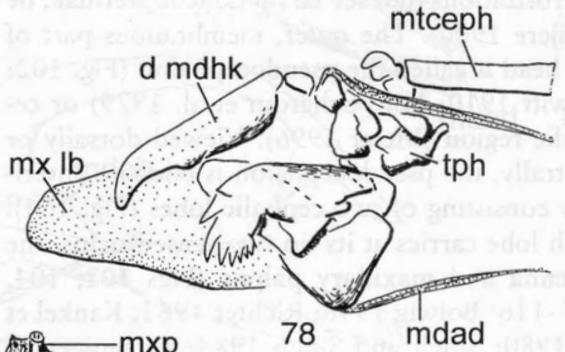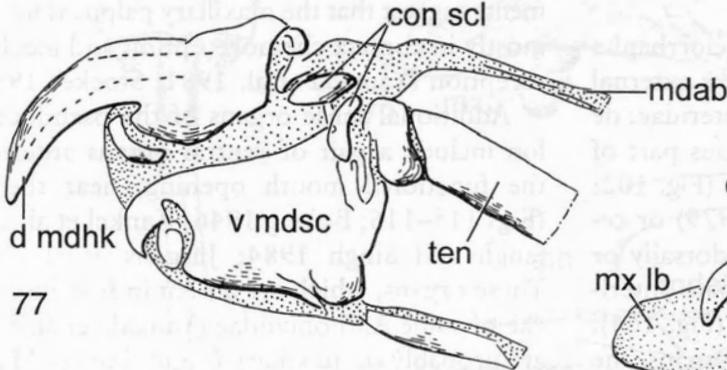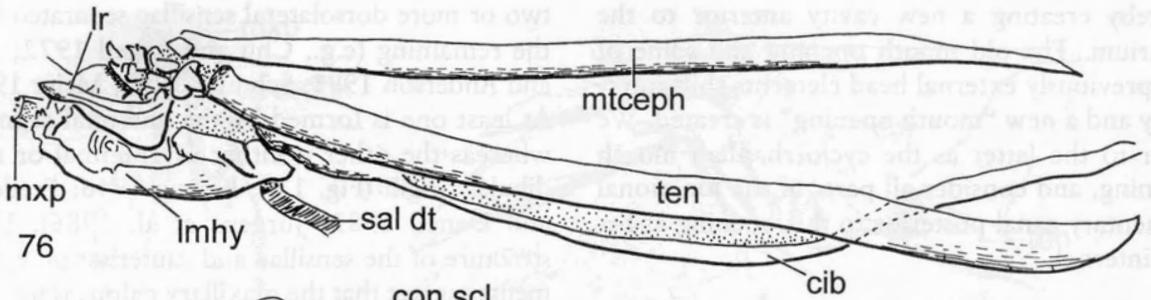
tremenduously between larval instars (Figs 113–115; Traxler 1977), between species of the same instar, and between species of different families (Ferrar 1987; Meier 1996). First-instar larvae generally have few cirri and oral ridges, whereas the facial mask of third-instar larvae is usually large and covers most of the cephalic lobes (Figs 113–115). Predatory, parasitoid, and truly phytophagous larvae have a strongly reduced facial mask and may lack cirri and oral ridges entirely (Fig. 116). A well-developed facial mask thus seems to be associated with saprophagy. The grooves between the oral ridges are thought to direct food-carrying liquids to the mouth. The function of cirri is less understood, but some Platypezidae use them as rasping devices (Teskey 1981a) and some Syrphidae use them to push food toward the mouth (Roberts 1970). In other Syrphidae the invagination of the larval head is even more extensive than in a typical cyclorrhaphan larva and involves a facial mask that is firmly attached to the mouthhooks, which are transformed into supporting structures for the facial mask. Its ridges and cirri may function as a filter apparatus that excludes large particles from ingested liquids (Roberts 1970).

Use of terms. We refer to the larval head as the pseudocephalon, a term not entirely satisfactory but certainly better than the commonly used "cephalic segment" or "pseudocephalic segment". The latter two terms are misleading because they imply that the head consists of a single segment. However, the cephalic lobes alone includes antennal, mandibular and maxillary elements (Schremmer 1956; Jürgens and Hartenstein 1993). The antennal segment is restricted to the antennal sense organ and the mandibular segment to a narrow strip between the antenna and maxillary palpus (and possibly some elements of the "maxillary" palpus) while most of the lobes are formed by the maxillary segment.

Previous interpretations. (1) The larval head of the Cyclorrhapha is invaginated into the thorax. When viewed from the outside, the internal elements of the head posterior to the labial lobe lie within the thorax. However, contrary to remarks in several publications (Hartley 1963; Roberts 1970, 1971a), there is no evidence that the externally visible part of the head, the pseudocephalon, includes any thoracic elements (Snodgrass 1953; Jürgens and Hartenstein 1993). It is correct that, during embryogenesis, a dorsal fold overgrows the dorsal part of the head, but this fold is formed by head segments (Turner and Mahowald 1979; Jürgens et al. 1986). (2) Most of the cephalic lobes are formed by the maxillary segment. Based on embryological evidence, the facial mask with all its cirri and oral grooves is of maxillary origin, but Hartley (1961), Roberts (1970), and Teskey (1981a) considered them part of the mandibular segment. Embryological and neuroanatomical evidence also indicates a maxillary origin of the ventral organs and a labial origin of the labial organs, which is incompatible with a mandibular origin of the facial mask.

Internal Morphology. The only sclerotized region of a typical Cyclorrhapha head is the largely internal **cephaloskeleton** (Figs 102, 104). The cephaloskeleton is secreted by the invaginated head segments and incorporates the larval tentorium. The size, shape, and degree of sclerotization vary tremenduously and are related to the feeding habits of the larva (Ferrar 1987). The invagination of the head segments creates the **atrium**, a new cavity anterior to the cibarium that among cyclorrhaphans is missing only in the Lonchopteridae (de Meijere 1900; Brauns 1954; Hennig 1973). The nomenclature for the different elements of the cephaloskeleton is for two reasons unusually confused. First, many elements have been named several times. Table 1 presents a list of commonly used synonyms (see Ferrar

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Figs 4.76–79. Mouthparts of Empidoidea. 76–77: *Oreogeton* sp.: 76: longitudinal section, left mandible and maxilla removed, 77: right mandible, adoral view. 78: *Hemerodromia* sp. (Empididae), right mandible, adoral view. 79: *Liancalus* sp. (Dolichopodidae), head capsule and prothorax, dorsal view (abbreviations: ant: antenna, a spir: anterior spiracle, b mdsc: basal mandibular sclerite, cib: cibarium, con scl: connecting sclerites, d mdhk: distal mandibular hook, lmhy: prementohypopharyngeal apparatus, lr: labrum, mdab: apodeme for mandibular abductor, mdad: apodeme for mandibular adductor, mtceph: metacephalic rod, mx lb: maxillary lobe, mxp: maxillary palpus, sal dt: salivary duct, ten: tentorial arm, tph: tentorial phragma, v mdsc: ventral mandibular sclerite).
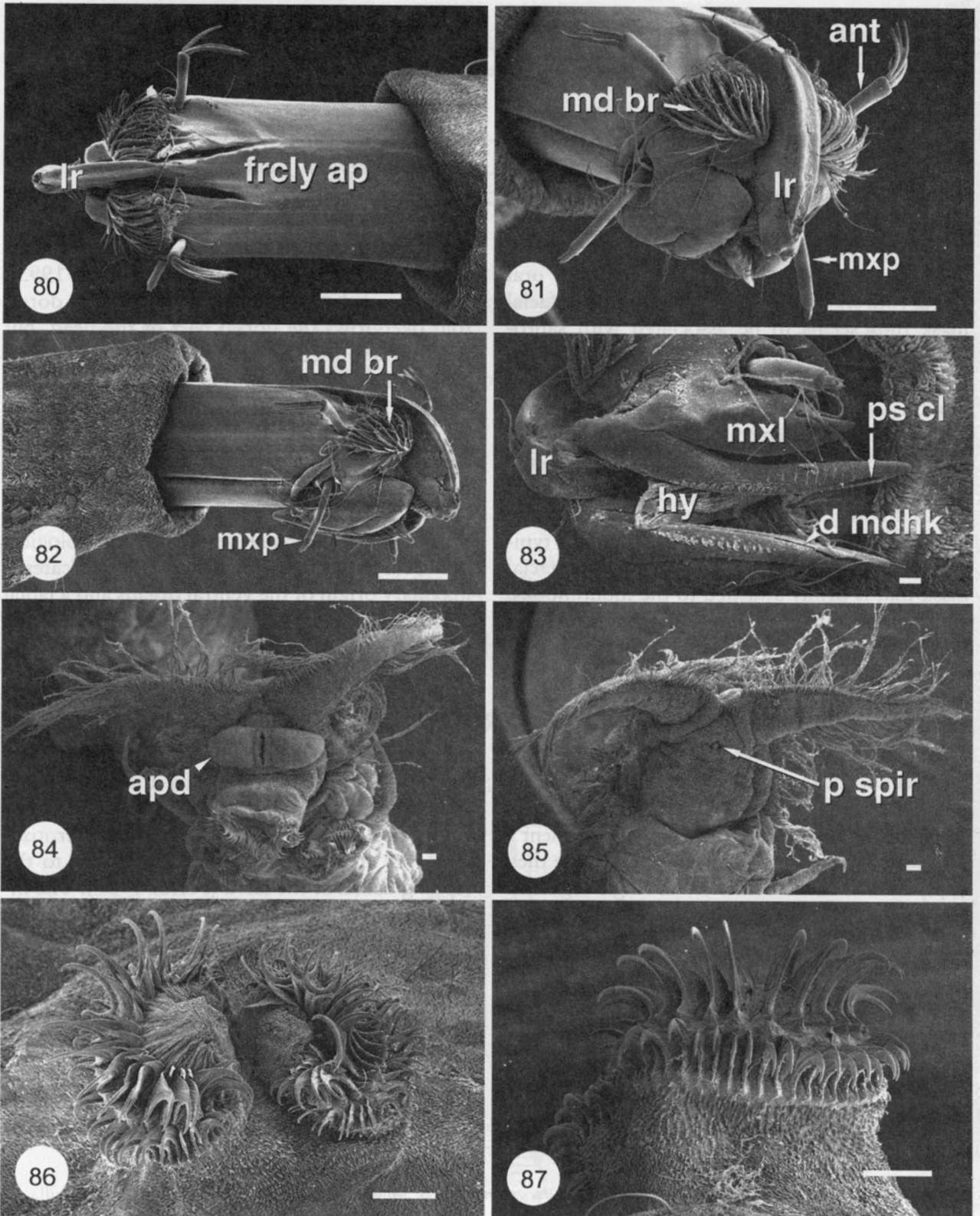
Figs 4.80–87. Scanning electron micrographs of *Atherix* sp. (Athericidae). 80–82: head capsule: 80: dorsal view, 81: oblique anterior view, 82: lateral view; 83: mouthparts, ventral view; 84–85: caudal end: 84: ventral view, 85: dorsal view; 86: pair of abdominal prolegs, ventral view; 87: abdominal proleg, lateral view (abbreviations: ant: antenna, apd: anal pad, d mdhk: distal mandibular hook, frcly ap: frontoclypeal apotome, hy: hypopharynx, lr: labrum, md br: mandibular brush, mxl: lacinia, mxp: maxillary palpus, ps cl: poison canal, p spir: posterior spiracle; all scale bars: 100µm, except Fig. 83 (10µm)).

[1987] for similar list, including German and French terms). Second, many of the smaller sclerites are difficult to homologize across the Cyclorrhapha and many new terms have been generated for similar sclerites in different groups. These terms are not reviewed herein. For our purposes, we divide the cephaloskeleton from anterior to posterior into three main parts: mouthhooks, intermediate sclerite, and basal sclerite (Figs 102, 104).

Mouthhooks – The anterior-most part of the cephalothorax comprises the mouthhooks, the tips of which often protude from the atrium into the preoral cavity (Figs 102, 108, 114). The mouthhooks are hollow and normally undivided. The inner sides of the distal mouthhooks are separated by a fleshy fold. A small pore at the base of the mouthhooks is probably homologous to the mandibular campaniform sensillum of many lower Diptera (Strasburger 1934; Teskey 1981a; Singh and Singh 1984; Sinclair 1992). The base of the mouthhooks is the attachment point for two apodemes, the dorsal mandibular abductor apodeme and the ventral mandibular adductor apodeme (Fig. 102). The corresponding muscles are attached posteriorly to the outer side of the ventral cornu. In many Schizophora, additional sclerites occur near the mouthhooks, including two dental sclerites that can be fused into a single transverse bar (Figs 102, 104). The name "dental sclerite" should be reserved for sclerites that carry part or all of the mandibular abductor apodeme (Fig. 102). Dental sclerites have not been reported from the admittedly poorly known cephaloskeletons of any "Aschiza" (Ferrar 1987). Accepting a paraphyletic "Aschiza" (see references in Yeates and Wiegmann 1999) implies that dental sclerites do not belong to the groundplan of the Cyclorrhapha and that Hennig's (1973) attempt to homologize them with sclerites in the orthorrhaphous Diptera is misguided.

The form of the mouthhook is often greatly modified as an adaption to particular food substrates. Common modifications include partial or complete fusion of both mouthhooks (Hartley 1963; Roberts 1970; Teskey 1981a; Ferrar 1987), reduction of one mouthhook in some

Agromyzidae (Teskey 1981a; Ferrar 1987), reduction of both mouthhooks in larvae with intrauterine nourishment (*Glossina* Wiedemann; Roberts 1971b), and slender, piercing mouthhooks with additional sclerites of unknown origin in predatory species (Roberts 1971b; Tinkeu and Hance 1998). At least two aschizan families include species with minute mouthhooks that have been functionally replaced by labial elements of the skeleton (Fig. 106; Teskey 1981a; Sinclair 1992). Except in predatory or parasitic species (Baker 1986; Schmidt 1993), the mouthhooks of first-instar larvae are usually small and weakly sclerotized.

Homologies. The question of whether the mouthhooks are mandibles, maxillae, both, or something novel is neither new nor solved (reviews in Ludwig 1949; Menees 1962; Hennig 1973; Sinclair 1992). Embryology supports a maxillary origin, but the evidence is inconclusive: (1) In studies of *C. vicina*, the removal of the maxillary anlage on one side of an embryo leads to a larva with a mouthhook on only the other side (Schoeller 1964). But experimental manipulation on the embryo is technically so difficult that doubt remains whether only the maxillary anlage was removed. (2) Jürgens et al. (1986) found that irradiation of the maxillary anlage of many embryos creates three times as many embryos with abnormal mouthhook morphology than if the mandibular anlage is irradiated. However, the irradiated area was about as wide as the anlagen and the technique thus was not especially precise. Jürgens and Hartenstein (1993: 701) thus reached only the following tentative conclusion: In *D. melanogaster* the "mouthhooks ... are included in the maxillary territory". (3) Turner and Mahowald (1979) suggested that a precursor of the mouthhooks can be seen on the maxillary anlage of the *Drosophila* embryo; however, their SEM images show the putative mouthhook rudiment on the border between the mandibular and maxillary anlage.

Traditional morphology supports that the mouthhooks are at least partially of mandibular origin. (1) Two apodemes are attached to the mouthhooks and connect to the mandibular adductor and abductor muscles (Fig. 102). The base
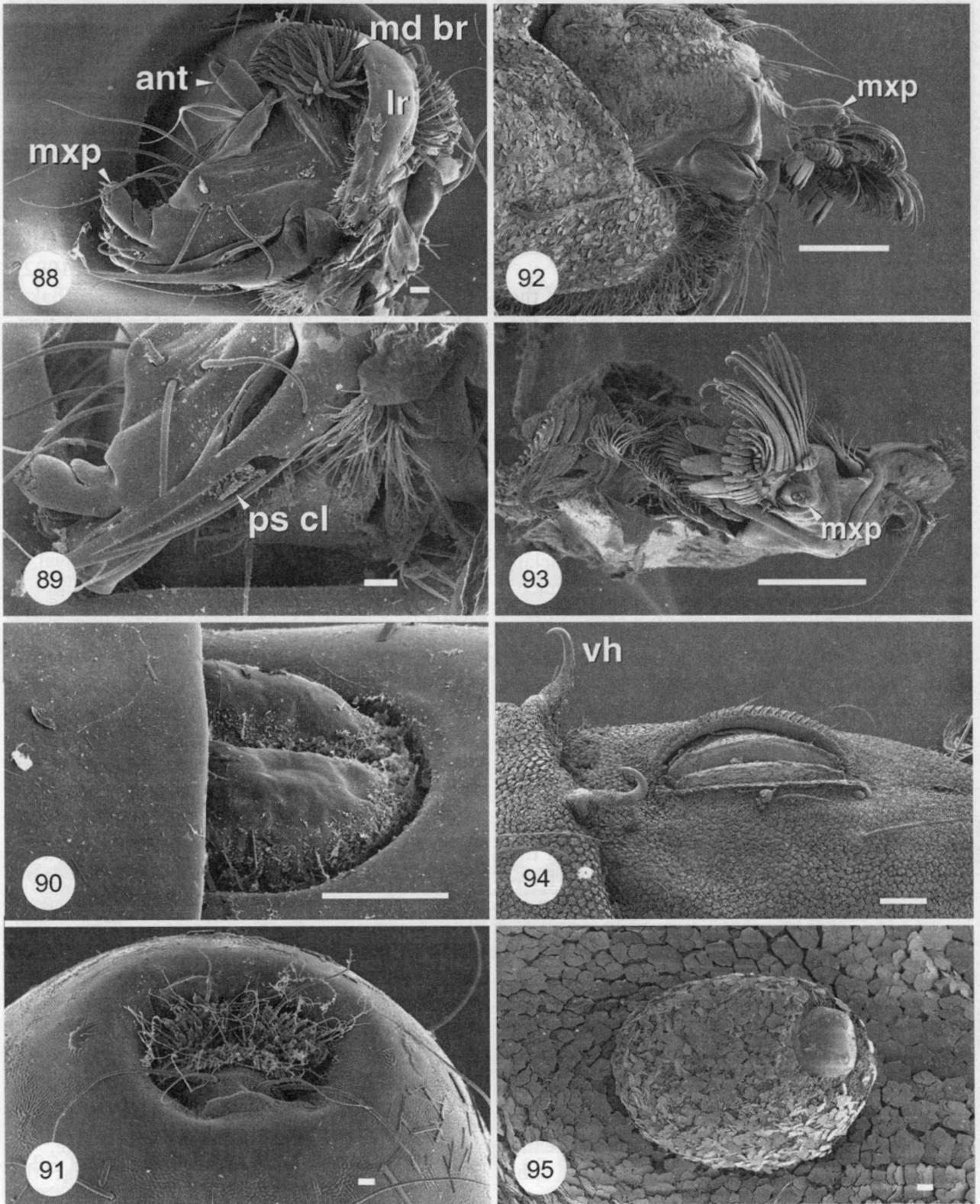
Figs 4.88–95. Scanning electron micrographs of mouthparts. 88–91: *Glutops* sp. (Pelecorhynchidae): 88: head capsule, oblique lateral view, 89: mouthparts, anteroventral view, 90: anal pads, ventrolateral view, 91: posterior spiracular cleft, posterior view. 92–95: *Caloparyphus* sp. (Stratiomyidae): 92: head capsule, lateral view, 93: mandibular-maxillary apparatus, ventral view, 94: anus and caudal hooks, ventrolateral view, 95: prothoracic spiracle (abbreviations: ant: antenna, lr: labrum, md br: mandibular brush, mxp: maxillary palpus, ps cl: poison canal, vh: ventral hook; scale bars: 10μm (Figs 88–89, 91, 95), 100μm (Figs 90–94)).

of the each maxillary remnant in orthorrhaphous Diptera appears to have at most one apodeme. A maxillary origin of the mouthhook base is thus unlikely based on position and number of apodemes. (2) The basal portion of the mouthhooks bears the porelike campaniform sensilla so typical of Diptera mandibles. The apo-demes and the sensillum are strong indications that the mouthhook base is mandibular in origin. We suggest that this evidence outweighs embryological evidence for a maxillary origin of the mouthhooks.

One should, however, keep in mind that morphological evidence applies only to the mouthhook base. The maxilla might be involved in formation of the distal part of the mouthhooks. Such a mixed origin could simultaneously explain the embryological and morphological data. It seems all the more conceivable because (1) the anlagen for these two segments fuse early in *Drosophila* development (Turner and Mahowald 1979), and (2) laser ablation study can yield damaged embryos in which the tip of the mouthhook is separated from the base (see figures in Jürgens et al. 1986), and (3) the maxilla and mandible are closely associated or fused in many orthorrhaphous Diptera.

Intermediate sclerite – The middle and posterior sections of the cephaloskeleton consist of the intermediate sclerite and basal sclerite, respectively (Figs 102, 104, 107–108). These sclerites are not separate in the paraphyletic "Aschiza" (Figs 105–106) and most first-instar larvae of Schizophora. A single large sclerite comprising both is therefore the groundplan condition for the Cyclorrhapha (Hartley 1963; Hennig 1973; Ferrar 1987; *contra* McAlpine 1989). Only in typical second- and third-instar larvae of the Schizophora is the intermediate sclerite separate (Strasburger 1934; Menees 1962; Ferrar 1987). If divided, the ventral and lateral support for the atrium comes mostly from the **intermediate sclerite** (Figs 102, 104, 107–108). In ventral view the intermediate sclerite resembles the letter H and it is thus widely known as the **H-shaped sclerite** (Figs 104, 107). The **salivary duct** enters the intermediate sclerite ventrally from the last third of the sclerite behind the transverse bar

(Fig. 102). The intermediate sclerite is therefore at least partially homologous to the V-shaped sclerite of the Empidoidea (Sinclair 1992). Anteroventrally, the atrium is supported by sclerites that are usually called **labial sclerites** and of which there can be several (Figs 102, 104, 107–108; Ferrar 1987). Often, one particularly large sclerite is in a median position. It is usually fenestrated for sensory processes from the labial sense organs that lie below the sclerite (Fig. 104; Jürgens and Hartenstein 1993). They are known as the hypophysis (Hertweck 1931; Singh and Singh 1984: "anteroventral group"; Stocker 1994) or hypostomal sense organ (Bolwig 1946). The hypophysis is thought to consist of chemoreceptors and mechanoreceptors (see Hertweck [1931] for details). Much less common are additional ventral sclerites in the atrium walls such as the **ligulate sclerite** or the toothed **ventral arch** of Sciomyzidae (Figs 107–108, 116).

Dorsally, stabilisation of the atrium is accomplished by two **parastomal bars** that project anteriorly and normally are continuous with the basal sclerite (Figs 102, 105, 108). In first-instar larvae of Cyclorrhapha and later instars of a few aschizan species (Syrphidae: Roberts 1970; Platypezidae: Sinclair 1992), a **labrum** is at the anterior end of these parastomal bars (Snodgrass 1953; Roberts 1970). Most first-instar larvae use the labrum as an egg burster or, in Tachinidae, for penetration of the host cuticle (Hennig 1973). Except for some predatory larvae of Syrphidae (Hartley 1963; Roberts 1970), later-instar larvae rarely possess a labrum. Additional dorsal skeletal elements of the atrium include the **epistomal sclerite**, which is either fused to the anterior tip of the parastomal bars or lies freely over the anterior half of the intermediate sclerite (Figs 107–108). The labral sense organs (Singh and Singh 1984: "dorsal group"; Jürgens and Hartenstein 1993), also known as the epiphysis (Hertweck 1931) or epipharyngeal sense organs (Bolwig 1946), are dorsal, above the epistomal sclerite. These organs send sensory projections through pores of the epistomal sclerite into the atrium (Bolwig 1946; Roberts 1970, 1971a; Hartenstein 1988; Younossi-Hartenstein et al. 1993). Labral sense organs and various scleroti-

zations of the epipharynx are known from nematocerous Diptera but it is unclear if these are homologous to the epistomal sclerite and epiphysis of the Cyclorrhapha.

The morphology of the intermediate section of the cephaloskeleton varies across the Cyclorrhapha, especially in the "Aschiza" (Figs 105, 106–108). For example, many "Aschiza" lack the transverse bar and in some species the intermediate sclerite becomes the functional mouthhooks. Substantial morphological changes to the intermediate sclerite are also typical between instars of the same species, but these changes are poorly documented. Functionally, the atrium is part of the suction pump used to ingest liquids, and the atrium sclerites function as attachment
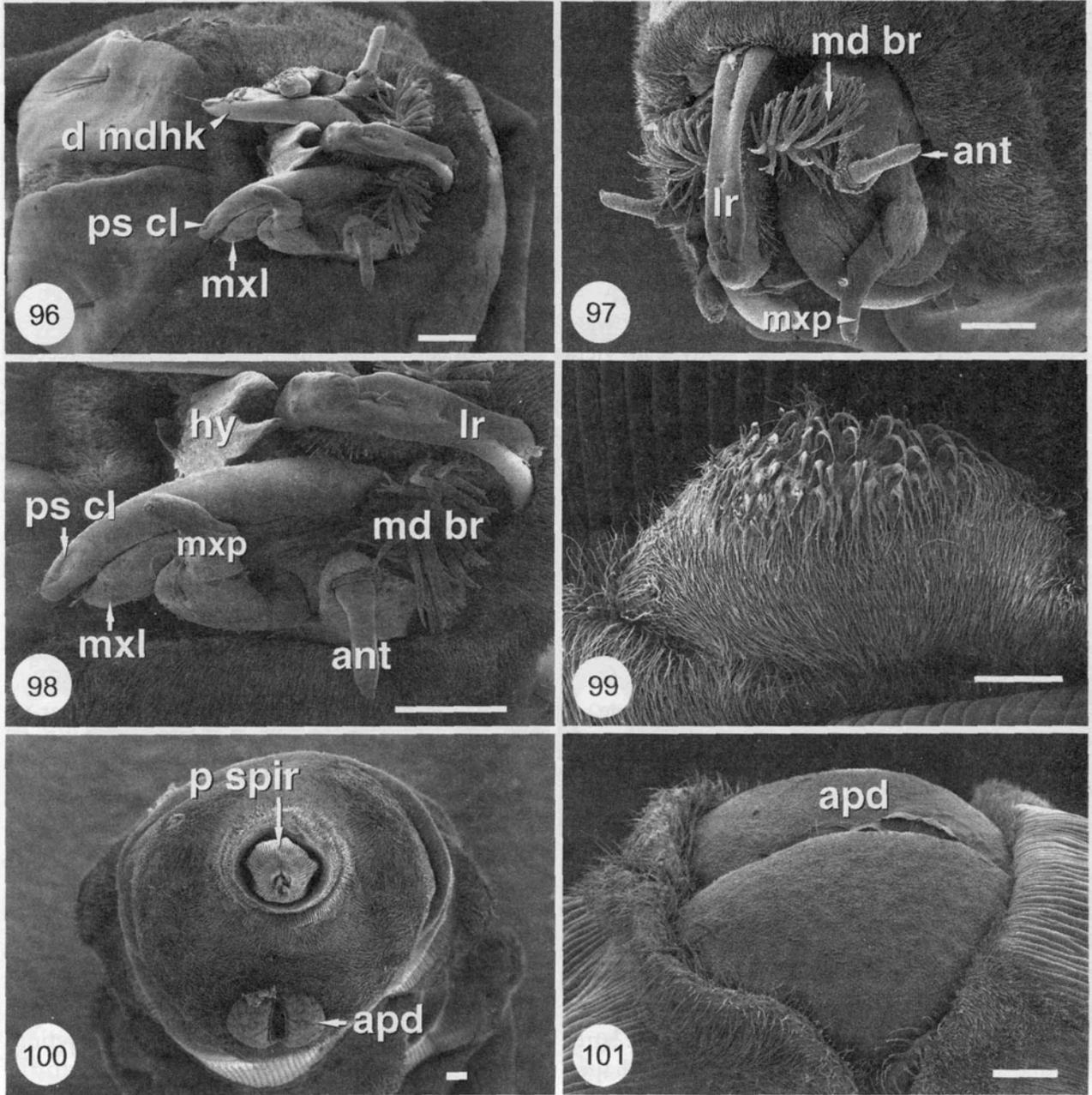
Figs 4.96–101. Scanning electron micrographs of Tabanidae. 96–98: *Tabanus* sp., mouthparts: 96: anterior view, 97: oblique anterior view, 98: left mouthparts, anterior view. 99–100: *Silvius* sp.: 99: abdominal proleg, lateral view, 100: caudal end, posterior view. 101: *Tabanus* sp., anal pads, oblique lateral view (abbreviations: ant: antenna, apd: anal pad, d mdhk: distal mandibular hook, hy: hypopharynx, lr: labrum, md br: mandibular brush, mxl: lacinia, mxp: maxillary palpus, p spir: posterior spiracle, ps cl: poison canal; all scale bars: 100μm).

sites for the complicated atrial musculature designed to dilate the atrium during food intake (Miller 1932; Roberts 1970, 1971a).

Homologies. Identifying the head segments that contribute to the sclerotized elements of the atrium is facilitated by sense organs of known segmental origin and by fate mapping studies in *D. melanogaster* (Jürgens et al. 1986). Furthermore, the salivary duct marks the border between the labial and intercalary segments. Except for the main labial sclerite and the labrum, the sclerotized elements of the middle section of the cephaloskeleton are probably *de novo* structures (Hennig 1973). We therefore only briefly indicate their segmental origin. There is little doubt that most ventral parts of the intermediate sclerite are formed by the labial segment, whereas other head segments, especially the maxillary segment, contribute to the lateral walls. The parastomal bars are of mandibular origin (Jürgens and Hartenstein 1993). Based on the position of the epiphysis, the epistomal sclerite and the labrum, if present, are formed by the labral segment (e.g., Younossi-Hartenstein et al. 1993).

Previous interpretations. (1) Teskey (1981a) argued that the intermediate sclerite should be called "hypopharyngeal" because it is at least partially formed by the hypopharynx. He also argued that part of the cibarium is enclosed by this sclerite. Based on the evidence presented previously, the ventral elements of the intermediate sclerite are largely of labial origin and the lateral walls of maxillary origin. Only a small part of the sclerite behind the salivary duct opening could potentially belong to the hypopharynx. We therefore prefer the neutral term intermediate sclerite. (2) Additional interpretations likely to be incorrect include the suggestion that the labrum of first-instar larvae is the mandible (Menees 1962), and the hypothesis that the lateral walls of the intermediate sclerite are part of the tentorial arms (Hartley 1963; Roberts 1970). During embryogenesis of *Drosophila* (Jürgens and Hartenstein 1993; Younossi-Hartenstein et al. 1993) and *Calliphora* (Schoeller 1964) the anterior arms of the tentorium move into the larval

body to a position below the posterior arm. The tentorium therefore lies posterior to the intermediate sclerite.

Basal sclerite – The largest and most posterior element of the cephaloskeleton is the **basal sclerite** (Figs 105, 108). It consists dorsally of the paired **dorsal cornua** (Fig. 102) whose size and shape vary with their function as an attachment site for muscles of the cibarial pump and dorsal protractor muscles (Snodgrass 1924). The **dorsal arms** (Fig. 102) are connected at their anterior end via the **dorsal bridge** (Fig. 102), which is usually weakly sclerotized and fenestrated. The larval stemmata are externally visible in many orthorrhaphous Brachycera, but they are internal, ventrolateral to the dorsal bridge, in the Cyclorrhapha. The stemmata are connected through Bolwig's nerve to the brain (Melzer 1994). In all Cyclorrhapha, the retinular pigment is reduced and functionally replaced by the dark background of two **optic depressions** in the basal sclerite (Fig. 102; Roberts 1971b; Teskey 1981a; Melzer and Paulus 1989). The stemmata of the Schizophora are called **Bolwig's organ** (Bolwig 1946; Melzer and Paulus 1989). They differ from the photoreceptors of orthorrhaphous and aschizan Brachycera by having the rhabdom replaced by stacks of flat lamellae (Melzer and Paulus 1989). Below the optic depressions, the dorsal cornua are fused to the posterior arm of the tentorium (i.e., the larval tentorium is the connecting element between the dorsal cornu and the ventral element of the basal sclerite; Schoeller 1964; Jürgens and Hartenstein 1993; Younossi Hartenstein et al. 1993). In this modified form the tentorial arms are known as the **vertical plate** (Fig. 102). During embryogenesis the tentorium consists of a pair of **tentorial rods** in the typical insectan orientation (i.e., anterior-posterior). Each is the product of fusion between the **anterior arm** and the **posterior arm**. During involution of the head segments, the anterior arm moves into the larva to below the posterior arm. The posterior arms are fused to the dorsal cornua, whereas the anterior arms are fused to the main ventral elements of the basal sclerite, the **ventral cornua** (Figs 102, 104). Size and

Figs 4.102–112. Cephaloskeleton and anterior spiracles of larval cyclorrhaphans. 102–104: *Phormia regina* (Meigen) (Calliphoridae): 102: lateral view of cephaloskeleton with left antennomaxillary lobe removed, 103: diagrammatic cross section through ventral cornu, 104: ventral view of cephaloskeleton and pseudocephalon. 105–108: cephaloskeleton: 105: *Spiniphora* sp. (Phoridae), lateral view; 106: *Platypeza* sp. (Platypezidae), lateral view; 107: *Sepedon* sp. (Sciomyzidae), ventral view of anterior elements; 108: *Sepedon* sp. (Sciomyzidae), lateral view. 109–112: anterior spiracles: 109: *Syrphus knabi* Shannon (Syrphidae); 110: *Desmometopa m-nigrum* (Zetterstedt) (Milichiidae); 111: *Lasiopiophila pilosa* (Staeger) (Piophilidae); 112: *Saltella sphondylii* (Schrank) (Sepsidae) (abbreviations: acth: accessory teeth, ant: antenna, bsc: basal sclerite, cib: cibarium, darm: dorsal arm, dbr: dorsal bridge, dcor: dorsal cornu, den: dental sclerite, epi: epipharynx, epsc: epistomal sclerite, fama: facial mask, insc: intermediate sclerite, hy: hypopharynx, insc: intermediate sclerite, lmlo: labial lobe, lmsc: labial sclerite, mdab: apodeme for mandibular abductor, mdad: apodeme for mandibular adductor, mdhk: mouthhook, mxp: maxillary palpus, opde: optic depression, pab: parastomal bar, psceph: pseudocephalon, sal dt: salivary duct, v arch: ventral arch, vcor: ventral cornu, vrpl: vertical plate) (102–104 after Teskey 1981a, 105 after Peterson 1987b, 106 after Kessel 1987, 107–108 after Knutson 1987, 109 after Vockeroth and Thompson 1987, 110 after Sabrosky 1987, 111 after McAlpine 1987a, 112 after Steyskal 1987).

shape of the ventral cornua vary tremenduously within the Cyclorrhapha, which reflects their significance as attachment sites for cibarial and mouthhook muscles. The name "ventral cornu" is unfortunate because the ventral cornu is not an extension of another structure but encloses the **cibarial pump** (Figs 102–103) and is therefore part of the functional alimentary canal. Its main components are the **hypopharynx** (Figs 103–104), which forms the floor of the pump, and the **epipharynx** (Fig. 103), which forms its roof. In saprophagous taxa, the hypopharynx bears prominent longitudinal ridges extending into the lumen of the cibarial pump. These **ventral cibarial ridges** have short, lateral, filamentous extensions that just touch the filaments of neighboring ridges. In cross-section, they are shaped like the letters T or Y and therefore also called **T-ribs** or **Y-ribs** (Fig. 103). The T-ribs are usually missing in non-saprophagous taxa, such as predatory, parasitoid, and phytophagous species (Dowding 1967; Roberts 1971b).

The largest muscle of the cibarial pump is the cibarial dilator, which originates on the roof of the cibarium and attaches to the inner sides of the dorsal cornua (Hewitt 1910; Roberts 1970, 1971a). Its interpretation as a cibarial dilator muscle sensu Snodgrass (1935) is at a first glance questionable because it does not originate on the labrum. However, in all Diptera the origin of the cibarial dilator has apparently moved from the labrum to the frons (see previous discussion). Contraction of the cibarial dilator lifts the epipharynx and sucks food-carrying liquids into the cibarium. Once the muscle is relaxed, the roof of the cibarium lowers and pushes liquid against the T-ribs. In at least some Schizophora and aschizans, this lowering is accomplished by **cibarial constrictor muscles** (Hartley 1963; Roberts 1969b, 1970, 1971a). Food particles are concentrated in the dorsal chamber of the cibarium while filtrated water is pushed out of the mouth through ventral canals formed by the lateral walls of cibarial ridges. Flow is directed anteriorly by an **atrial valve** and posteriorly by a **pharyngeal constrictor muscle** (Dowding 1967; Roberts 1970). Most pumping is accomplished by the cibarial pump, but contraction of its dilator muscles is preceded by contraction of atrium dilator muscles. In some species the pharynx is modified into a grinding mill (Roberts 1969b, 1970).

Homologies. The segmental origin of the posterior part of the basal sclerite is very complicated. A discussion of its ontogenetic origin is nevertheless necessary to evaluate previous hypotheses about homology. Most of the following description is based on *D. melanogaster* (Jürgens et al. 1986; Jürgens and Hartenstein 1993). The basal sclerite is of dual origin because dorsal elements are secreted by the dorsal pouch, whereas the ventral elements are produced by epidermis invaginated through the mouth of the embryo (Jürgens and Hartenstein 1993; Schoeller 1964). Most of the dorsal pouch is formed by the invaginated acron, and the acron undoubtedly contributes Bolwig's organs, probably much of the dorsal bridge, and most of the dorsal cornua (but see Diederich et al. 1989). However, more ventrally, the dorsal pouch includes epidermis from several other head segments. Most prominent is the maxillary segment, which probably forms the anteroventral parts of the dorsal cornua. These parts are attached to the posterior arms of the tentorium, which are also of maxillary origin (Younossi-Hartenstein et al. 1993).

The anterior arm of the tentorium, which is derived from the intercalary segment, is fused dorsally to the posterior arm. Ventrally, the anterior arm is continuous with the hypopharynx (= floor of cibarium), which is at least partially of intercalary origin, whereas the epipharynx (= roof of cibarium) is derived from the labral segment (Younossi-Hartenstein et al. 1993). Far posterior, toward the end of the cibarium, lies a sense organ that is often called organ X (Hertweck 1931; Singh and Singh 1984: "posteroventral group"). It is derived from the intercalary segment, which is compatible with a cibarial origin of the pump (Hartenstein 1988). The T-rib anlagen becomes visible early in embryogenesis in an area probably belonging to the intercalary segment (Schoeller 1964; Turner and Mahowald 1979; Ajidagba et al. 1985). However, fate mapping indicates that a narrow strip of the mandibular segment also contributes to the lateral
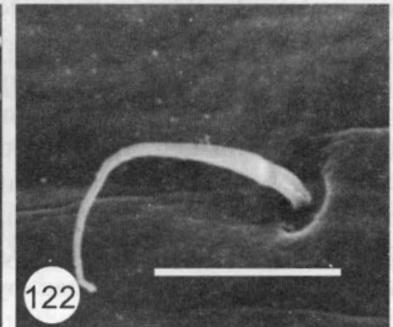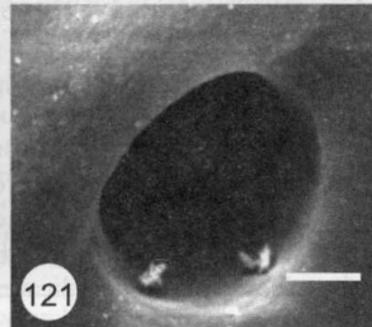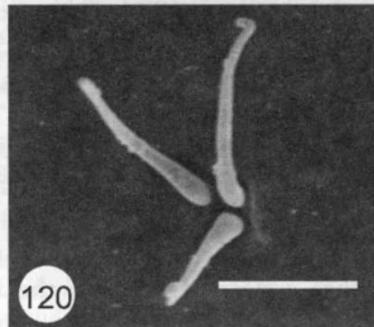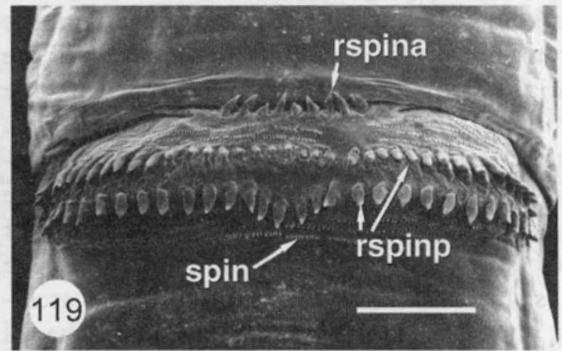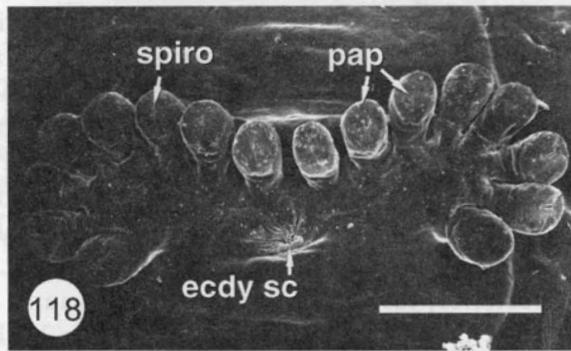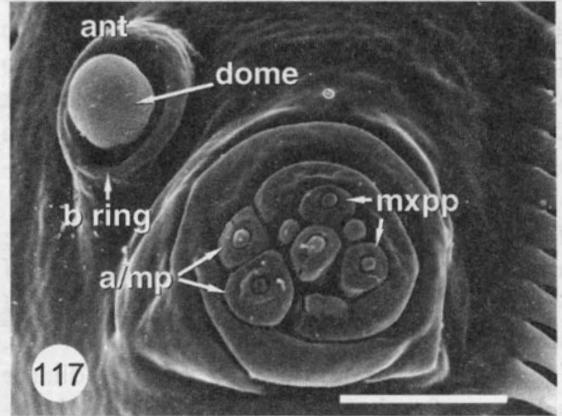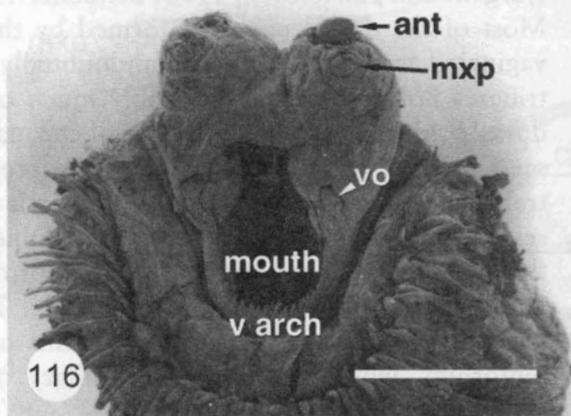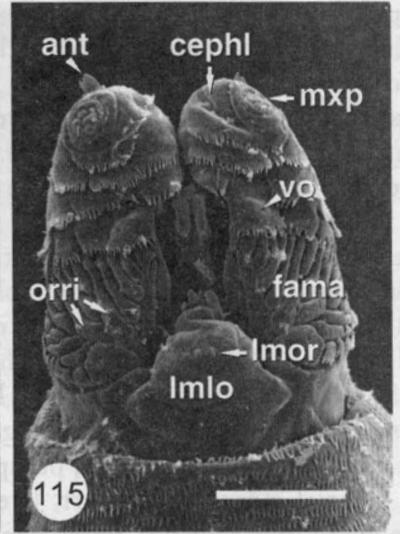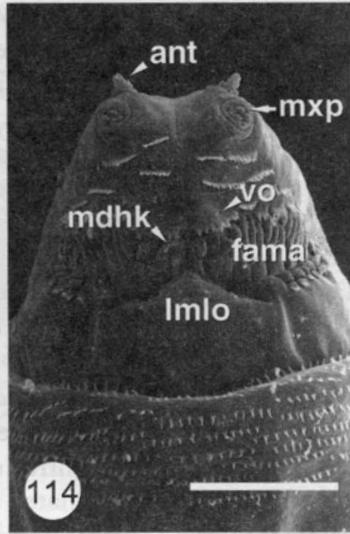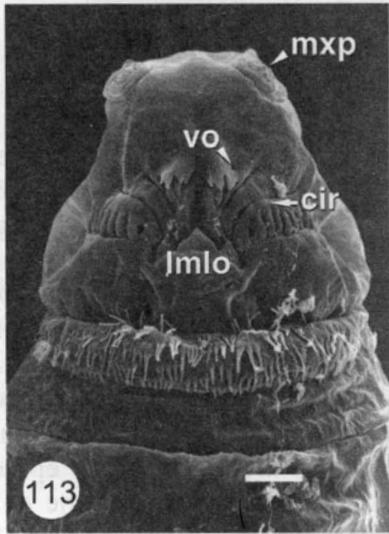
side and floor of the cibarium. This strip termi-
nates at the posterior end of the T-ribs and prob-
ably delimits the border between cibarium and
pharynx. This interpretation is confirmed by the
position of the frontal ganglion (Ludwig 1949;
Fraser 1959; Ranade 1967; Roberts 1970).

Previous interpretations. (1) We are carefully
avoiding terms that imply homology between
elements of the cephaloskeleton and pharynx. By
definition the anterior part of the stomodeum is
called "pharynx" (Snodgrass 1935), but there is
compelling evidence that the cephaloskeleton is of
cibarial rather than pharyngeal origin (Snodgrass
1953). First, the floor is formed by the hypo-
pharynx and the roof by the epipharynx, which is
characteristic for the cibarium. Second, the fron-
tal ganglion, which indicates the border between
the end of the cibarium and the beginning of the
pharynx, is near the end of the basal sclerite, and,
as is typical of cibarial muscles, most dilator mus-
cles are innervated from this ganglion (Snodgrass
1953; Ludwig 1949; Fraser 1959; Ranada 1967;
Roberts 1970, 1971a). Third, elements of the
mandibular segment are on the basal sclerite as
far posterior as the end of the T-ribs, and a sto-
modeal pharynx should never comprise material
from any head segment. And fourth, the sense

organ X at the posterior end of the cibarial pump
is of intercalary origin (Hartenstein 1988;
Stocker 1994). This evidence is incompatible
with a pharyngeal origin of the cyclorrhaphan
pump. Most morphological and embryological
literature on the cephaloskeleton describe the
atrium and/or ventral cornu as enclosing the
pharynx or use terms that suggest a pharyngeal
origin of these elements. Some authors are ap-
parently aware of the correct morphological situ-
ation (Snodgrass 1935; Roberts 1971b), but oth-
ers seem to have been misled by the terminology.
To prevent further confusion over the correct
morphological origin of the filter pump, we ad-
vocate a terminology that avoids reference to a
pharyngeal origin of the cephaloskeleton. (2) Ac-
cording to Hartley (1963) and Roberts (1970,
1971a), the dorsal bridges connecting the dorsal
cornua are of labral origin in some Syrphidae.
This interpretation is incompatible with embryo-
logical evidence. As mentioned previously, the
labrum is farther anterior, at the tip of the paras-
tomal bars. (3) Roberts (1971a) considered the
dorsal cornu to be partially of thoracic origin,
but there is no embryological evidence for any
participation of thoracic material in the forma-
tion of the cephaloskeleton of the Cyclorrhapha.

THORAX AND ABDOMEN

Body shape – Body form of Diptera larvae
varies almost as much as does cranial diversity
and ecological habits. In many nematocerous
groups (e.g., most Chironomidae, Bibionidae,
Anisopodidae, Tipulidae), the body is subcylin-
drical (Figs 123–124, 133–136). Other groups

are predominantly fusiform (e.g., Cecidomyii-
dae) or elongated and serpentine (e.g., Ceratopo-
gonidae). The latter body form is common in
groups inhabiting soil and interstitial aquatic
habitats. Larval Culicidae, Chaoboridae, and
Corethrellidae are unusual because the thoracic

Figs 4.113–122. Scanning electron micrographs of larval cyclorrhaphans. 113–115: *Sepsis lateralis* Wiedemann (Sepsidae),
pseudocephalon, ventral view: 113: instar I, 114: instar II, 115: instar III. 116: *Dictya umbroides* Curran (Sciomyzidae),
pseudocephalon, ventral view. 117: *Drosophila melanogaster* Meigen (Drosophilidae), cephalic lobe of instar II. 118:
Coelopa frigida (Fabricius) (Coelopidae), anterior spiracle of instar III. 119: *Archisepsis diversiformis* (Ozerov) (Sepsidae),
abdominal creeping welt. 120: *Liodrosophila aerea* Okada (Drosophilidae), Keilin's organ. 121: *Drosophila micromettleri*
Heed (Drosophilidae), pit sensillum. 122: *Liodrosophila aerea*, trichoid sensillum (abbreviations: ant: antenna, a/mp: an-
tennal or mandibular sensilla, b ring: basal ring, cephl: cephalic lobe, cir: cirri, ecdy sc: ecdysial scar, fama: facial mask,
lmlo: labial lobe, lmor: labial organ, mdhk: mouthhook, mxp: maxillary palpus, mxpp: maxillary palpus sensilla, orri: oral
ridges, pap: papillae, rspina: anterior reclinate spines, rspinp: posterior reclinate spines, spin: spinules, spiro: spiracle open-
ing, v arch: ventral arch, vo: ventral organ; scale bars: 1μm (Fig 121), 10μm (Figs 113, 117, 120, 122), 50μm (Figs
114–115), 100μm (Figs 116, 118–119)).

segments are indistinctly differentiated and form a single large segment wider than the rest of the body (Sæther 1997: Figs 2.17.23–28). The Simuliidae are also unusual in body form, characterised by swollen posterior segments (Fig. 125). The larvae of other aquatic groups (e.g., Deuterophlebiidae, the psychodid *Horaiella*) are dorsoventrally compressed (Figs 129, 132) and sometimes bear distinct protuberances or locomotory devices (see later). Larval Nymphomyiidae are laterally compressed (Fig. 126), a possible adaptation to life among aquatic mosses and bryophytes (Courtney 1994). Blephariceridae larvae, which have fused anterior segments (i.e., cephalothorax) and a row of ventral suckers (see below), are among the most aberrant groups in body form. In most groups (e.g., most *Blepharicera* Macquart, *Bibiocephala* Osten Sacken), larvae are cylindrical dorsally but flattened ventrally (Fig. 130), whereas others can be markedly
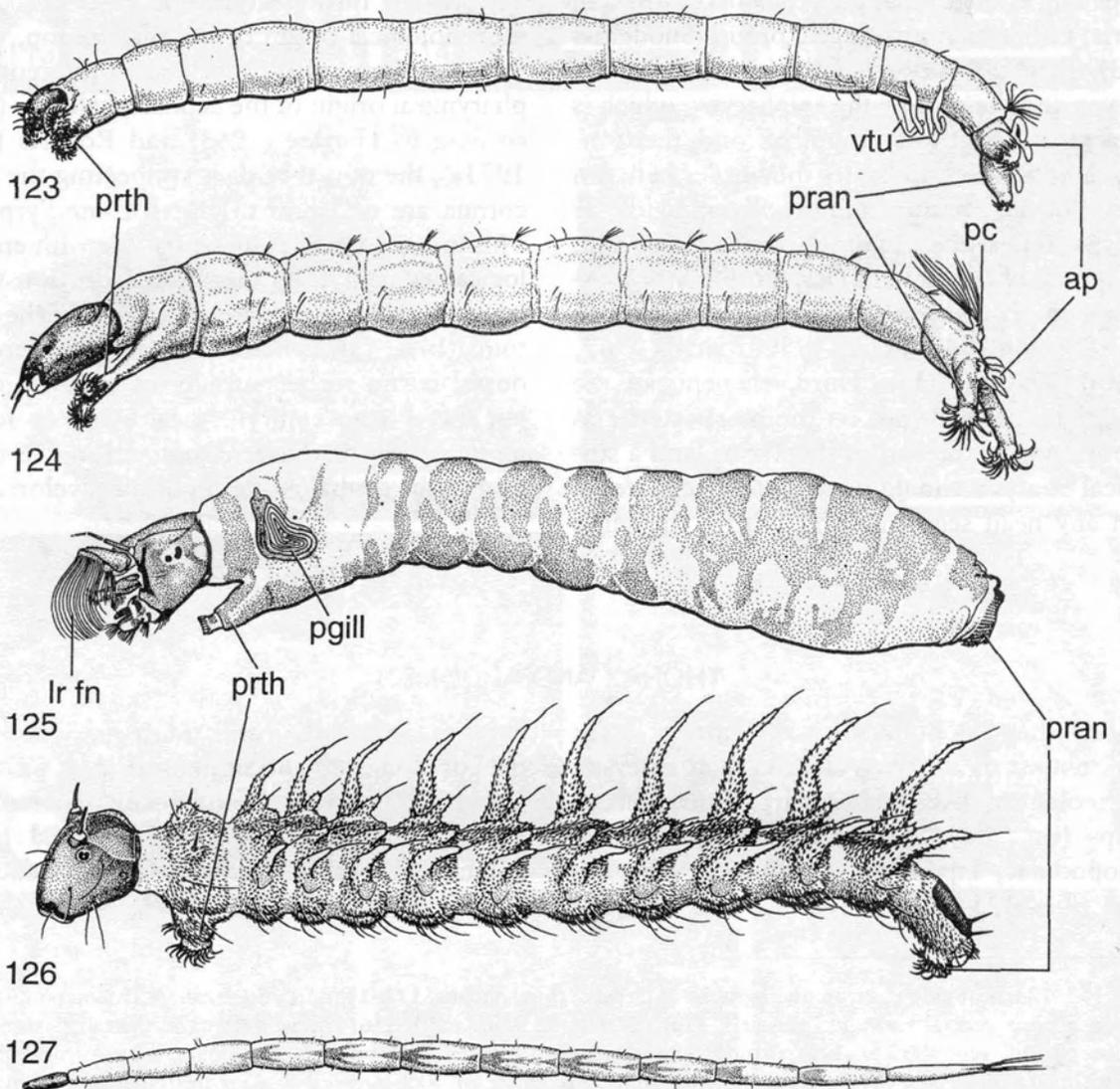
Figs **4.123–127.** Lateral habitus views of larval nematocerans. **123**: *Chironomus* sp. (Chironomidae – Chironominae); **124**: *Ablabesmyia* sp. (Chironomidae – Tanypodinae); **125**: *Simulium* sp. (Simuliidae); **126**: *Atrichopogon* sp. (Ceratopogonidae); **127**: *Bezzia* sp. (Ceratopogonidae) (abbreviations: ap: anal papillae, lr fn: labral fan, pc: procercus, pgill: pupal gill (histoblast), pran: anal proleg, prth: thoracic proleg, vtu: ventral tubules) (123–124 after Oliver 1981, 125 after Peterson 1981, 126–127 after Downes and Wirth 1981).

flattened dorsoventrally (e.g., *Horaia* Tonnoir) or possess prominent protuberances along the dorsal midline (e.g., some *Blepharicera*).

Among orthorrhaphous Brachycera, larval Xylomyidae and Stratiomyidae are moderately broad, compressed, and with segments that are usually wider than long (Nagatomi and Rozkošný 1997: Fig. 22.27; Rozkošný 1997b: Figs 24.59–65). Larvae of most Tabanidae are fusiform or spindle-shaped, being wide in the middle and narrow towards both ends (Fig. 139). The larvae of Athericidae are dorsoventrally compressed and bear distinct prolegs and protuberances (Rozkošný and Nagatomi 1997: Figs 29.10–14). Therevidae, Scenopinidae, and Pelecorhynchidae larvae are long, slender, cylindrical, and tapered at the head and apex of the abdomen (Krivosheina 1997b: Fig. 36.14; Majer 1997: Fig. 35.24). Late-instar endoparasitic larvae of Acroceridae, Bombyliidae, and Nemestrinidae are robust and grublike (Greathead and Evenhuis 1997: Fig. 33.2; Nartshuk 1997: Figs 32.48, 49).

The typical body shape of a cyclorrhaphan larva is that of a maggot (i.e., pointed at the anterior end, with the thoracic segments approaching the maximum body diameter (Figs 146, 149)). The larval body is usually long, slender, and more or less cylindrical in cross section. The posterior end of a typical maggot ranges from blunt to somewhat rounded. The variation in body form is staggering (Figs 145–153; Ferrar 1987) and particularly impressive in families whose larvae feed on a variety of substrates (e.g., Syrphidae). Cyclorrhapha larvae can be dorsoventrally flattened (e.g., Lonchopteridae, Fanniidae, and some Syrphidae (Figs 145, 153)), a feature often associated with the presence of segmental or branched body protuberances (Fig. 153). Some groups are exceptionally flat and bear complex lateral projections (e.g., Platypezidae). The syrphid *Microdon* has one of the most aberrant larvae, being ventrally flattened, dorsally dome-shaped, and sluglike in overall appearance (Fig. 148). These larvae are so unusual that they were described initially as molluscs. In

contrast are the extremely long, thin larvae of cambium miners in the Agromyzidae. Larvae with parasitoid and parasitic life styles (e.g., Conopidae, Pipunculidae, Oestridae) are often extremely stout or pear-shaped (Figs 150, 152; Teskey 1981b), their body form being closely adapted to that of the host. For example, third-instar conopid larvae, which are stout posteriorly and slender anteriorly (Fig. 150), position themselves with the posterior part of the maggot in the gaster of the aculeate host while the slender anterior end penetrates through the petiole into the thorax. In predatory Syrphidae, the pseudocephalon, mesothorax, and metathorax are greatly reduced in size (Rotheray and Gilbert 1989). Well-illustrated overviews of the body shapes in Cyclorrhapha are provided by Teskey (1981a, b), Ferrar (1987), and Teskey and Foote (1991).

Segmentation – In a Diptera embryo, the basic number of externally visible segment anlagen is 19, of which six form the head, three the thorax, and 10 the abdomen. The head segments and their various modifications are covered in the first half of this chapter, whereas the postcranial segments are described here. Although Diptera embryos possess 13 postcranial segments (Craig 1967; Matsuda 1976), fusion of one or more segments is typical of larvae. The Diptera groundplan probably included larvae with 12 body segments, a condition found in several nematocerous groups (e.g., Anisopodidae, Bibionidae). In all groups, the first three postcranial segments are thoracic and the remainder abdominal. Although nine abdominal "segments"* are typical of some groups, there is considerable variation among Diptera families, most involving fusion of posterior segments. In Simuliidae, Deuterophlebiidae, and most higher Nematocera, there are at most eight abdominal segments, with the number reduced further in Axymyiidae and Blephariceridae.

Secondary subdivision of abdominal and sometimes thoracic segments occurs in Trichoceridae, Anisopodidae, most Psychodidae and Tipulidae, and some Blephariceridae. This arrangement also

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* Here and elsewhere in this section, we use the term "segment" rather loosely. As discussed later (see Anal division), the terminal "segment" comprises several abdominal segments. This body region is hereafter called the anal division.
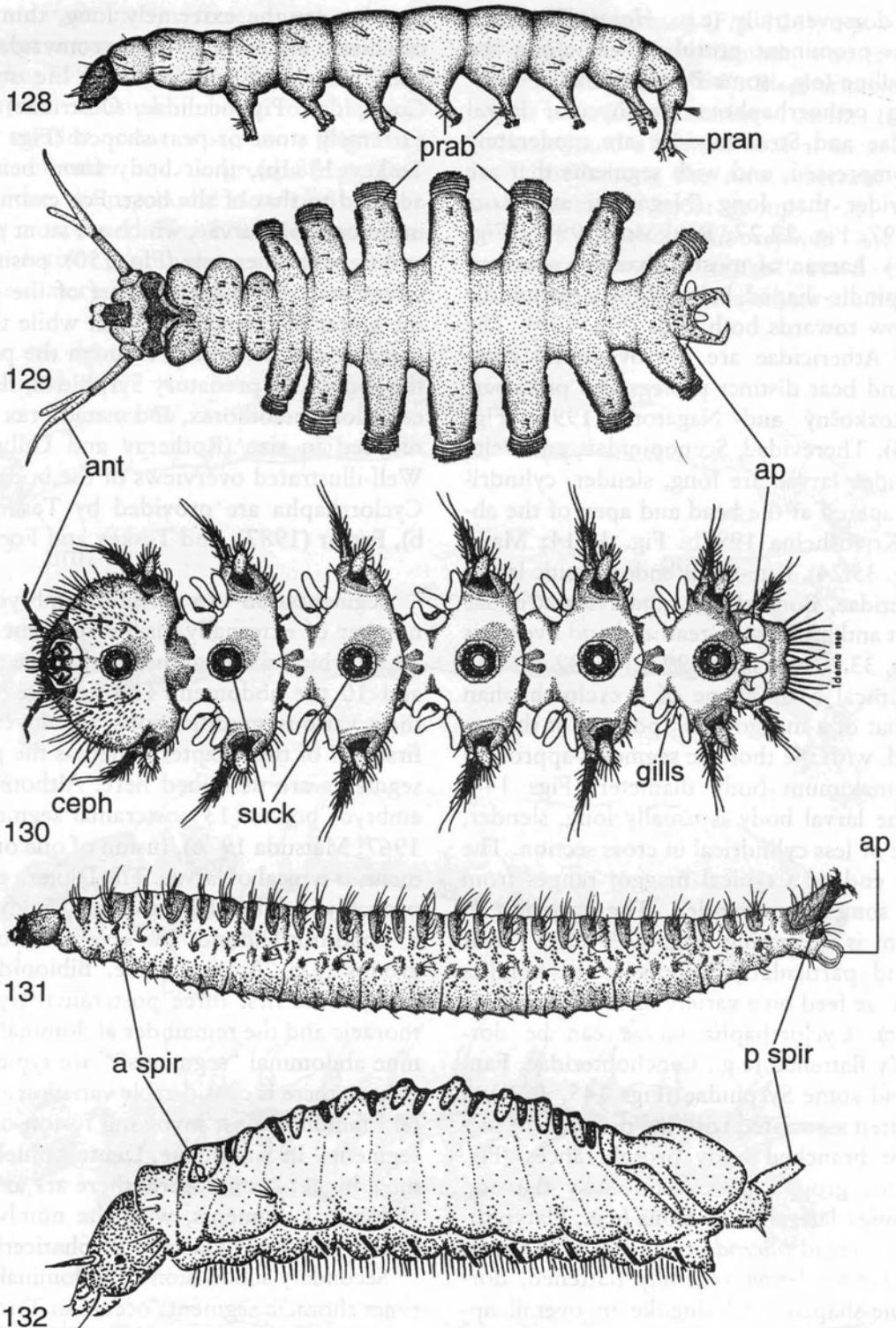
Figs 4.128–132. Habitus views of larval nematocerans. 128: *Nymphomyia* sp. (Nymphomyiidae), lateral view; 129: *Deuterophlebia* sp. (Deuterophlebiidae), dorsal view; 130: *Agathon* sp. (Blephariceridae), ventral view; 131: *Pericoma* sp. (Psychodidae), lateral view; 132: *Horaiella* sp. (Psychodidae), lateral view (abbreviations: ant: antenna, a spir: anterior spiracle, ap: anal papillae, ceph: cephalothorax, prab: abdominal prolegs, pran: anal proleg, p spir: posterior spiracle, suck: suctorial disc) (128 after Courtney 1994, 129 after Courtney 1990b, 130 after Hogue 1981, 131 after Quate and Vockeroth 1981, 132 adapted from Tonnoir 1933).

occurs in a few derived clades within the Ceratopogonidae (*Leptoconops* Skuse (Borkent et al. 1987)) and Sciaroidea (some Keroplatidae: Plachter 1979; Matile 1990). In spite of conflicting information regarding segmentation in Psychodidae, the abdomen apparently consists of eight segments (Keilin and Tate 1937; Satchell 1953; Jung 1958a, b; Quate and Vockeroth 1981).

Larval Blephariceridae are unique in that the head, thorax and first abdominal segment are fused into a cephalothorax (Fig. 130). Fusion and compression of anterior segments are probably related to the feeding mechanism, and serve to bring the mouthparts closer to the first of six ventral suckers (Fig. 165). Posteriorly, blephaericerid larvae are markedly compressed, their anal division comprising fused abdominal segments 7–10 (Craig 1967).

Brachyceran larvae typically have eight abdominal segments, the first seven of which are normal. In Asilidae, Apioceridae, and Mydidae, the terminal, or anal division is subdivided, with the posterior spiracle lying dorsolaterally or dorsally on the penultimate abdominal segment. Secondary subdivision of segments occurs in some families (e.g., Therevidae, Scenopinidae, and some Sepsidae and Syrphidae); in these groups, the true segments can sometimes be recognised by creeping welts or other segment-specific features. The body segments in Vermileonidae bear transverse wrinkles that are particularly evident as secondary annulations on the thorax (Nagatomi 1997: Fig. 30.48). Establishing homologies of the anal division has been controversial. Different techniques of studying the embryology of *D. melanogaster* suggest different results regarding the number of segments that produce the last abdominal division (see later).

Cuticle – The cuticle of Diptera larvae is usually soft, thin, non-pigmented, and thus largely translucent. The thickness and lack of pigment is probably related to larval life in moist substrates. Although the mechanism of pigmentation is known in relatively few nematocerans, some taxa (e.g., Thaumaleidae) apparently possess chromatocytes in the epidermis (Hinton 1958). Among other Diptera, diurnal larvae that feed in ex-posed situations often have thicker cuticle and darker body coloration. The cuticle itself is rarely pigmented but, if thick and leathery, is often yellowish. Dense pubescense (Figs 126, 133, 147, 151, 155) or small warts can shift the color to dark brown and the surface texture to matt (e.g., many Bibionidae and Sciomyzidae). Some Tabanidae are greenish to brownish in color with taxonomically important patterns of microtrichia (Figs 96, 100). In the aquatic family Athericidae, the cuticle is clothed with distinct microscopic pile (Figs 82, 84–86; Webb 1995; Thomas 1997). Yet another way to change body coloration is with pigmented haemolymph (Syrphidae: Rotheray and Gilbert 1989) or fat body (Sciomyzidae: Knutson and Berg 1963; Syrphidae: Rotheray and Gilbert 1989). The latter is, however, present in only late third-instar larvae. All modifications allow either for a uniform color of the larval body or for various patterns such as banding and spotting (Bhatia 1939). One of the most dramatically colored species is the blue *Microdon aeolidiformis* Wheeler (Syrphidae), which is covered with white scales and has a red fringe (Ferrar 1987). Coloration often changes from one instar to the next, with early instars usually being less pigmented.

Although the cuticle is often smooth and glabrous, many larvae possess at least some pubescence, and hairs of various size and structure. Tubercles (small, fleshy processes) may occur on one or more segments (Figs 126, 133, 153), particularly on the anal division and near the posterior spiracles (e.g., Tipulidae; Figs 137–138). These hairs or processes can serve various sensory, locomotory, or other purposes (see later). The larvae of some groups bear sclerotized plates on one or more thoracic segments (e.g., Xylophagomorpha; Teskey 1976) or on most body segments (e.g., many Psychodidae; Figs 131–132). Sclerotized, cuticular plates are uncommon in Cyclorrhapha larvae, but present in Lonchopteridae (Fig. 145), Fergusoninidae, and Tachinidae (e.g., Brauns 1954; Whitten 1956; Ferrar 1987). These plates are thought to protect larvae against predation or desiccation.

The larvae of Stratiomyidae and Xylomyidae are unique among Diptera in having the cuticle

encrusted with "warts" of calcium carbonate, forming a honeycomb or mosaic appearance (Fig. 95) (Rozkošný 1982; Woodley 1989). McFadden (1967) briefly reviewed the structure of these faceted cuticular deposits. Stratiomyidae also bear characteristic transverse rows of setae and a 'sternal patch' on abdominal segment 6. This patch is an oval field of specialised, presumably glandular, cuticular facets with a central pore

(Rozkošný 1982). In aquatic larvae, the posteroventral margins of the penultimate and occasionally antepenultimate segments are armed with a pair of strong sclerotized hooks (Fig. 94). In addition, anteroventral setae on the abdominal segments of some taxa are hooklike, similar to the large caudal spines (Sinclair 1989).

The larval cuticle also carries a multitude of sense organs that are of great diagnostic value
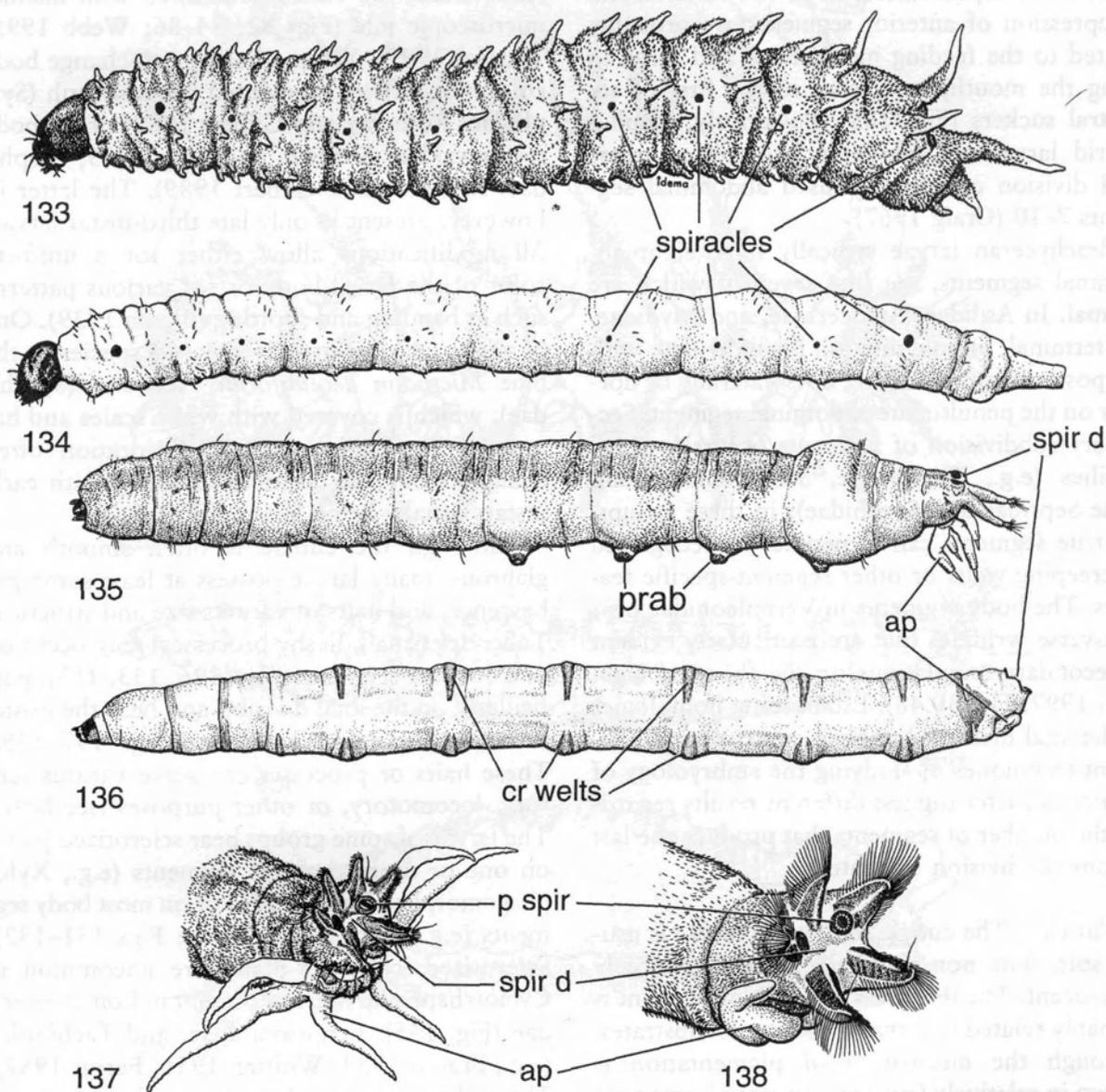
Figs 4.133–138. Larval nematocerans. 133: *Plecia* sp. (Bibionidae), habitus, lateral view; 134: *Hesperinus* sp. (Hesperinidae), habitus, lateral view; 135: *Pedicia* sp. (Pediciidae), habitus, lateral view; 136: *Limonia* sp. (Limoniidae) habitus, lateral view; 137: *Tipula* sp. (Tipulidae), anal division and spiracular disc; 138: *Ormosia* sp. (Limoniidae), anal division and spiracular disc (abbreviations: ap: anal papillae, cr welts: creeping welts, prab: abdominal prolegs, p spir: posterior spiracle, spir d: spiracular disc / plate) (133–134 after Hardy 1981, 135–138 after Alexander and Byers 1981).

and phylogenetic potential (Figs 120–122). However, their distribution is poorly known, except for a few groups (Hartley 1961; Hogue 1978; Lohs-Schardin et al. 1979; Harbach and Knight 1980; Kankel et al. 1980; Sæther 1980; Gasc et al. 1984; Colwell 1986; Dambly-Chaudiere and Ghysen 1986; Green and Hartenstein 1997; Rotheray and Gilbert 1989; Courtney 1990a; Colwell and Scholl 1995). Available information suggests that the distribution of sense organs (setae) is stable across instars and could be evolutionarily conservative to homologize across major Dipteran subgroups. Often the number and position of sense organs are stable but differences occur in the type of sense organ that forms in a particular position. The most important and easily recognised sense organs in Cyclorrhapha are trichoid sensilla (Figs 120–122), basiconic sensilla, papilla ("pit") sensilla (Fig. 121; Kankel et al. 1980; Singh and Singh 1984; Green and Hartenstein 1997), and subepidermal chordotonal organs, which are difficult to detect externally but genetically related to external sense organs (Bodmer et al. 1987; Merritt 1997).

Morphologists generally have been more interested in the conspicuous, often very large, fleshy cones, processes, and protuberances (Figs 126, 133, 146, 149, 153). Such cones are often segmentally arranged, and range from small to large, and simple to branched. They are usually associated with sense organs carrying sensilla in either a terminal position or nearby. Different instars and closely related species within the same family can differ considerably with regard to these cones (e.g., Rhinophoridae: Ferrar 1987) suggesting that the cones are less conservative than their associated sense organs. It is therefore important to study the distribution of sense organs before establishing homology of the larger and more conspicuous fleshy protuberances.

One of the most conspicuous and widespread sense organs of the Diptera is **Keilin's organ**, which is also known as the tuft organ (Lanfranchi and Belcari 1990; Ross and Anderson 1991; but see Colwell 1986). One pair of Keilin's organs occurs ventrally on each thoracic segment. In the Cyclorrhapha, these sense organs consist of three hair sensilla that emerge from a single

opening of the cuticle (Fig. 120; Lanfranchi and Belcari 1990). Homologous sensilla are known to occur on the larvae of some nematocerous Diptera and orthorrhaphous Brachycera, but the fine structure differs throughout the Diptera. Keilin's organs are apparently sensitive to humidity and are the last remains of thoracic legs in larval Diptera. During metamorphosis, they are transformed into tarsal sense organs of the adult (Melzer et al. 1999).

Locomotory structures – In spite of the absence of jointed thoracic legs in larval Diptera, locomotion is highly diverse, reflecting the group's diversity in habitat and habits. Most forms of locomotion use a combination of turgor pressure and antagonistic contraction of muscles. Body wall muscles typically include bundles oriented in various directions: dorsals (typically longitudinal), ventrals (typically longitudinal), laterals (typically dorsoventral), and transverse (Snodgrass 1935). Many (most) longitudinal muscles are intersegmental, but their homologies can be established through studies of innervation (Birket-Smith 1984). Birket-Smith's (1984) investigation of the larval musculature in insects included one dipteran (*Tipula*).

Basic locomotion in many groups is initiated at the posterior end (Roberts 1971c). Typically, this end is lifted and preceding segments are contracted. The posterior end is then placed back on the substrate and a wave of contraction moves to the anterior part of the body, thus stretching the anterior end forward while the segments behind the wave are placed back on the substrate. Larvae that inhabit loose sediments (e.g., *Hexatoma*) can sometimes inflate their posterior segments, using them as an anchoring device. Other types of unusual locomotion include the quick, zig-zag movement of larval Thaumaleidae (Thienemann 1909) and the rapid, lateral shifting of larval Blephariceridae (Frutiger 1998). Both behaviors are presumably a response to disturbance (Tonnoir 1930).

Because larval Diptera lack jointed thoracic legs, various kinds of hooks, tubercles, and fleshy organs can be particularly useful for locomotion. Locomotory appendages operate through a combination of turgor pressure and muscle action,

and include creeping welts, prolegs, and other specialised structures (e.g., suctorial discs).

Creeping welts. Creeping welts are transverse, swollen ridges that bear one-to-several modified setae, spines, or spinules. They are usually present on the anterior margin of abdominal segments, but in cyclorrhaphan larvae typically also involve adjacent segments. In the latter, a few anterior rows of proclinate spines can occur on the posterior edge of the anterior segment, whereas the more extensive part of the welt is on the an-

terior side of the following segment (Fig. 119). The orientation of spines and spinules is usually reclinate (Fig. 119). Rows of proclinate spinules and spines might aid in backward movement.

Distinct creeping welts occur on the larvae of several nematocerous groups, including Dixidae, many Tipulidae (Figs 135, 154–155), and several Bibionomorpha. Among orthorrhaphous taxa, ventral creeping welts are common in Rhagionidae and Empidoidea, and both dorsal and ventral welts occur in Xylophagidae (Teskey 1976). Larval Acroceridae have one to three ventral welts
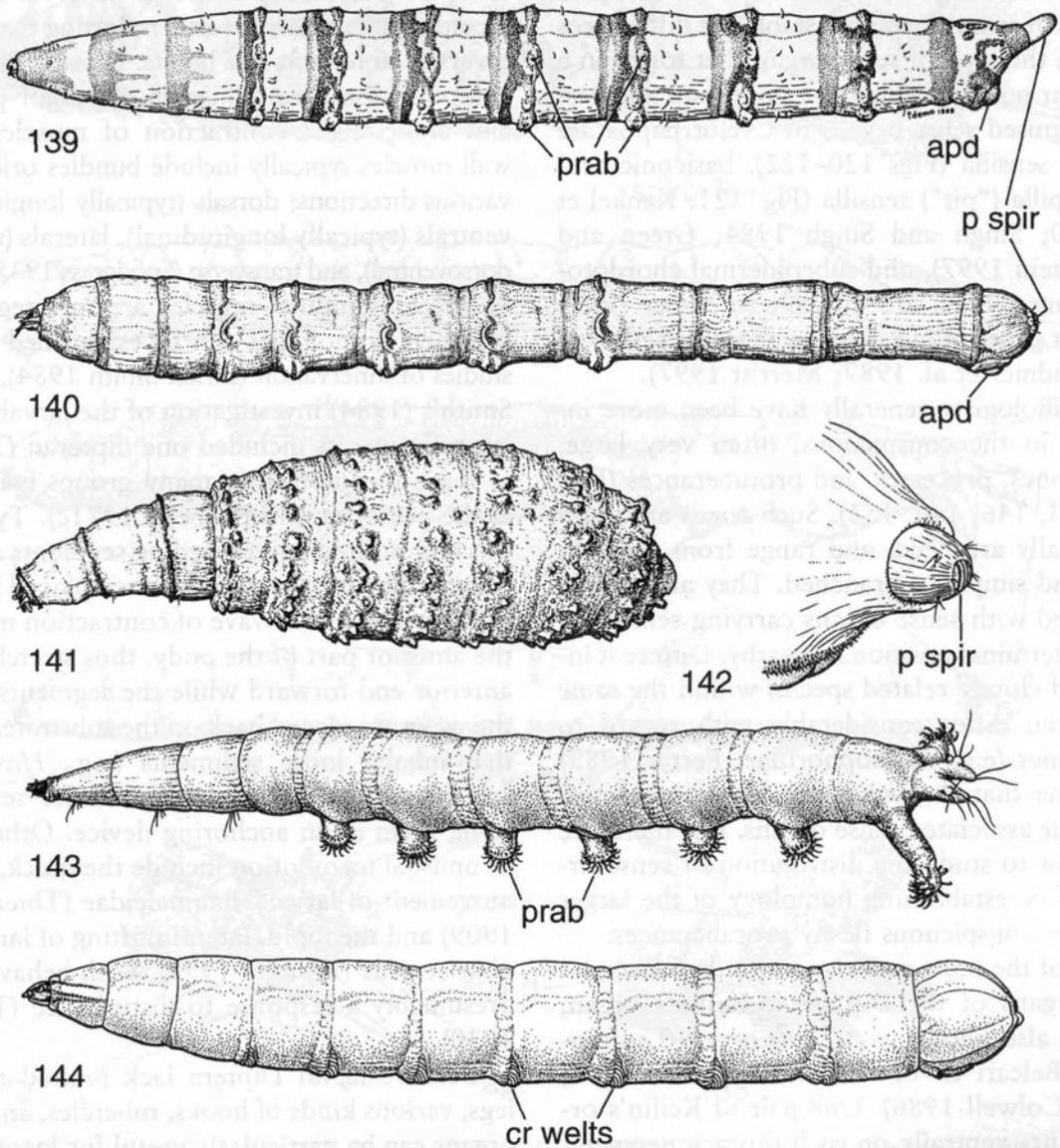
Figs 4.139–144. Tabanomorpha and Empidoidea. 139–141: habitus of Tabanidae, lateral view: 139: *Tabanus* sp.; 140: *Esenbeckia* sp.; 141: *Goniops* sp. 142: *Tabanus* sp. (Tabanidae), posterior spiracle. 143–144: habitus of Empididae, lateral view: 143: *Hemerodromia* sp.; 144: *Rhamphomyia* sp. (abbreviations: apd: anal pad, cr welts: creeping welts, prab: abdominal prolegs, p spir: posterior spiracle) (139–142 after Pechuman and Teskey 1981, 143–144 after Steyskal and Knutson 1981).

or pads of minute setae on the abdominal segments (Schlinger 1981). Cyclorrhapha larvae typically use creeping welts as anchoring devices (Figs 119, 147). These welts are found mostly on abdominal segments and often consist of bands of spinules or spines on un-elevated cuticle. The distribution and morphology of creeping welts vary considerably between segments, instars, species, and families. In general, creeping welts are more developed in later instars (but see Colwell and Scholl 1995), most prevalent on abdominal segments (but see Rotheray and Gilbert 1989), and have more or larger spines on the ventral side of the body. Many creeping welts consist only of rows of tiny spinules. Others have large, strongly sclerotized, darkly pigmented spines of variable shape. Unusual creeping welts occur in larvae from unusal substrates (e.g., agromyzid larvae that orient sideways in leaf mines have creeping welts only on the lateral side of the body). In many endoparasitic larvae, the creeping welts have more or less disappeared, but spines occur all over the body (Teskey 1981a; Ferrar 1987).

Prolegs. Prolegs are paired, fleshy, round to elongate, retractable processes that bear apical spines or crochets (small, curved hooks). Prolegs come in a diversity of shapes, sizes, and positions, and their characteristics can be extremely important in the identification of families, genera, and species. Depending on the group, prolegs occur on the thorax, abdomen, and/or anal division (Table 2).

Thoracic (prothoracic) prolegs occur in many Chironomoidea, including Thaumaleidae (Fig. 157), Simuliidae (Fig. 125), Chironomidae (Figs 123–124, 158–159), and plesiomorphic Ceratopogonidae (Fig. 126). In fact, this feature is one of the frequently cited synapomorphies of the superfamily (Hennig 1973; Wood and Borkent 1989; Oosterbroek and Courtney 1995). First-instar corethrellid larvae have similar prolegs (Borkent and McKeever 1990), suggesting the possibility that thoracic prolegs define a more inclusive clade, perhaps all Culicomorpha. With few exceptions (e.g., some Syrphidae), larval Brachycera lack thoracic prolegs.

Abdominal prolegs occur on the larvae of many Diptera (Table 2), including the nematoceran groups Ptychopteridae (Fig. 156; Rozkošný 1997a: Fig. 15.13), Dixidae, Tipulidae (Fig. 136), and all Blephariceromorpha. Among the latter, first-instar larvae of most Blephariceridae (Zwick 1977; Courtney 1990a) and all larval instars of Deuterophlebiidae (Courtney 1990a) and Nymphomyiidae (Fig. 128; Courtney 1994: fig. 65) have prolegs on abdominal segments I-VII. deuterophlebiid larvae are unusual in that their prolegs vary between instars (Courtney 1990a), with striking differences between the first instar (Fig. 162) and subsequent instars (Figs 129, 163).

Among the Brachycera, several aquatic larvae possess abdominal prolegs. Athericidae bear seven pairs of prolegs and a single, median proleg posteriorly (Figs 84, 86–87; Webb 1995; Thomas 1997). Seven or eight pairs of ventral prolegs occur in many aquatic Empididae. Rings of three or four pairs of small tubercles or short prolegs occur in Tabanidae (Fig. 99) and Asilidae (Melin 1923; Teskey 1969). Larvae of Vermi-leonidae are unique among terrestrial larvae in that the first abdominal segment bears a ventral, median proleg, and segments 6 and 7 have a posterodorsal comb of recurved flattened spines (Nagatomi 1997: Figs 30.52–56). In the aquatic larvae of certain Cyclorrhapha (e.g., some Syrphidae, Ephydridae, and Muscidae), creeping welts have apparently transformed into prolegs (Figs 147, 151). Except in certain Syrphidae, such prolegs are restricted to the abdomen.

Because abdominal prolegs occur on various segments in several unrelated Diptera (Table 2), their evolution may be susceptible to convergence (Hinton, 1955). However, several authors (Wood and Borkent 1989; Courtney 1990a, 1991; Oosterbroek and Courtney 1995) have used the presence of abdominal prolegs to help define certain clades (e.g., Blephariceromorpha).

Anal prolegs are present on larval Tanyderidae, Thaumaleidae, Simuliidae (Fig. 125), Chironomidae (Figs 123–124, 160), plesiomorphic Ceratopogonidae (Fig. 126), and Nymphomyiidae (Fig. 128; Courtney 1994: fig. 66). Within these groups, the form of the prolegs is highly
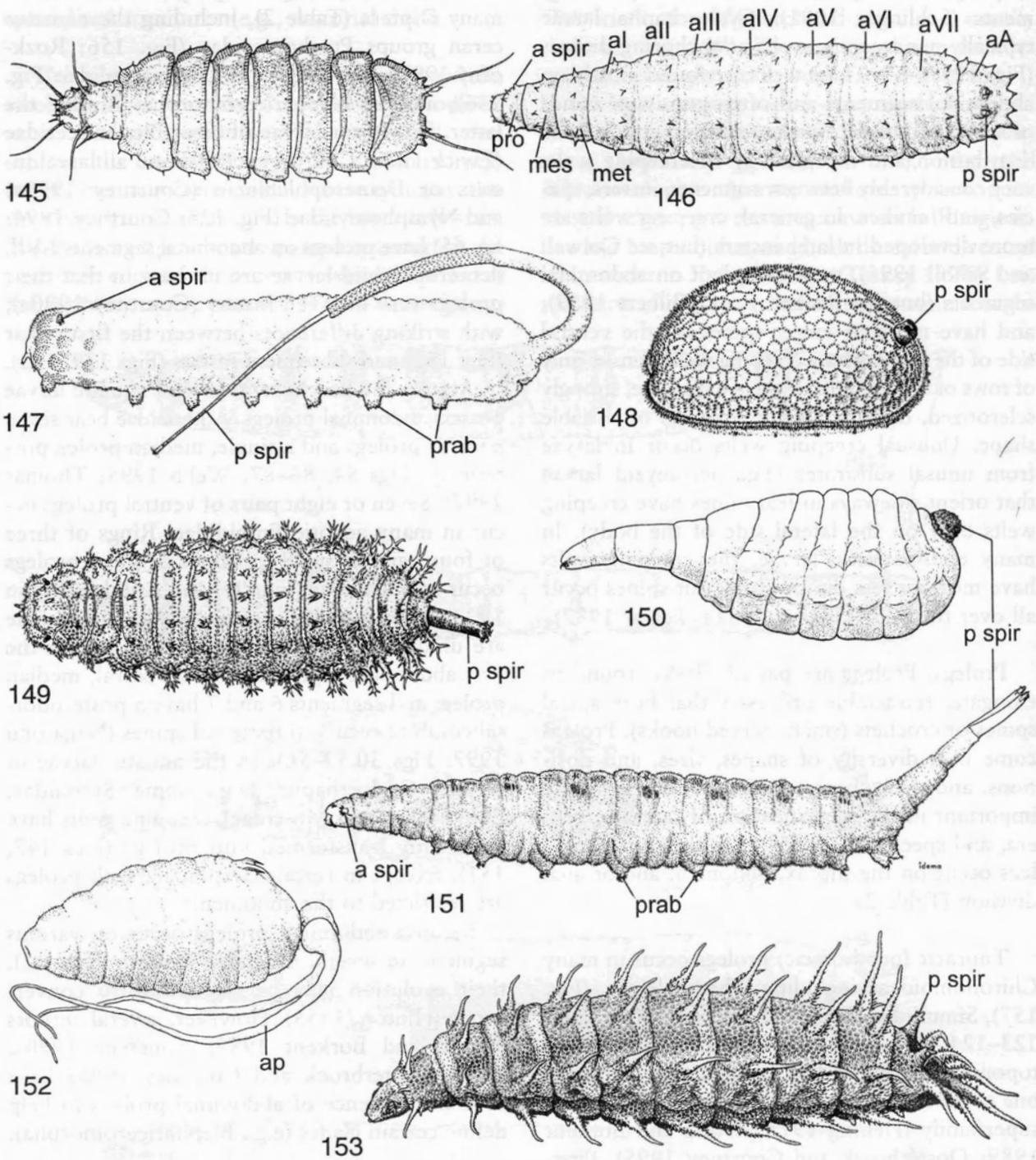
Figs 4.145–153. Habitus of larval cyclorrhaphans. 145: *Lonchoptera* sp. (Lonchopteridae), dorsal view; 146: *Megaselia* sp. (Phoridae), dorsal view; 147: *Eristalis* sp. (Syrphidae), lateral view; 148: *Microdon* sp. (Syrphidae), dorsolateral view; 149: *Brachyopa* sp. (Syrphidae), dorsal view; 150: *Physocephala* sp. (Conopidae), lateral view; 151: *Ephydra* sp. (Ephydridae), lateral view; 152: *Cryptochetum* sp. (Cryptochetidae), lateral view; 153: *Fannia* sp. (Fanniidae), lateral view (abbreviations: aA: anal division, aI-aVII: abdominal segments 1–7, ap: anal papillae, a spir: anterior spiracle, mes: mesothorax, met: metathorax, pro: prothorax, prab: abdominal prolegs, p spir: posterior spiracle) (145 after Peterson 1987a, 146 after Peterson 1987b, 147–149 after Vockeroth and Thompson 1987, 150 after Smith and Peterson 1987, 151 after Wirth et al. 1987, 152 after McAlpine 1987b, 153 after Huckett and Vockeroth 1987).

variable. Many of these groups apparently use anal prolegs to anchor the larva in the substrate or in flowing water. The latter characterise Simuliidae, an abundant and economically important group in streams. Larvae of these flies use a crochet-tipped anal proleg and silk pad to adhere to submerged rocks or vegetation. Among orthorrhaphous Brachycera, the Athericidae have a single, median proleg on the terminal end (Fig. 84). Both Scenopinidae and Therevidae are characterised by a pair of retractable, glabrous, fingerlike, apical prolegs on the posterior abdominal segment (Irwin and Lyneborg 1981: fig. 37.23, Krivosheina 1997b: Figs 36.23–24).

Other locomotory devices. Other specialised structures used for locomotion or attachment include friction pads and suctorial discs. Several genera of Psychodidae possess **friction pads**, which are areas of modified cuticle on the ventral surface of the thorax and/or abdomen. These areas are often elongate (e.g., *Maruina*), oblong (*Horaiella*; Fig. 132), or circular (*Neotelmatoscopus*; Fig. 164), and fringed with dense marginal hairs. These structures probably help to diminish drag on larvae in flowing water. Functionally similar structures may occur in certain Ephydridae (Mathis and Hogue 1986), particularly in groups inhabiting waterfalls and thin films of flowing water.

Suctorial discs are true hydraulic suckers on the ventral surface of larval Blephariceridae (Figs 130, 165–167) and are an obvious adaptation to life in torrential streams. Dipterists have been interested in the structure of suctorial discs for nearly a century, and several authors have provided detailed descriptions (Kellogg 1900; Komarek 1914; Bischoff 1928; Rietschel 1961). Suctorial discs, which function as true vacuum pumps, contain a rigid piston housed within a central opening and surrounded by several layers of complex cuticle (Fig. 165). From the central opening to the disc margin are layers of flexible, ridged cuticle; finely reticulate cuticle; and at least two layers of macrotrichia (Fig. 167). Near the transitional zone between the ridged and reticulate cuticle are several setiform sensillae (usu-

ally three pairs). The outer margin of the suctorial disc is smooth, highly folded, and flexible (Fig. 166). The suctorial disc creates a vacuum primarily through contraction of strong muscles inserted on the central piston. Anteriorly, the disc bears a distinctive notch, through which the vacuum is released. Smaller muscle bundles attached to the lateral margins permit additional disc mobility. Suctorial disc operation and general movement of blepharicerid larvae are complex, behavior dependent, and apparently predictable (Frutiger 1998). Some authors (Tonnoir 1933b; Craig 1967) discussed the evolution of ventral suckers in Blephariceridae, and others (Hora 1930; Hinton 1955) evaluated the hypothesis that ventral suckers are homologous to the lateral abdominal prolegs of Deuterophlebiidae. Although it is possible that suctorial discs evolved from a structure comparable to a friction pad (Tonnoir 1933b), there is general agreement that suctorial discs are not homologous with lateral prolegs.

Another form of locomotion in larval nematocerans is active swimming (e.g., serpentine movements in Ceratopogonidae; antennal propulsion in Chaoboridae). Larvae of aquatic Stratiomyidae can use their mouthparts for propulsion. Swimming also occurs in some sciomyzid larvae, and skipping is known in some terrestrial larvae. The latter is best known in the cheese skipper (*Piophila casei* (Linneaus)) but widespread among acalyptrate groups. During skipping, the larval mouth attaches to the terminal end of the larva. Muscle contraction increases tension in the body, the release of which causes the larva to skip. Another specialised form of locomotion, unique among the Cyclorrhapha, occurs in some terrestrial Syrphidae. In these larvae, the ventral abdominal surface is conspicuously grooved (Rotheray and Gilbert 1989) and the larva moves on a slimy trail (Roberts 1971c) thought to aid in locomotion. The liquids are produced in the salivary gland and anus (Roberts 1971c; Rotheray and Gilbert 1989). Contrary to many reports, mouthhooks play a minor role in the normal locomotion of Cyclorrhapha larvae (Roberts 1971c).
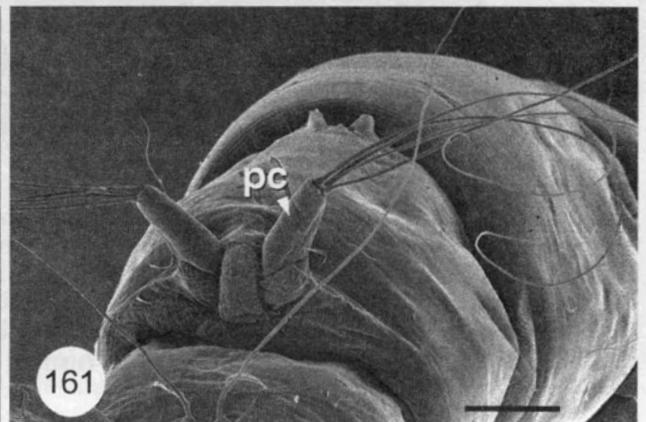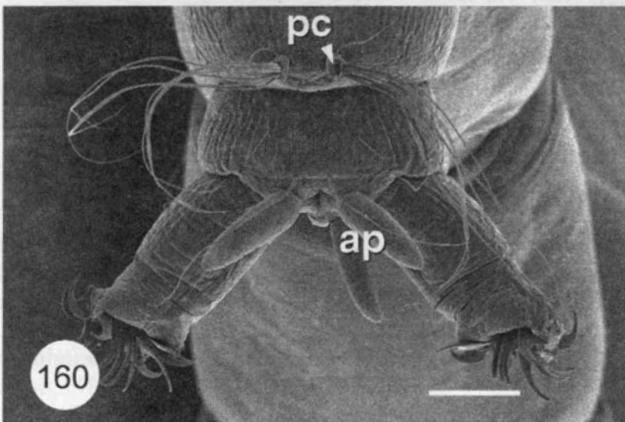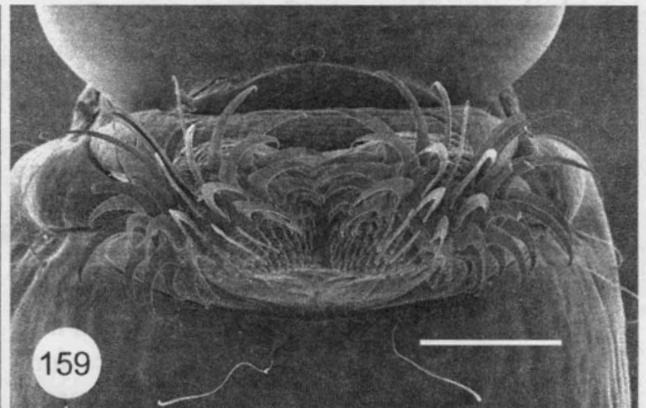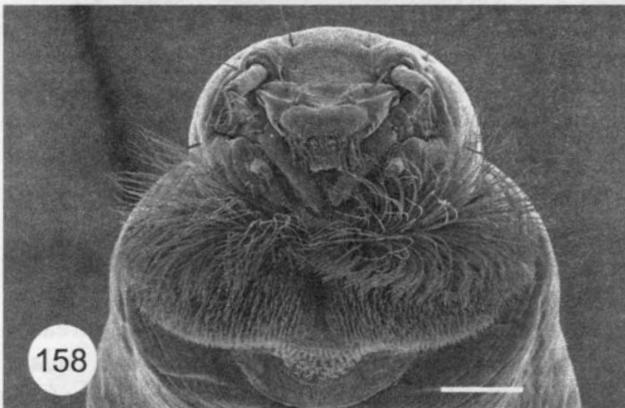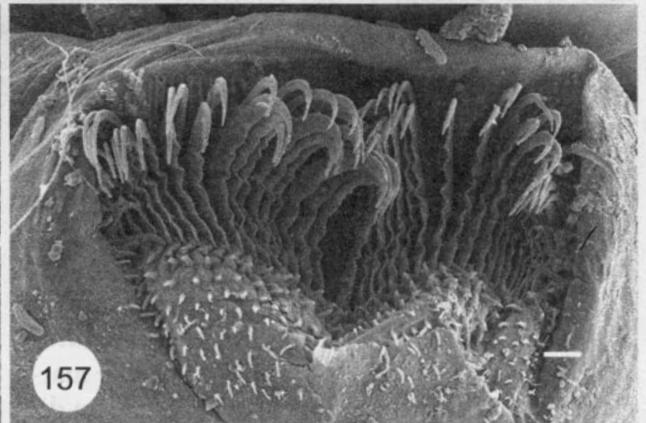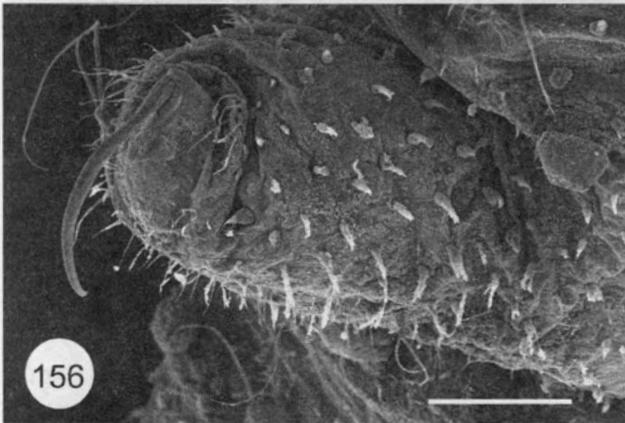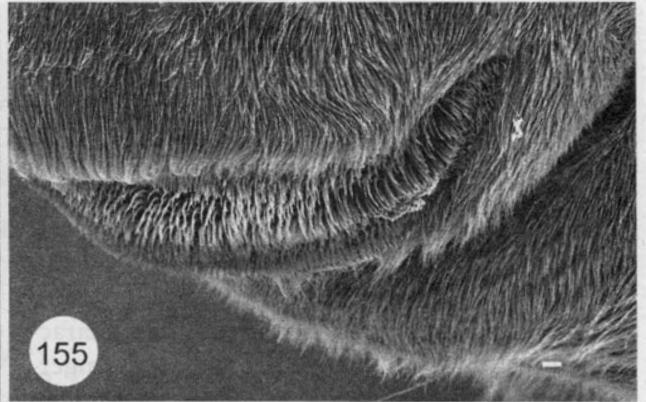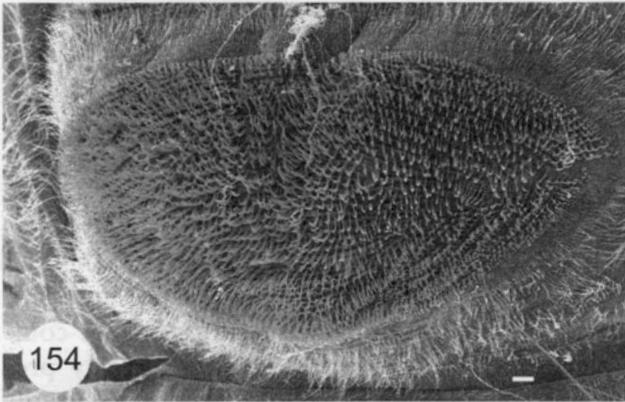
Respiratory system – Larval Diptera show a variety of respiratory adaptations, many a reflection of life in fluid or semi-fluid habitats. The basic respiratory system comprises an internal system of tracheae and the external spiracles. The tracheal system has been well-documented by Keilin (1944) and Whitten (1955), and reviewed in several general texts (e.g., Teskey 1981a). The basic arrangement includes two dorsal and two lateral longitudinal trunks, each of which is united by a series of anastomoses and connectives (Teskey 1981a: fig 3.15); reductions in this basic scheme occur in several groups (Whitten 1963). Most larvae possess 10 pairs of spiracular tracheae, but some may be non-functional. Larvae of the Bibionidae, some higher Nematocera, and the Brachycera possess a full compliment of tracheae and anastomoses (Whitten 1960; Teskey 1981a), whereas most other groups have lost certain connectives. The dorsal tracheal trunks of some larval Chaoboridae and Culicidae are modified as hydrostatic organs, an adaptation to help larvae maintain their position in water (Keilin 1944).

The cyclorrhaphan tracheal system is remarkably constant (Keilin 1944; Whitten 1955, 1956, 1960; Tatchell 1960) and is distinguished from the system of nematocerans and orthorrhaphous brachycerans by the following characters (Whitten 1960): (1) the first dorsal anastomosis is markedly broad; (2) the ventral ganglionic tracheae are extended to the concentrated nervous system, which is in an anterior position; and (3) the last visceral tracheae are well-developed. These characteristics occur in basal aschizans such as *Lonchoptera* Meigen and in derived Schizophora such as *Calliphora* (Whitten 1960). Larval *Lonchoptera* are the only known cyclorrhaphan in which the last dorsal anastomosis is not short and broad as in lower Brachycera, but is long as in most of the remaining anastomoses. Given that *Lonchoptera* is a basal aschizan, this

condition is probably plesiomorphic. Even the tracheal system of *Gasterophilus* Leach, whose larvae live under the largely anaerobic condition of the horse digestive system, can be easily derived from the typical cyclorrhaphan condition (Tatchell 1960). The main new structure is a tracheal organ connected to haemoglobin-carrying cells. Other respiratory modifications in the Cyclorrhapha are known from some Syrphidae where the second and third anastomoses are reduced (Whitten 1960). A suite of adaptations occur in larvae from aquatic environments. Some Syrphidae have tracheae enlarged into rows of bladders (Keilin 1944) and some Ephydridae carry an external gas bubble (physical gill) around the posterior spiracles (Hennig 1973).

Number and distribution of spiracles. The anlage of three pairs of thoracic and eight pairs of abdominal spiracles appear early in the embryo of *Drosophila* (Fullilove et al. 1978; Martinez-Arias and Lawrence 1985), *Bactrocera* Macquart (Anderson 1966), *Stomoxys* Geoffroy (Ajidagba et al. 1983), and *Lucilia* Robineau-Desvoidy (Davis 1967: 11 anlagen in fig. 6). The same arrangement is probably typical of most Diptera. However, only 10 pairs of spiracles occur in larval flies, and most groups have fewer that are open and used for respiration. Most spiracles are functional only during molting, when the old tracheae of a given segment are withdrawn through these spiracles (Whitten 1980). Larvae of only the Bibionidae and genus *Pachyneura* (Pachyneuridae) possess a full compliment of functional spiracles. In these taxa, paired spiracles occur on the prothorax, metathorax, and each of eight abdominal segments. Spiracles on the prothorax are apparently mesothoracic spiracles that migrated forward (Hinton 1947). Keilin (1944) proposed that originally all spiracles were intersegmental but that the spiracle between the prothorax and mesothorax shifted

Figs 4.154–161. Scanning electron micrographs of locomotory devices and anal appendages of larval nematocerans. 154–155: *Antocha* sp. (Limoniidae), abdominal segment: 154: ventral creeping welt, 155: dorsal creeping welt. 156: *Bittacomorpha* sp. (Ptychopteridae), abdominal proleg. 157–159: thoracic prolegs: 157: *Androprosopa* sp. (Thaumaleidae); 158: Chironomidae – Chironominae sp.; 159: Chironomidae – Orthocladiinae sp. 160: Chironomidae – Orthocladiinae sp., anal division. 161: Chironomidae – Tanypodinae sp., procercus (abbreviations: ap: anal papillae; pc: procercus; scale bars: 10μm (Figs 154–155, 157), 100μm (Figs 156, 158–161)).

anteriorly while all others were displaced posteriorly. For these reasons, we recommend that the term **anterior spiracles** is preferred over the commonly used term prothoracic spiracles. Likewise, the posterior-most pair, which represents the eighth abdominal spiracle but is often located on the apparent ninth segment, is referred to as **posterior spiracles**.

The number and distribution of spiracles are summarized in Figure 170. All systems can be found among representatives of larval nematocerans. As discussed previously, the basic arrangement is characterised by a full compliment of 10 pairs of spiracles. This **holopneustic** system occurs in only a few Bibionomorpha. Loss of posterior thoracic (metathoracic) spiracles characterises the **peripneustic** system, which occurs in several Bibionomorpha (Cecidomyiidae, the mycetophilid subfamily Ditomyiinae, and the Pachyneuridae exclusive of *Pachyneura* Zetterstedt) and higher Nematocera (Scatopsidae, Synneuridae). The **hemipneustic** system, which is a slight variant of the peripneustic system, involves loss of the posterior thoracic spiracles and posterior spiracles, and occurs in most Mycetophilidae and Sciaridae. The **amphipneustic** arrangement includes only anterior and posterior spiracles, and occurs in Tanyderidae, Thaumaleidae, Axymyiidae, and many higher Nematocera (Trichoceridae, Anisopodidae, most Psychodidae). The **propneustic** system is characterised by the presence of only anterior spiracles and is found only in certain Mycetophilidae. A more common arrangement is the presence of only posterior spiracles, the **metapneustic** system. This system is typical of many aquatic nematocerans (e.g., Dixidae, Culicidae, Ptychopteridae, Tipulidae). Many other aquatic groups (e.g., Simuliidae, Ceratopogonidae, most Chironomidae, all Blephariceromorpha) lack spiracles and are **apneustic**.

In the larvae of most Brachycera, the spiracles of the metathoracic and abdominal segments 1–7 are rudimentary and probably non-functional; these larvae are, therefore, functionally amphipneustic. Among orthorrhaphous groups, the larvae of Nemestrinidae (Fuller 1938) and Tabanidae (Teskey 1969) are metapneustic. Acroceridae are peripneustic but most spiracles are probably nonfunctional. The family should therefore be considered amphipneustic. Apneustic larvae have been reported in Rhagionidae (James and Turner 1981) and many aquatic Empidoidea (e.g., Hemerodromiinae, Clinocerinae). The respiratory system of cyclorrhaphan larvae is either apneustic, metapneustic, or amphipneustic. The apneustic condition is rare but reported in first-instar larvae of Pipunculidae and the first- and second instars of Cryptochetidae (Keilin 1944; Ferrar 1987). Both groups are obligatory endoparasitoids of Homoptera. Metapneustic larvae are common in the Cyclorrhapha because all first instars apparently have no functional anterior spiracles (Keilin 1944). However, a single porelike opening at the anterior end of the dorsal longitudinal trunk has been reported in various calyptrate flies (Kitching 1976; Ajidbaga et al. 1983). Whether they are functional remains contentious (Roberts 1981). Metapneustic second- and third-instar larvae are comparatively rare in Cyclorrhapha, but known in Braulidae, Pupipara, and some Ephydridae and Syrphidae (Keilin 1944; Hinton 1947; Hartley 1958, 1961). Functionally metapneustic larvae with anterior spiracles hidden in grooves or pockets are known from several families (e.g., Drosophilidae, Ephydridae, Cuterebrinae, Gasterophilinae, Canacidae, Aulacigasteridae). The spiracles of these species are either everted rarely during larval life or functional only during a brief period before pupation. An amphipneustic arrangement is typical of second- and third-instar larvae of Cyclorrhapha (Figs 146–149, 151).

Anterior spiracles. As mentioned, the segmental origin of the anterior spiracles is controversial. Snodgrass (1924; 1935) argued that they are not homologous to any adult spiracle because they are part of the dorsal longitudinal tracheal trunk (i.e., adult spiracles attach to the ventral longitudinal trunk). His argument is not very convincing because anteriorly both trunks are fused (Whitten 1955, 1956, 1960). The anterior spiracles are on the prothorax (Fig. 146), a segment that lacks spiracles in most Pterygota; consequently, several authors propose that anterior spiracles are mesothoracic spiracles that migrated

forward (Hinton 1947; Ludwig 1949). However, during early embryogenesis there are anlagen for spiracles on all thoracic segments, and, before connecting with the internal tracheal system, the felt chamber of the anterior spiracle forms on the prothoracic segment (Anderson 1966; Fullilove et al. 1978; Ajidagba et al. 1983). Thus, the possibility that anterior spiracles are of prothoracic origin cannot be eliminated until it is known which of the three thoracic tracheal anlagen fails to produce a functional spiracle.

The anterior spiracles of larval nematocerans and orthorrhaphous brachycerans are usually sessile and located on the dorsolateral margin of the prothorax (Figs 95, 172–174). The anterior spiracles of Cyclorrhapha larvae have a similar position but are often situated on conspicuous cuticular projections. The latter consist of a projecting felt chamber with one to many openings. In the Schizophora, the openings are usually at the end of lobe-like projections (Figs 110–112, 118). In most "Aschiza" the openings are sessile at the end of a stalk (Fig. 109; Teskey 1981a; Ferrar 1987). A perispiracular gland of unknown function is associated with these spiracles (Keilin 1944; Whitten 1980), and in third-instar larvae the ecdysial scar of the spiracle of the second-instar larva is posterior to the functional spiracle (Fig. 118).

In most groups, the first noticeable anterior spiracles occur in second-instar larvae and have only a single opening. Later instars have from few to "thousands" of lobes, with 5–20 lobes being an average number for a typical third-instar larva (Figs 110–112, 118; Ferrar 1987). The position of the lobes on the felt chamber is highly variable and of great diagnostic value. Terms such as rosette-shaped, fan-shaped, broadly fan-shaped, bifurcate spread, vertically elongate, and tree-shaped have been used to describe the arrangement of lobes (Figs 110–112, 118). The position of the anterior spiracle on the cyclorrhaphan body is remarkably constant; however, in larval Agromyzidae the spiracles have moved to a dorsal position, which is probably related to the sideways feeding position in leaf mines (Ferrar 1987). Another remarkable shift in position occurs in some predatory Syrphidae, where the anterior spiracles are on the mesothorax (Rotheray and Gilbert 1989).

Posterior spiracles. The posterior spiracles are on the terminal abdominal division, which usually represents a composite of several embryological segments. In the larvae of nematocerous Diptera, the posterior spiracles are usually sessile and in a dorsal or posterodorsal position. Spiracles are often surrounded by complex lobes, hairs, or sclerites (Figs 135–138) and can be of considerable value in the identification of families and genera (Alexander 1981; Teskey 1981b). The area surrounding the posterior spiracles is often called the **spiracular disc**, and is especially well-developed in certain groups (Figs 137–138). In several groups (e.g., Culicidae, Axymyiidae, several higher Nematocera), the spiracular disc is borne on an elongated projection or lobe (Figs 131–132). These lobes usually bear apical hooks or elongate hairs (Figs 175–178), the latter of which can prevent wetting of the spiracular field in aquatic larvae. Aquatic groups show a variety of respiratory adaptations. In many, respiration via the posterior spiracles may be directly from the atmosphere (e.g., Dixidae, most Culicidae) or from plant tissues (e.g., some Culicidae). The larvae of some families remain close to the air-water interface, and the upper 5 cm of damp-to-saturated sediments is among the favored habitats of many species (e.g., many Tipulidae). The larvae of Ptychopteridae overcome this need to remain near the surface by having a slender terminal respiratory siphon that can extend two or three times the body length (Rozkošný 1997a: Fig. 15.13). The presence of haemoglobin in the blood of some Chironomidae may assist the absorption of oxygen.

In larvae of orthorrhaphous Brachycera, the posterior spiracles are located anterodorsally in Xylophagomorpha, Acroceridae, Nemestrinidae, and Bombyliidae (*Heterotropus*) and mid-dorsally in Vermileonidae. In Asiloidea, the posterior spiracles are on the penultimate abdominal segment, a condition considered synapomorphic of the superfamily (Woodley 1989). The spiracles of Therevidae and Scenopinidae are on the antepenultimate segment, a more derived state
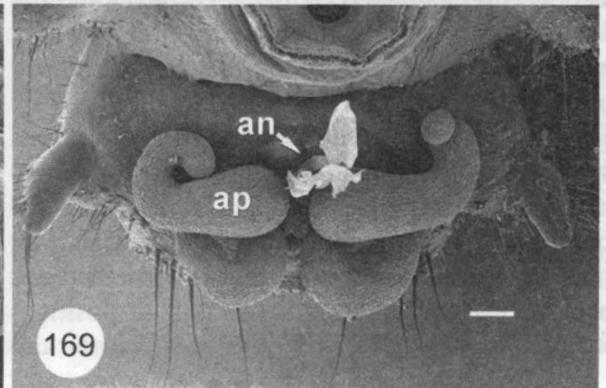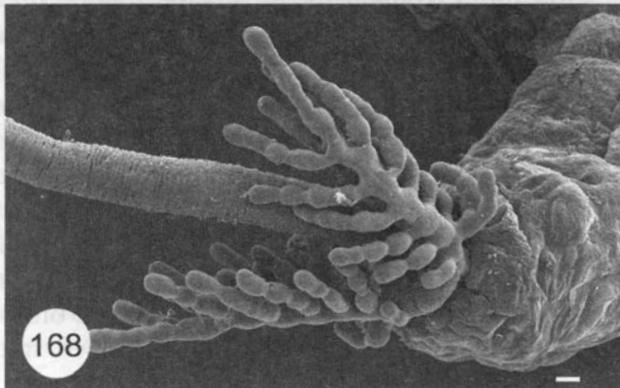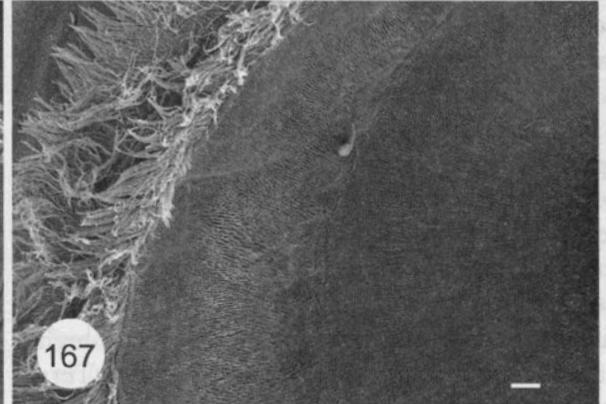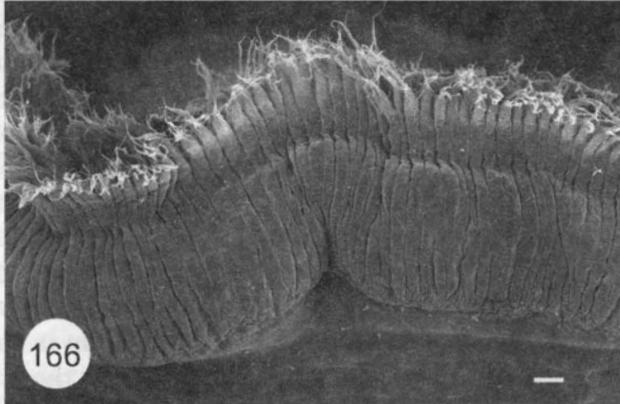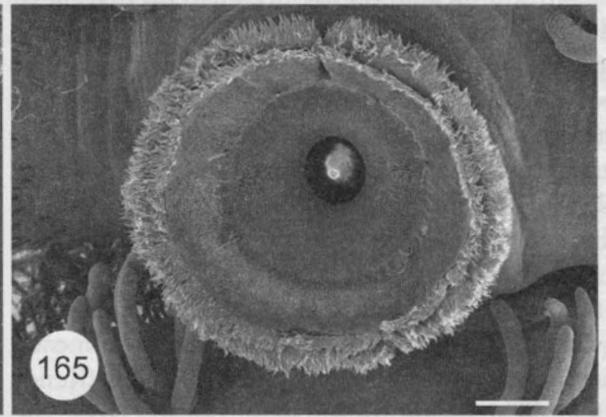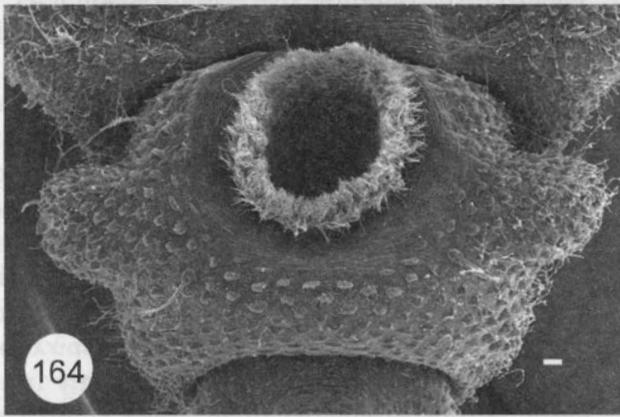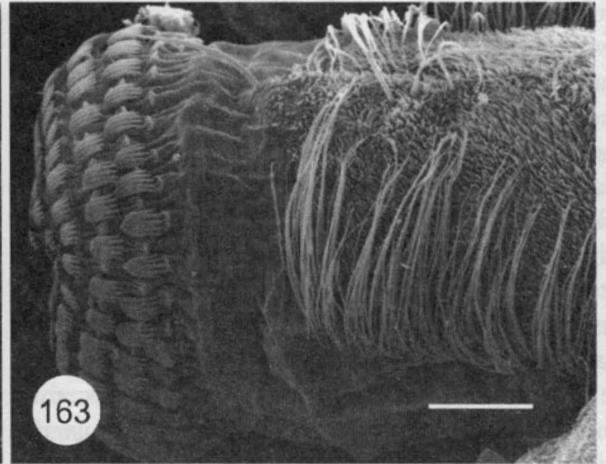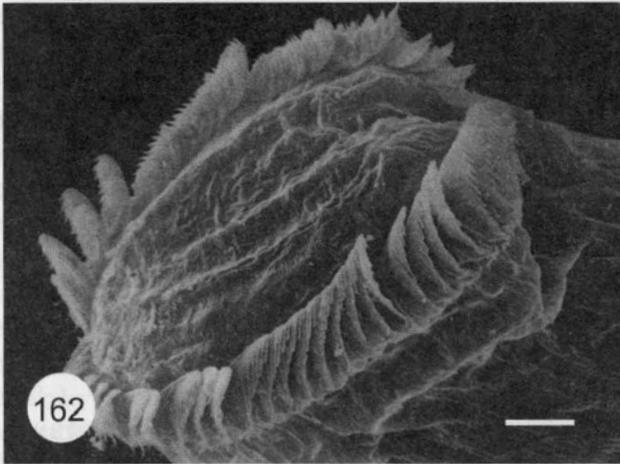
than that of the remaining asiloids (Woodley 1989). The position of the posterior spiracles on the segment is variable in asiloids. They are dorsolateral in the final-instar larvae of Asilidae, Mydidae, and Bombyliidae (Teskey 1976; Yeates 1994). First-instar larvae of Mydidae (*Tongamya* Stuckenberg) have a group of three spiracular openings posterolaterally (Irwin and Stuckenberg 1972). The spiracles are distinctly lateral in Therevidae and Scenopinidae and are lateral in the intersegmental area between segments 7 and 8 in Apioceridae (English 1947; Toft and Kimsey 1982). Outgroup comparison suggests that dorsally positioned spiracles are a groundplan condition of the Asiloidea, including Bombyliidae. The posterior spiracles are terminal in Pelecorhynchidae and Tabanidae (Figs 91, 100), and dorsomedial in Athericidae (Fig. 85). In both Athericidae and Tabanidae, these spiracles are united, whereas they remain separate in *Pelecorhynchus* Macquart (Mackerras and Fuller 1942). Despite fully developed tracheal trunks, the posterior spiracle of Athericidae is apparently closed (Russ 1953). The posterior spiracles of Stratiomyidae and Xylomyidae are in a narrow chamber surrounded by upper and lower sclerotized lips, bearing hydrofuge setae in most aquatic species (Rozkošný 1982). In Empidoidea and Rhagionidae, the spiracles are terminal, situated apically on a somewhat truncate face of the caudal segment. In some aquatic Stratiomyidae, the apex of the abdomen is drawn out into a breathing tube or respiratory siphon, with the apical spiracular cleft surrounded by a fringe of setae (Rozkošný 1982). Some aquatic Stratiomyidae also use a physical gill, which comprises air bubbles carried on a fringe of setae surrounding the posterior spiracles.

The posterior spiracles are the main opening of the respiratory system in larval Cyclorrhapha. They usually form the terminus of the larval body and occur at the end of the dorsal longitu-dinal tracheal trunks (Figs 179–180). The spiracular openings are usually located on a strongly sclerotized **spiracular plate** that is surrounded by a more-or-less complete, thickened cuticular ridge, the **peritreme** (Figs 181–182, 185). In a typical second- or third-instar larva, each spiracle has three slitlike openings (Figs 181–182, 185). In most species, these slits radiate from the medially situated **ecdysial scar** or **button**, which is the remnant of the second-instar spiracle (Figs 181–182; Keilin 1944; Teskey 1981a). The cyclorrhaphan posterior spiracle is thus a type III spiracle (*sensu* Keilin 1944). Associated with each spiracular opening are several single-celled, hypodermal **perispiracular** or **spiracular glands**, which produce an oily, water-repellent substance that prevents liquids from penetrating into the felt chamber of the openings (Keilin 1944; Hartley 1958; Whitten 1980; Jarial and Engstrom 1995). Another prominent feature of most posterior spiracles is **spiracular hairs**, which are arranged in four separate, water-repellent **peristigmatic tufts** (Figs 181–185; Whitten 1980). When larvae are in water, they float with the spiracular hairs spread on the water surface. The presence of one dendrite at the base of each peristigmatic tuft suggests that the hairs also have a sensory function (Singh and Singh 1984; Dambly-Chaudiere and Ghysen 1986).

The posterior spiracles of cyclorrhaphan larvae are exceptionally variable structures of great diagnostic value. The elements most frequently useful for species identification are as follows: (1) Size of slits: The three slits can be extremely elongated. They are usually coiled or folded multiple times to fit on the spiracular plate. Long openings can be stablised either by **rimae**, which are sclerotizations along the edges of the slits, or **trabeculae**, which are cross struts and serrations (Teskey 1981a). Elongated slits are particularly common in parasitic and parasitoid larvae. (2) Shape of slits: Even if not elongated, the slits can

Figs 4.162–169. Scanning electron micrographs of locomotory devices and anal papillae of larval nematocerans. 162–163: *Deuterophlebia* sp. (Deuterophlebiidae): 162: instar I abdominal proleg, apicolateral view, 163: instar IV abdominal proleg, lateral view. 164: *Neotelmatoscopus* sp. (Psychodidae), abdominal friction pad (suctorial disc), ventral view. 165–167: *Blepharicera* sp. (Blephariceridae), suctorial disc: 165: ventral view, 166: lateral view, 167: ventral view, higher magnification. 168: *Axymyia* sp. (Axymyiidae), anal papillae. 169: *Agathon* sp. (Blephariceridae) anal division (abbreviations: an: anus / anal opening, ap: anal papillae; scale bars: 10µm (Figs 162, 164, 166–167), 30µm (Fig 163), 100µm (Figs 165, 168–169)).

either be straight (Fig. 181), curved, or sinuate (Figs 182, 185; Ferrar 1987; Meier 1996). (3) Number of openings: The normal number of openings is three (Figs 181–182, 185), but occasionally many more slits or pores are found. Both conditions are common in parasitic or parasitoid groups (e.g., Tachinidae, Glossinidae, Conopidae, Pyrgotidae: Ferrar 1987; Ždárek et al. 1996). Reduction in the number of slits is apparently rare in third instars (Ferrar 1987). (4) Arrangement of slits: The relative position of slits can vary tremendously (Figs 181–182, 185), sometimes even within a single family (Hartley 1961; Ferrar 1987; Meier 1996). (5) Position of ecdysial scar (Figs 181–182): The relative position between the ecdysial scar and the openings also varies considerably (Hartley 1958; Ferrar 1987). (6) Morphology of peristigmatic tufts: The four tufts of spiracular hairs can lose their individual identity and the hairs are then equally spaced around the peritreme (Coelopidae: Ferrar 1987). Individual tufts can differ in number and branching pattern of hairs (Fig. 185; Sepsidae: Meier 1996) and tufts can be lost altogether (Heterocheilidae: Backlund 1945) (7) Shape of spiracular plate: In lateral view the spiracular plate can be flat (Fig. 181), rounded (Glossinidae: Keilin 1944) or, in species with spiracle elongation, be partially extended onto spiracle-bearing horns (Fig. 185; Sepsidae: Meier 1996). (8) Respiratory spines: In aquatic, parasitic, and parasitoid Cyclorrhapha, the frequently fused spiracular

plates or projections from them ("respiratory spines") can be modified to tap into the aerenchyma of water plants or the tracheal system of hosts (e.g., Ephydridae, Syrphidae, Conopidae; Hinton 1953; Hartley 1958; Ferrar 1987). (9) Position of spiracular plate: Larvae of aquatic larvae frequently have their posterior spiracles translocated onto long extensions of the stigmatophores (Figs 147, 151; e.g., Syrphidae, Ephydridae). The longest siphon occurs in the syrphid *Eristalis*. It can be up to 15 cm in length and has its own musculature for adjusting its length to water depth (Fig. 147; Keilin 1944). (10) Fusion of spiracular plates: The two spiracular plates often fuse to various degrees. In most cases only the base of the spiracles is involved, but in other species the entire medial area fuses into a single two-lobed plate (Fig. 181; e.g. Syrphidae: Hartley 1958, 1961; Drosophilidae: Okada 1968). (11) Posterior spiracle chambers: Species from various families have special muscular flaps that can be used to completely separate the openings of the posterior spiracles from the surrounding medium (e.g., Muscidae, Sarcophagidae, Calliphoridae, Gasterophilinae; Ferrar 1987). The flap of *Gasterophilus* has been shown to be gas-tight (Tatchell 1960).

Although the previous discussion was based largely on the spiracles of third-instar cyclorrhaphans, certain modifications in third instars also are known in the first-instar larva. However, in general, the spiracles of first-instar larvae are

holopneustic   peri-   hemi-   amphi-   pro-   meta-   a-
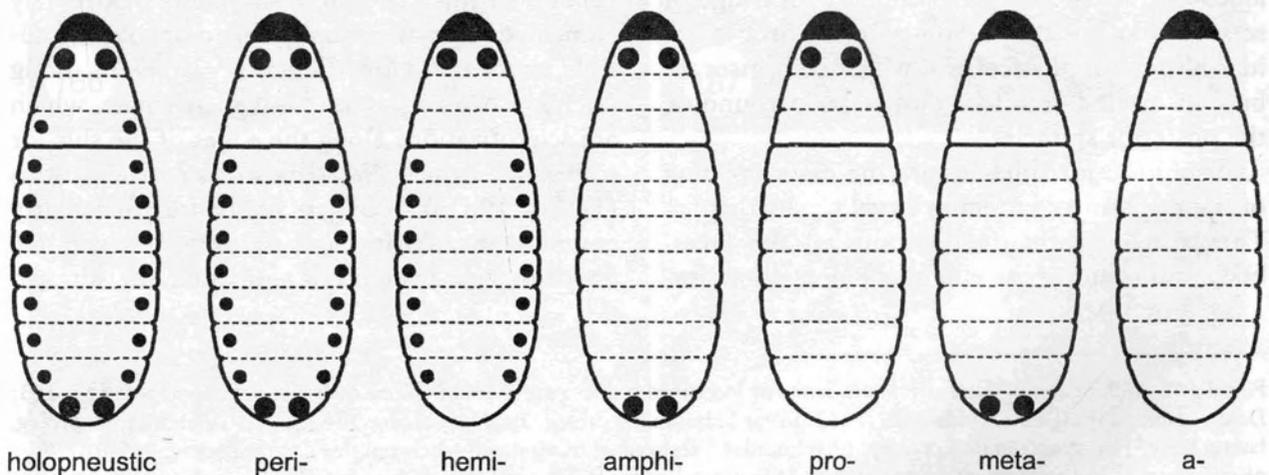
Fig. **4.170.** Diagrammatic representations of spiracular systems in larval Diptera (adapted from Teskey 1981a).

more uniform (Ferrar 1987; Colwell 1989). Most first-instar larvae have two, somewhat oval spiracular slits that are fused apically (Fig. 183; Ferrar 1987). A few first-instar larvae also possess a third, porelike opening. Most second-instar larvae have three spiracular slits (Fig. 184). In many details, these slits closely resemble the posterior spiracles of third-instar larvae.

Tracheal gills. Except for the occasional misleading reference to anal papillae as tracheal gills, these structures are rare in Diptera larvae. True tracheal gills (i.e., structures that apparently have only a respiratory function) occur in few groups, including some Chironomidae and later-instar larvae of all Blephariceridae (Figs 130, 171). In the latter family, first-instar larvae and, in some genera, second instars lack these structures. Among Brachycera, the larvae of Athericidae may possess paired tracheal gills (Russ 1953: fig. 21).

Anal division – After the head, the posteriormost division of a Diptera larva is arguably the most complex region of the body. This complexity partly reflects the composite nature of the region, and partly the division's significance to bodily activity (locomotion, respiration, osmoregulation, digestion). Among the more conspicuous features of the anal division are anal prolegs and posterior spiracles (see earlier), and the anal papillae and anus. Other structures are present in some groups (e.g., **paracercus** of certain Chironomidae: Figs 160–161).

The anal division has many names, including the anal segment, terminal segment, caudal segment, telson, pseudotelson, and terminalia (Jürgens 1987; Meier 1996). We prefer the term **anal division** because all other terms imply that the region consists of only a single segment. As discussed previously (see Segmentation), the anal division comprises multiple segments and, during embryology, four externally visible segment anlagen are indeed found (Turner and Mahowald 1979, but see Jürgens 1987). However, more recent studies using molecular markers and laser ablation on *D. melanogaster* embryos have lead to conflicting results regarding the number of abdominal segments involved in the anal divi-

sion (Turner and Mahowald 1979; Sato and Denell 1986; Jürgens 1987; Kuhn et al. 1992, 1995; Jürgens and Hartenstein 1993). Uncontroversial is that (1) abdominal segments 8–10 participate in its formation, (2) most of the anal division is formed by segment 8, (3) the ventral region of segment 9 is either reduced in size or lost, and (4) the ventral side of segment 10 is entirely lost. Controversial are Jürgens and Hartenstein (1993) interpretations that the **anal pad** (Figs 84, 90, 100, 179; see later) is a highly modified abdominal segment 11 and the **anal tuft**, a tuft of spines posterior of the anal opening, constitutes the telson (Fig. 179). Alternatively, the anal pad belongs to abdominal segment 10 and the anal tuft might be of a mixed segmental origin (Sato and Denell 1986; Kuhn et al. 1992, 1995).

The anal division of Xylophagomorpha often bear sclerotized plates, with the anal plate usually bearing terminal tubercles (Teskey 1976). A similar configuration occurs in some Asilidae (Melin 1923), and a large terminal shield is known in Pantophthalmidae (Greene and Urich 1931; Thorpe 1934). In many families, the last body division is truncate with lobes or tubercles surrounding the apical margin (e.g., Rhagionidae, Dolichopodidae). Most Empidoidea possess four or more lobes surrounding the posterior spiracles, with the spiracles on the caudoventral face of the upper pair of lobes and often fringed with setae (Dyte 1967). Additional smaller secondary lobes can occur mid-dorsally and laterally between primary lobes. The anal division of some dolichopodid larvae is rounded and lacks lobes, a condition also found in Pelecorhynchidae (Fig. 91). In these and related groups, the form of the anal division can provide many useful diagnostic characters. The larvae of Athericidae bear a pair of long, slender, terminal processes that are usually fringed with fine, filamentous setae (Figs 84–85). These processes are exceptionally long in *Atrichops* Verrall and, together with similar filaments on segments 6 and 7, remain exposed above the substrate when the larva is buried (Thomas 1985). The anal division of Vermileonidae bears short, broad, flat, fingerlike terminal processes.
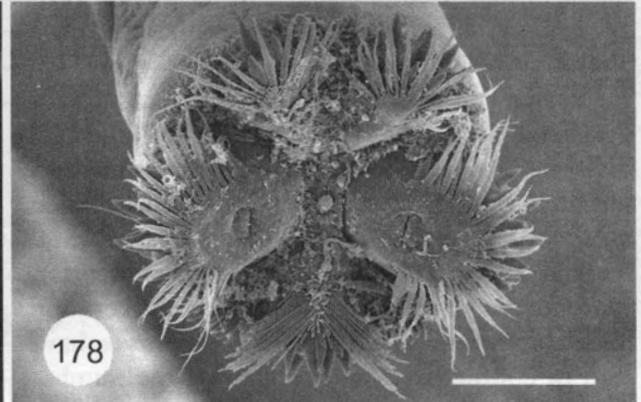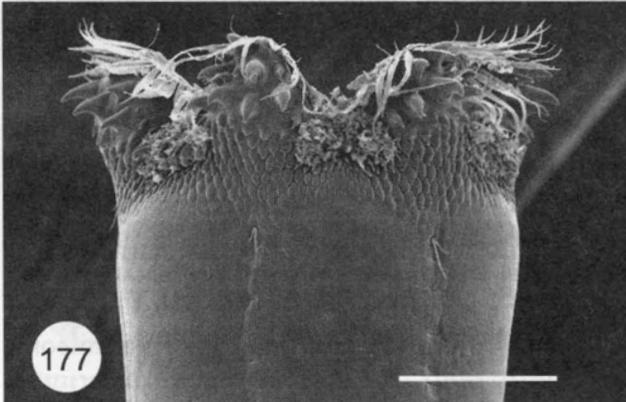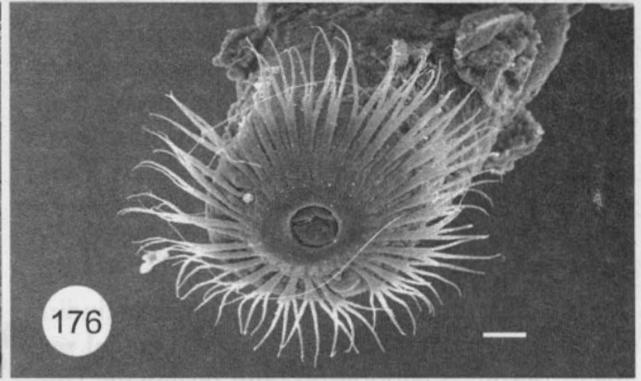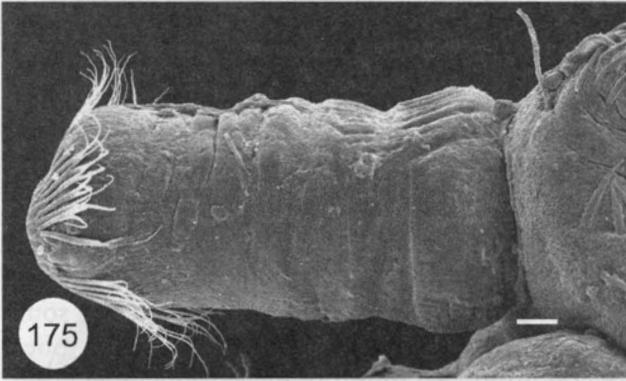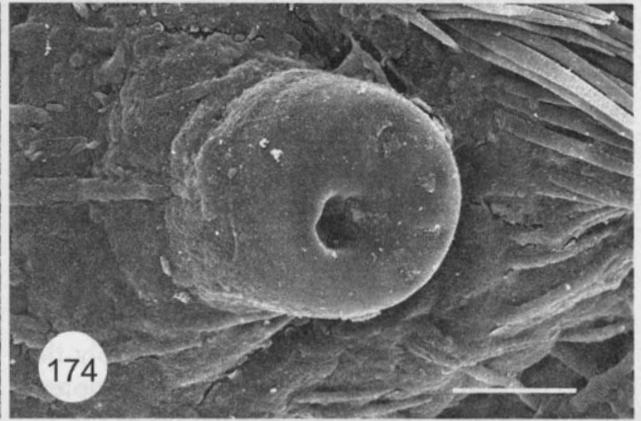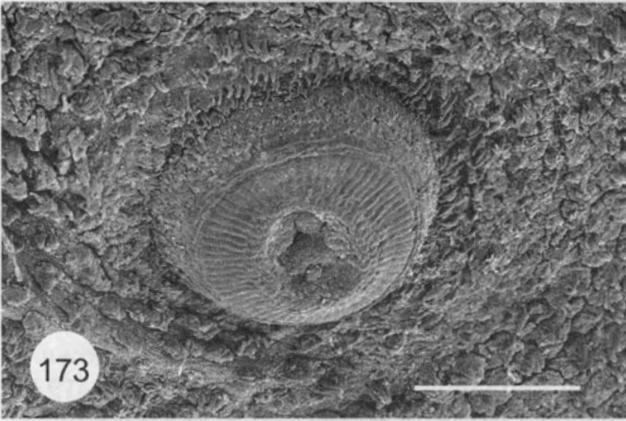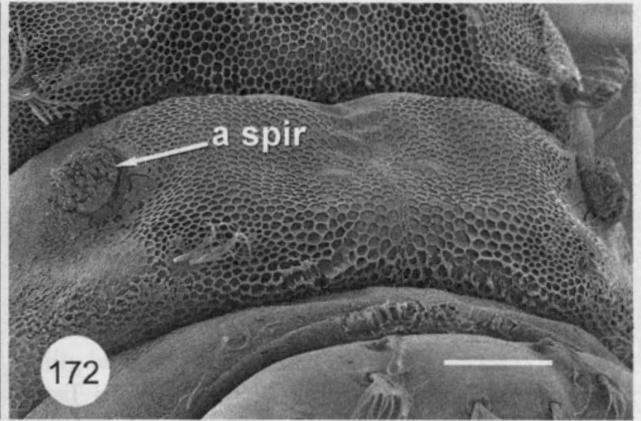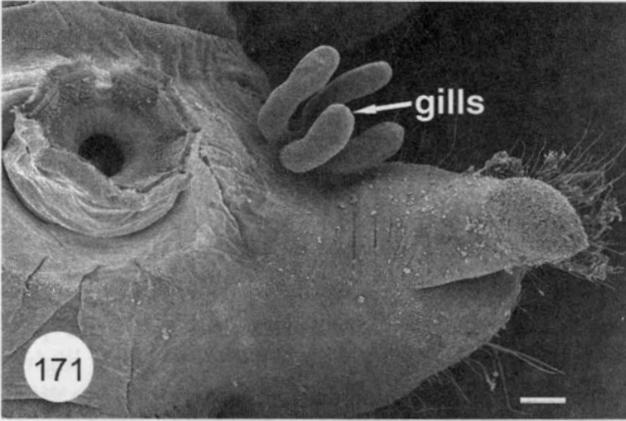
In cyclorrhaphan larvae, the most conspicuous features of the anal division are the ventral, longitudinal, slitlike **anus**, which is flanked by the anal pad (Fig. 179), and the posterior spiracles, which often occur at the end of long spiracle bearing horns (Ferrar 1987) or **stigmatophores** (Figs 147, 149, 151; Jürgens 1987). Many cyclorrhaphan larvae are adorned with pairs of fleshy cones posteriorly (Figs 179–180; Ferrar 1987). The presence, distribution, and position of these processes have received much attention from systematists, but attempts to homologise them across families have had mixed success (Hennig 1948, 1950, 1952). As mentioned, these cones are usually associated with sense organs, and the presence and position of sense organs are more conservative than the presence and position of associated cones. Thus, the study of these cones must begin with the study of associated sense organs. A good starting point for comparisons in aschizan families is the extensive work on the sense organs and cones and processes of Syrphidae (Hartley 1961; Rotheray and Gilbert 1989). For the Schizophora, the best point of comparison is work on *D. melanogaster*, where the ontogeny and innervation of cones and sense organs are well known (Kankel et al. 1980; Sato and Denell 1986; Jürgens 1987; Hartenstein 1988; Kuhn et al. 1992, 1995). In *Drosophila* but probably also in many other Schizophora, cones can be used to identify approximate borders between the fused abdominal segments (Jürgens 1987, but see Dambly-Chaudiere and Ghysen 1986 and Kuhn et al. 1992). In third-instar larvae, the anal division has seven pairs of sensory cones (Sato and Denell 1986; Jürgens 1987; Kuhn et al. 1992, 1995). The two most anterior ones are called the dorsomedial cones and anterior-lateral cones (Figs 179–180). Both are apparently derived from abdominal segment 8. The two more posterior pairs are the posterior-lateral cones and are located on seg-

ment 9 (Figs 179–180). Lastly, a single pair of anal cones is immediately posterior of the anal pad and belongs to segment 10 (Figs 179–180).

The shape of the anal division varies tremendously in larval Cyclorrhapha (Figs 145–153). One common modification is elongation of the stigmatophore. Different parts of the anal division can be elongated, and careful study of cone position can help establish homologies between elongations. Retractile elongated stigmatophores are called **respiratory siphons** (Fig. 147). They are often subdivided by a fold that allows for retraction of the distal part of the stigmatophore into the proximal element. These folds are sometimes interpreted as the borders between segments 8 and 9 (Colwell and Scholl 1995). However, there is little doubt that such folds are secondary and do not follow segmental borders. Secondary folds in the anal division are common in many families and can be of great diagnostic value (Ferrar 1987; Rotheray and Gilbert 1989). The cuticle of the anal division is frequently similar to that of the remaining abdominal segments, and spines are usually restricted to the creeping welts on abdominal segment 8. However, in many Sepsidae, spines also occur on the lateral and dorsal side.

Anus. In most Diptera larvae, the anal opening is situated posteriorly, near the terminus of the anal division. In larval nematocerans that have elongate respiratory siphons (e.g., Ptychopteridae, Axymyiidae, Perissommatidae, some Psychodidae), the anus is usually located posteroventrally at the base of the siphon. In larvae of many higher Nematocera and lower Brachycera, the anus is a ventral opening or slit in the middle of the anal division (Figs 84, 90, 101), usually somewhat removed from the terminus. In Stratiomyidae, the anus is sometimes lined with spines or teeth (Fig. 94). In Xylomyidae the anus is bordered by pair of rounded swellings and an

Figs 4.171–178. Scanning electron micrographs of respiratory structures of larval nematocerans. 171: *Agathon* sp. (Blephariceridae), abdominal gills, ventral view. 172: *Androprosopa* sp. (Thaumaleidae), anterior (thoracic) spiracle. 173: *Plecia* sp. (Bibionidae), anterior (thoracic) spiracle. 174–176: *Rhexoza* sp. (Scatopsidae): 174: anterior (thoracic) spiracle, 175: posterior spiracular lobe, lateral view, 176: apex of posterior spiracular lobe. 177–178: *Axymyia* sp. (Axymyiidae): 177: posterior spiracular lobe near apex, lateral view, 178: apex of posterior spiracular lobe (abbreviation: a spir: anterior spiracle; scale bars: 10μm (Figs 174–176), 100μm (Figs 171–173, 177–178)).
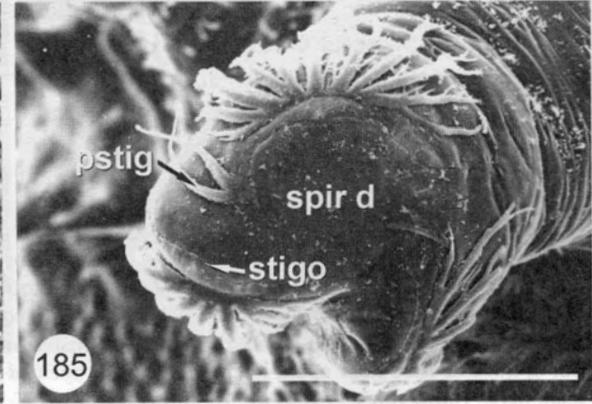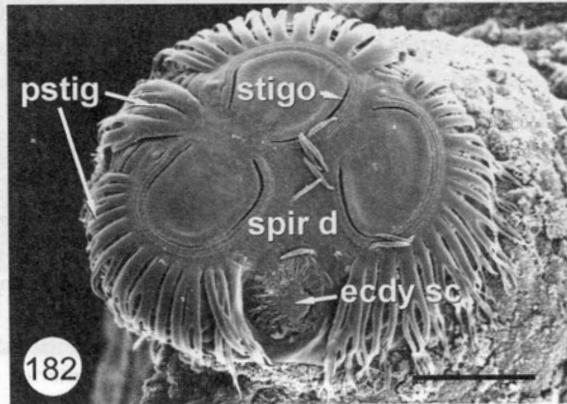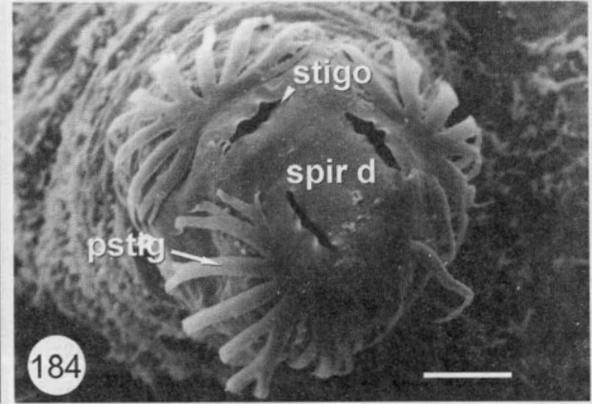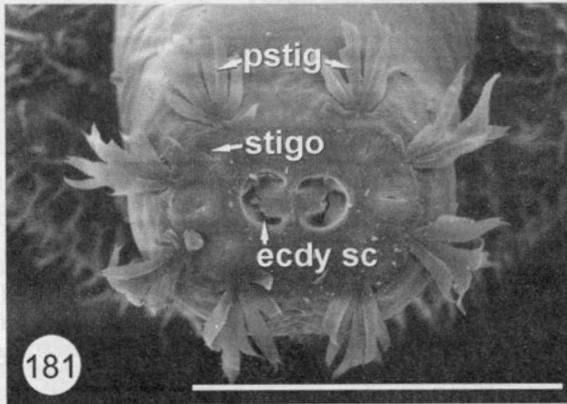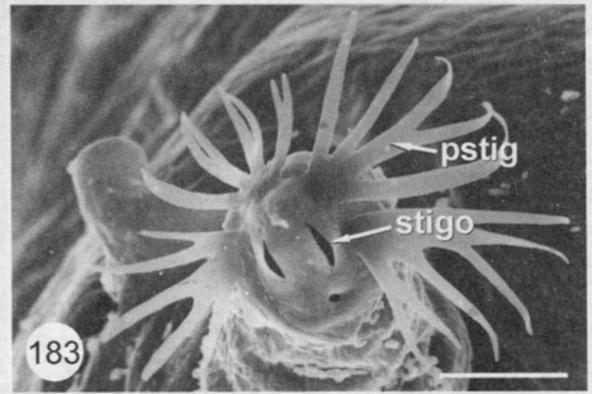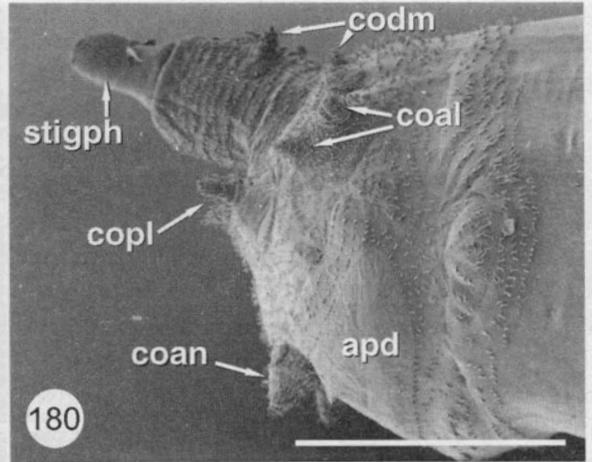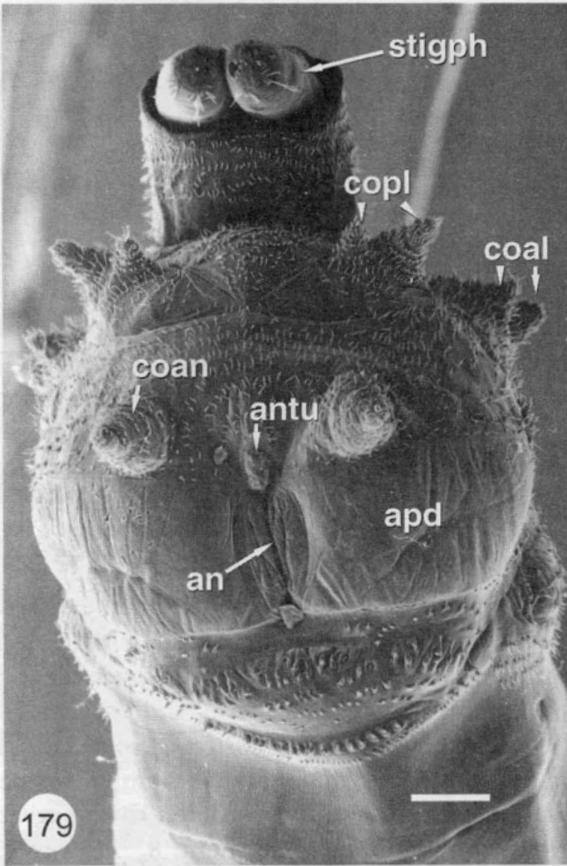
anterior transverse row of strong, posteriorly directed teeth.

Anal papillae / anal pads. Anal papillae occur in the larvae of almost all aquatic and semi-aquatic nematocerans (Table 3). These structures are absent in groups that are predominantly terrestrial, including most Bibionomorpha, several higher Nematocera (e.g., Synneuridae, Scatopsidae, Anisopodidae), and nearly all Brachycera (Courtney 1991). In families with anal papillae, the typical number is four; however, some families demonstrate considerable variation in papillae number (e.g., Tipulidae have between 2 and 8, Psychodidae between 0 and 8). With few exceptions (Deuterophlebiidae with five papillae, Simuliidae with three), papillae occur in multiples of two. Although typically elongate (Figs 124, 135, 137, 160) or sausage-shaped (Figs 130, 138, 169), the papillae of some larvae are padlike (Fig. 136), bulbous (Fig. 131), or intricately branched (Fig. 168). Anal papillae are retractable in Trichoptera (Neboiss 1991), some Mecoptera including Nannochoristidae (Pilgrim 1972), and many nematocerous families (Table 3). Permanently exserted anal papillae are present in larval Tanyderidae, Ptychopteridae, Corethrellidae, Chaoboridae, Culicidae, Chironomidae, Deuterophlebiidae, Blephariceridae, and Axymyiidae (Courtney 1991). Anal papillae apparently provide an osmoregulatory function and, in some species, are involved in unspecialised integument-tracheal respiration (Komnick and Wichard 1975); however, there is no structural evidence indicating that anal papillae function as tracheal gills or blood gills.

Anal papillae are rare in orthorrhaphous Brachycera, known only in the wood-boring larvae of Pantophthalmidae (Thorpe 1934). These structures arise ventrolaterally from the intersegmental membrane between segments 7 and 8 (Greene and Urich 1931). Their precise function is unclear, but they are connected to a dense tuft of fine tracheae and may have a respiratory function. Anal papillae are also rare in the Cyclorrhapha. They have been described for Syrphidae, where they can be elaborate and a nomenclatural system has been developed for describing their morphology (Hartley 1961). They consist of eversible, tracheal tubes that can be protruded through the anal fold via turgor pressure and retrieved through contraction of special musculature. The respiratory processes of the endoparasitoid Cryptochetidae are apparently also anal papillae (Fig. 152; Hennig 1973).

Although anal papillae are rare in larval Brachycera, these flies have functionally similar structures: **anal pads.** Alternative names for these anal pads include anal plates, anal organ, perianal pads, ventral hypodermal organ, and anal papillae. The shape and size of the anal pads, which are located on either side of the anal opening (Figs 84, 90, 100, 179), vary considerably and can be used for species identification (Meier 1996). The cuticle of the anal pads is thin, glabrous, and often creased and folded. The thin cuticle, the underlying large epidermal cells with giant chromosomes, and an increase of anal-pad size in *Drosophila* strains selected for survival in salty media suggests an osmoregulatory function (Stoffolano 1970). Anal pads are apparently missing (e.g., Coelopidae) or invaginated (Ropalomeridae) in some larvae. The tracheal gills of Syrphidae and the long, tracheated, anal processes of Cryptochetidae (Fig. 152) are possibly derived from more normal-shaped anal pads (Hartley 1961; Hennig 1973).

Courtney (1991) discussed three alternatives regarding the evolution of anal papillae in Diptera, ranging from independent evolution in several clades of [nematocerous] flies, to the possibility that these structures belong to the Diptera groundplan and were lost independently in several lineages. Anal papillae do not occur in Si-

Figs 4.179–185. Scanning electron micrographs of anal division and respiratory structures of larval cyclorrhaphans. 179–180: *Drosophila melanogaster* Meigen, anal division: 179: posteroventral view, 180: lateral view. 181–182: posterior spiracles: 181: *Drosophila anceps* Patterson et Mainland; 182: *Orygma luctuosum* Meigen. 183–185: *Sepsis neocynipsea* Melander et Spuler, posterior spiracles: 183: instar I, 184: instar II, 185: instar III (abbreviations: an: anus / anal opening, antu: anal tuft, apd: anal pad, coal: anterolateral cones, coan: anal cones, codm: dorsomedial cones, copl: posterolateral cones, ecdy sc: ecdysial scar, pstig: peristigmatal tuft, spir d: spiracular disc / plate, stigo: stigmatal opening, stigph: stigmatophore; scale bars: 10µm (Figs 183–184), 100µm (Figs 179–182, 185), 0.5mm (Fig. 180)).

phonaptera, but apparently homologous structures are present in Nannochoristidae and other Mecoptera (Pilgrim 1972), and in some Trichoptera (Neboiss 1991). Oosterbroek and Courtney (1995) considered anal papillae part of the Diptera groundplan.

Hypermetamorphosis.

The families Acroceridae, Nemestrinidae, and Bombyliidae exhibit hypermetamorphosis, which is characterised by an active, slender first-instar (planidium), and grub-like, endoparasitic later instars (Nartshuk 1997: Figs 32.47–49). Acrocerid planidia lack prolegs and are covered with spines and stiff scales. This larval stage is metapneustic, with posterior spiracles positioned dorsolaterally on segment 8 or at the base of segment 9, and the caudal segment bears a suction- or adhesive disc (King 1916; Schlinger 1981). In Nemestrinidae, the planidium is metapneustic and has long ventral setiform projections (Teskey 1981b)

The planidium in Bombyliidae is apparently amphipneustic and has long and slender paired mandibular hooks, thoracic segments bearing a pair of long setae ventrally, abdominal segments with pair of short prolegs, and long terminal setae (Bohart et al. 1960). The dorsal sclerite or plate is continuous with the cranium and the labrum and is not articulated (Berg 1940). Hypermetamorphosis is typical of all Bombyliidae except *Glabellula arctia* (Zetterstedt), a scavenger in ant nests (Andersson 1974), and *Heterotropus*, which is free-living (Yeates and Irwin 1992). The mode of parasitism in Bombyliidae has apparently evolved independently from that in Acroceridae and Nemestrinidae (Woodley 1989).

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