ADULT MORPHOLOGY AND TERMINOLOGY 3

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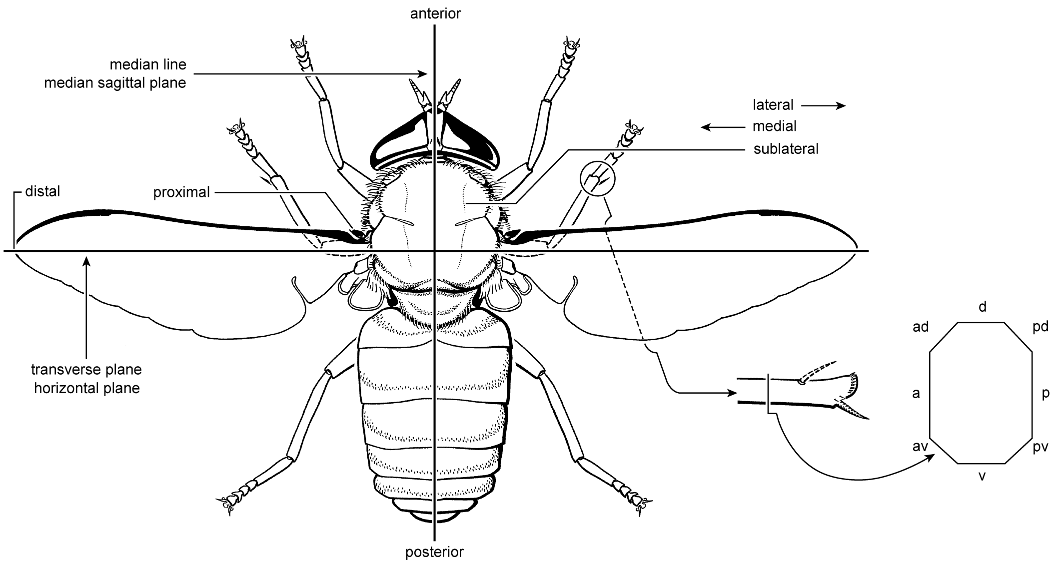
Introduction

This chapter introduces and describes the terms used for the identification of adult flies in this *Manual*, although the discussion of terms is not exclusively restricted to Diptera occurring in the Afrotropical Region. The information provided herein is based mainly on the terminology presented by Cumming & Wood (2009), which largely followed McAlpine (1981), with certain modifications subsequently adopted by Kotrba (2000), Merz & Haenni (2000) and Sinclair (2000). The most significant changes made to the previous treatment presented by Cumming & Wood (2009) include definitions of a few additional terms now in common usage (*e.g.*, postpedicel, pseudacanthophorites) and a more complete listing of synonyms. Three additional wing figures are also included, which depict some modified terms for venation (Wootton & Ennos 1989; Saigusa 2006), that are used as an alternative to the system presented in McAlpine (1981). This alternative system, which is based on a better homologised Diptera and Mecoptera fore wing base, is now used throughout this *Manual* and should be considered the standard.

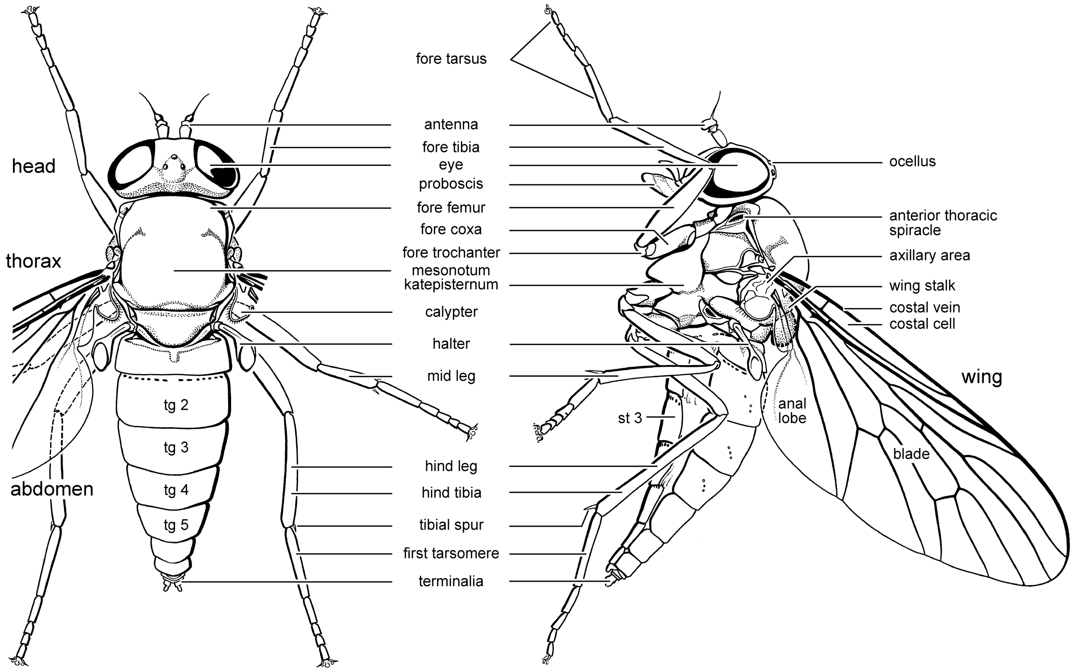
Terms are arranged alphabetically by major body region for the **head**, **thorax** and **abdomen** (Figs 1–3). Within the three major regions general discussions of components of the **compound eye**, **antenna**, **mouthparts**, **wing**, **legs**, **female terminalia** and **male terminalia** are followed by glossaries of terms used, grouped together under each of these headings. Preferred terms appear in *boldface* font followed by synonyms within brackets in *regular* font. Sometimes the corresponding singular (sing.) or plural (pl.) form is also given in brackets.

Each thoracic and abdominal segment is organised into a dorsal **tergum** (with a sclerotised **tergite**) and a ventral **sternum** (with a sclerotised **sternite**), connected together by a lateral **pleuron**, or **pleural membrane** (Figs 2, 3). The **tracheae** of the respiratory system open externally as **spiracles** on the sides of some of these segments. Parts of the integument, including the cuticle of the head, are variously covered in vestiture of different types. **Macrotrichia**, which are innervated and project from sockets called **alveoli** (sing. **alveolus**), include **bristles**, **setae**, **setulae** and **hairs**, depending on their relative size, as well as some enlarged spines on certain structures (*e.g.*, **acanthophorite spines** in female terminalia). Larger macrotrichia are generally referred to as setae and smaller macrotrichia are referred to as setulae; the terms bristle and hair are less frequently used. The arrangement of macrotrichia on the integument is referred to as **chaetotaxy**. Macrotrichia often function as sense organs or **sensilla** (sing. **sensillum**) with over 15 different types of sensilla having been defined in insects, including Diptera, based on their morphology and function (Nichols 1989: 670). **Microtrichia** include various minute projections of the cuticle that lack alveoli, such as the dust-like **pruinescence** (pollinosity) and the pubescent-like **tomentum** that dulls the surface of many sclerites, providing pattern and colour. Microtrichia that form spots are referred to as **maculae** (sing. **macula**), whereas microtrichia that form lines are referred to as **fasciae** (sing. **fascia**). Transverse lines of microtrichia are called **bands**, whereas longitudinal lines are termed **stripes,** or **vittae**.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 89–133.



1 *Tabanus* ♀



2 *Symphoromyia* ♀

3 *Symphoromyia* ♀

Figs 3.1–3. Main anatomical divisions and parts of adult flies: (1) dorsal view of *Tabanus americanus* Forster (Tabanidae) ♀, to show orientation and anatomical planes (inset of vertical section through distal portion of right mid tibia showing external surfaces); (2) *Symphoromyia montana* Aldrich (Rhagionidae) ♀, dorsal view; (3) same, lateral view (both non-Afrotropical). Figs 1–3 (after McAlpine 1981, figs 1–3).

Abbreviations: a – anterior; ad – anterodorsal; av – anteroventral; d – dorsal; p – posterior; pd – posterodorsal; pv – postero-ventral; st – sternite; tg – tergite; v – ventral.

Head

The segments that make up the head are fused into a somewhat spherical, or oval head capsule bearing hypognathous **mouthparts** formed into a **proboscis** (a synapomorphy of all Diptera, in which the **labrum**, **mandibles**, **hypopharynx** and **maxillae**, when present, are enclosed in a trough-like **labium**). Except for the mouthparts, these head segments are no longer clearly recognisable. For descriptive purposes, however, the head capsule has been arbitrarily divided into regions: the **frons** above the **antennae** and between the **compound eyes** anterodorsally, the **vertex** at the top of the head bearing the **ocellar triangle** when present, the **genae** below the eyes, the **face** and **clypeus** between the eyes and below the antennae and the **occiput** behind the eyes forming the usually flattened posterior surface of the capsule (Figs 4–7). The inner skeleton of the head capsule is formed by the arms of the **tentorium**.

The chaetotaxy of the head is diagnostically important in many groups of Diptera. The orientation of setae is described as **proclinate** (= directed forward), **reclinate** (= directed backward), **inclinate** (medioclinate) (= directed inward), or **lateroclinate** (eclinate, exclinate) (= directed outward).

In Tipulidae and in a few members of other families, the face, clypeus and genae are elongated anteriorly to form a **rostrum**, carrying the mouthparts further forward, similar to a weevil (Fig. 40). A condition referred to as **colocephaly**, in which the head is disproportionately small with reduced widely separated eyes and vestigial non-functional mouthparts, occurs in both sexes of some species of Blephariceridae (Stuckenberg 2004).

Glossary

anteclypeus, see **clypeus**.

anterior tentorial pit, see **tentorium**.

callus (pl. **calli**): bare, sometimes swollen areas on the frons of many female Tabanidae, including the **basal callus** (frontal callus), at the ventral limit of the frons above the subcallus and level with the lower margins of the compound eyes and the **median callus**, a narrow oval area between the ocellar triangle and basal callus (see **subcallus**). Calli also occur on the frons and face of some Therevidae.

cerebral sclerite, see **vertex**.

cibarium, see below under Mouthparts.

clypeal ridge, see below under Mouthparts.

clypeus (frontoclypeus) (Figs 4, 30, 33, 34, 36, 37, 39): that part of the head capsule between the labrum ventrally and the face dorsally, often extending almost to the antennal bases. In blood-feeding nematocerous families and Tabanomorpha, the clypeus is particularly prominent as a roundish convex sclerite (Fig. 30). By contrast, the clypeus of Cyclorrhapha and of Schizophora especially, has become reduced to a U- or Y-shaped sclerite hinged to and distinctly delineated dorsally from, the lower facial margin and often somewhat separated from it by the frontoclypeal membrane (Figs 4, 6, 37). In a few groups (e.g., Blephariceridae) the clypeus is divided into a proximal **postclypeus** and a distal **anteclypeus** (see also under Mouthparts).

cornicula (sing. **corniculum**) (patagia): permanently everted sac-shaped structures on the posterior surface of the head of males of some Psychodidae (*i.e.*, certain Psychodinae) that are presumed to be scent organs.

coronal suture, see under **frontal vitta**.

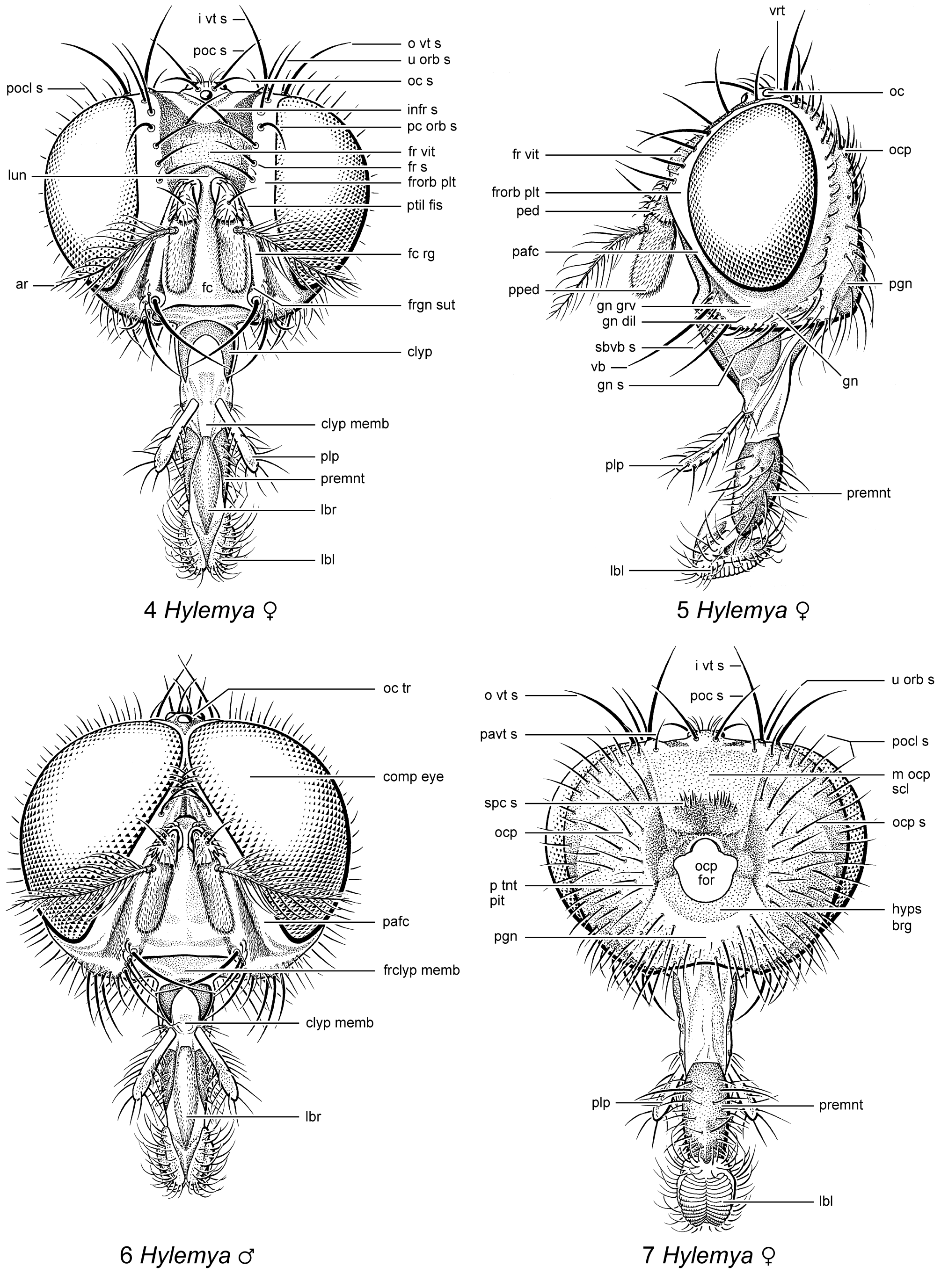
face (Figs 4, 32): in Diptera the region on the anteroventral surface of the head capsule between the antennal sockets dorsally, the compound eyes laterally (or ptilinal fissures in Schizophora, which separate the face from the parafacial) and the clypeus ventrally, often partially surrounding the clypeus dorsolaterally. Among nematocerous families and orthorrhaphous Brachycera, especially among blood-feeding forms, the face has become greatly reduced and the convex sclerite between antennal bases and mouthparts is the clypeus, which internally supports the insertion of muscles that dilate the cibarium. In Muscomorpha *sensu* Woodley (1989) generally and in Cyclorrhapha in particular, the clypeus is reduced and the face has become the major sclerite between the antennae and mouthparts. The face may be concave (and thus invisible in profile), or convex, with a midlongitudinal ridge, or bulge. It is usually bare, although it is variously adorned with stout, curved setae (the mystax) in most Asilidae.

facial carina: a midlongitudinal (vertical) ridge on the face, extending forward between the first flagellomeres in many Schizophora and in some species extending up between the antennal bases to unite with the lunule.

facial ridge (Fig. 4): the lateral margin of the face of Schizophora, delineated laterally by the ptilinal fissure and especially obvious in those forms in which the face is concave. The facial ridge often supports a vertical row of setae, or setulae, some of which can be stout, or elongate (see **supravibrissal seta** and **vibrissa**).

facial tubercle: a medial swelling on the face, especially among some Syrphidae.

frons (front) (Fig. 32): in Diptera the frons refers to the area between the compound eyes above the antennae. Morphologically, this is the postfrons, which is only part of the true frons of a generalised insect (McAlpine 1981) that extends to the clypeus as the prefrons. This latter region is, in Diptera, called the face. The frons is almost always complete in females, but may be partially or entirely reduced by medial enlargement of the compound eyes that meet in the midline in many flies, especially in males (see **holoptic** under Compound eye). Among nematocerous families and orthorrhaphous Brachycera, the frons is a simple sclerite, continuous from eye-to-eye and usually without setae, although hairs or scales are often present. In most Tabanidae bare shiny patches, termed calli (see **callus** above), are present on the frons, including the subcallus, basal callus and median callus. In Schizophora the frons becomes subdivided into a midlongitudinal frontal vitta and paired lateral fronto-orbital plates. The frontal vitta is expandable, allowing enlargement of the head and protrusion of the ptilinum during eclosion, while the lateral area, the fronto-orbital plate, is



4 *Hylemya* ♀

5 *Hylemya* ♀

6 *Hylemya* ♂

7 *Hylemya* ♀

Figs 3.4–7. Anatomical features of adult fly head: (4) *Hylemya alcathoe* (Walker) (Anthomyiidae), anterior view ♀; (5) same, lateral view ♀; (6) same, anterior view ♂; (7) same, posterior view ♀ (non-Afrotropical). Figs 4–7 (after McAlpine 1981, figs 8–11).

Abbreviations: ar – arista; clyp – clypeus; clyp memb – clypeolabral membrane; comp eye – compound eye; fc – face; fc rg – facial ridge; fr s – frontal seta; fr vit – frontal vitta; frclyp memb – frontoclypeal membrane; frgn sut – frontogenal suture; frorb plt – fronto-orbital plate; gn – gena; gn dil – genal dilation; gn grv – genal groove; gn s – genal seta; hyps brg – hypostomal bridge; i vt s – inner vertical seta; infr s – interfrontal seta; lbl – labellum; lbr – labrum; lun – lunule; m ocp scl – median occipital sclerite; o vt s – outer vertical seta; oc – ocellus; oc s – ocellar seta; oc tr – ocellar triangle; ocp – occiput; ocp for – occipital foramen; ocp s – occipital seta; p tnt pit – posterior tentorial pit; pafc – parafacial; pavt s – paravertical seta; pc orb s – proclinate orbital seta; ped – pedicel; pgn – postgena; plp – palpus; poc s – postocellar seta; pocl s – postocular seta; pped – postpedicel; premnt – prementum; ptil fis – ptilinal fissure; sbvb s – subvibrissal seta; spc s – supracervical seta; u orb s – upper orbital seta; vb – vibrissa; vrt – vertex.

sclerotised, usually bears setae and is usually different from the vitta in colour and texture, especially among Calyptratae. Secondary sclerotised plates, the interfrontal plates, which may bear rows of interfrontal setae, have developed in a few acalyptrate families (*e.g.*, Sphaeroceridae, Milichiidae).

frontal plate (Fig. 41): the anteroventral portion of the fronto-orbital plate, between the frontal vitta and the compound eye in Cyclorrhapha. It usually bears a longitudinal row of setae; the frontal setae (see **fronto-orbital plate**).

frontal setae (Fig. 4): a longitudinal row of setae arising on the frontal plate in most Cyclorrhapha; bordering the frontal vitta in Calyptratae and many acalyptrates. Frontal setae may be proclinate, or reclinate and are inclined medially to interdigitate with each other over the vitta. In most Phoridae these setae are quite large relative to the size of the head and they may be oriented in transverse rows as well as longitudinal rows.

frontal vitta (interfrons, interfrontal area, mesofrons) (Figs 4, 5): among Schizophora, during eclosion, the midlongitudinal area of the frons is expandable, thereby facilitating protrusion of the ptilinum and swelling of the head capsule. After eclosion and escape from the soil, or host cocoon, the ptilinum is retracted inside the head (leaving only the ptilinal fissure as external evidence of its former presence) and the cuticle of the frontal vitta shrinks, hardens and darkens. The vitta is bounded laterally by the sclerotised and usually setose and tomentose frontal plates. Although generally bare, the vitta may bear scattered setae and in some acalyptrate families (*e.g.*, Clusiidae, Milichiidae), a pair of larger setae, the **interfrontal setae** (Fig. 4). In some families (*e.g.*, Sphaeroceridae), paired longitudinal strap-like plates, the **interfrontal plates**, are present on the frontal vitta; each usually bears a row of interfrontal setae. In others (*e.g.*, Clusiidae, Chloropidae), the entire frontal vitta becomes more fully sclerotised and virtually indistinguishable from the frontal plates and may bear setae over its entire surface (*e.g.*, many Ulidiidae), thus resembling the frons of lower Cyclorrhapha. In many Phoridae a midlongitudinal line on the frons, which has been termed the coronal suture, may be the precursor of the frontal vitta.

frontoclypeal membrane, see **clypeus** below under Mouthparts.

frontoclypeal pit, see **anterior tentorial pit** under **tentorium**.

frontoclypeal suture, see **clypeus** below under Mouthparts.

frontogenal suture (Fig. 4): a paired line, in Cyclorrhapha, on the face, seldom used taxonomically. Usually faintly impressed, this suture extends from the vibrissal angle to the base of the antenna and delineates the facial ridge laterally, from the rest of the face, or facial plate, medially.

fronto-orbital plate (parafrontal plate) (Figs 4, 5, 42): the paired seta-bearing sclerite between the frontal vitta and the compound eye in Cyclorrhapha. Among nematocerous families and orthorrhaphous Brachycera, the entire frons is a simple sclerite, usually without setae (although hairs or scale-like setae may be present). Among Cyclorrhapha, however, the median area (frontal vitta) of the frons is expandable, allowing protrusion of the ptilinum during eclosion, while the lateral area, the fronto-orbital plate, is sclerotised and usually different from the vitta in colour and texture. In its simplest form, found in most acalyptrates and all calyptrates, the fronto-orbital plate is undivided and extends from the vertex to the level of the antennal bases. In a few acalyptrate taxa, however, this plate is subdivided into an anteroventral plate, the **frontal plate**, and a posterodorsal plate, the **orbital plate**, best exhibited by some Tephritidae.

fronto-orbital seta (Figs 4, 41, 42): any seta on the fronto-orbital plate sometimes differentiated into frontal and orbital setae. When differentiated into two longitudinal rows, the frontal setae are usually medial and anterior to the orbital setae. In Calyptratae, frontal and orbital setae form a continuous row and may not be readily differentiated, except by a change in size; the uppermost frontal setae are the smallest, while the adjacent orbital setae above and behind them are larger, becoming shorter towards the vertex.

gena (pl. **genae**) (cheek) (Fig. 5): that part of the head capsule between the compound eye and the subcranial margin. The gena is seldom of taxonomic importance in nematocerous families, or orthorrhaphous Brachycera, but in Cyclorrhapha, concurrent with the development of bristle-like setae, it has taken on greater importance. In Cyclorrhapha the setae on the occiput are continuous with those of the gena and may extend ventrally to the lower cranial margin, obliquely toward the vibrissa, or may curve up toward the eye margin to form a genal dilation. This setose part of the gena may be narrow, or broad, depending on the size of the eye in relation to the height of the head capsule. Along the ventral cranial margin there is usually a row of setae in Calyptratae that extends anteriorly almost to the vibrissae, separated from the subvibrissal setae by a narrow gap. McAlpine (1981: 15) separated the gena into two areas, the gena dorsally and a narrow bare ventral strip adjacent to the subcranial margin, the **subgena**, separated from the gena by the subgenal suture; however, from a taxonomic viewpoint this separation may not be of vital importance.

genal dilation (Figs 5, 42): of importance only in Schizophora, the widened part of the setose portion of the gena, just behind the vibrissa.

genal groove (Figs 5, 42): at the ventral terminus of the ptilinal fissure, lateral to the vibrissa, at the point of intersection of the facial ridge, parafacial and gena, is a triangular area of cuticle that was expanded during ptilinal eversion. In a well-hardened adult (it often collapses in a teneral specimen), the genal groove shows evidence of having been once expanded, similar to the cuticle of the frontal vitta. The cuticle of the genal groove is often coloured differently from adjacent cuticle of the parafacial, or gena and in some Tachinidae it may be quite extensive and rugose. Setae are seldom present.

genal seta (Fig. 5): in addition to the row of setae along the ventral margin of the gena, some setae and setulae may also be present on the surface of the gena itself.

inner vertical seta (**medial vertical seta**): (Figs 4, 7, 41, 42): a paired seta, usually the largest seta arising from the top of the head, lateral to the ocellar triangle. It is the uppermost in the row of postocular setae that extends from the vertex, behind the eye, to the gena. McAlpine (1981: 14) and Cumming &

Wood (2009: 13) applied the term inner vertical seta, while Merz & Haenni (2000: 34) preferred medial vertical seta. The inner and outer, or medial and lateral, vertical setae are adjacent to each other and the terms are equivalent, with usage depending on whether one prefers English, or latinised adjectives. McAlpine is here followed on the grounds that more dipterists are likely to be familiar with inner and outer, rather than medial and lateral. The inner vertical setae are often reclinate, or inclinate and may be parallel, or cruciate medially (see **outer vertical seta**).

interfrontal plate, see **frontal vitta**.

interfrontal seta (Fig. 4): any paired setae, other than scattered hairs, on the frontal vitta, between the frontal setae; found in Phoridae, Lonchopteridae and certain acalyptrate taxa (*e.g.*, some Clusiidae). In a few families of acalyptrates (*e.g.*, Sphaeroceridae and Milichiidae), a pair of strap-like sclerites has developed in the frontal vitta and the row of setae on these plates is referred to as the interfrontal setae (see **frontal vitta**).

lateral vertical seta, see **outer vertical seta**.

lunule (Figs 4, 41): present only in Schizophora, the narrow crescent-shaped part of the frons between the ptilinal fissure at its dorsal extremity and the antennal bases. Usually bare and shiny, it bears small setae in some Lonchaeidae (*e.g.*, *Dasiops* Rondani, Lonchaeini), many Ulidiidae and some Tachinidae (*e.g.*, *Oestrophasia* Brauer & Bergenstamm).

medial vertical seta, see **inner vertical seta**.

median occipital sclerite (Fig. 7): the somewhat rectangular mid-dorsal region of the back of the head in most Brachycera, between the ocellar triangle dorsally and the occipital foramen ventrally and delineated laterally by a suture extending from a point between the inner and outer vertical setae to the occipital foramen. Paired groups of small setae, the **supracervical setae**, may be present above the occipital foramen.

mystax (Fig. 34): a patch of stout, curved setae on the face of most Asilidae extending anteriorly like a moustache, probably to protect the head from struggling, or stinging prey.

nasus, see **rostrum**.

occipital foramen (Fig. 7): the opening in the middle of the back of the head where it is connected to the cervix.

occipital setae (Fig. 7): the setae scattered over the surface of the back of the head, not including postocular setae, which form a fringe behind the eyes.

occiput (Figs 5, 7): the upper portion of the postcranium, or back of the head; it may be convex, as in most nematocerous families; relatively flat as in most Schizophora; or concave, as in some other Brachycera (*e.g.*, Pipunculidae, some Bombyliidae and Syrphidae) (see **median occipital sclerite** and **postcranium**).

ocellar triangle (Figs 6, 41): on the midline, at the vertex, or uppermost part of the head, a triangular setose sclerite bears the three ocelli in most Diptera. It and the ocelli are absent in all members of Culicomorpha, Psychodidae and Tipulidae, as well as in several other nematocerous families (*e.g.*, many Cecidomyiidae), but they are almost always present in Cyclorrhapha (absent in Ctenostylidae and most Pygotidae). Although usually approximately equilateral, the triangle, which points forward, may be elongate as in some Chloropidae and Cryptochetidae, extending anteriorly to partially split the frontal vitta in half. In the phorid genus *Stichillus* Enderlein, the triangle is extremely broad, such that the ocelli form a nearly straight transverse line. If the ocellar triangle is raised, as in some Tabanidae, Bombyliidae and Asilidae, it is referred to as an **ocellar tubercle**. In some Mycetophilidae the ocellar triangle is absent, although two, or three ocelli may be present.

ocellar tubercle, see **ocellar triangle**.

ocellar seta (Figs 4, 41): in Cyclorrhapha and some other Brachycera, a single pair of small to large setae, larger and distinctly differentiated from the surrounding hairs, arising on the ocellar tubercle between the anterior and posterior ocelli (rarely on either side of the anterior ocellus, as in the heleomyzid subfamily Trixoscelidinae and the tachinid genus *Actinodoria* Townsend). Ocellar setae may be proclinate, reclinate, or inclined laterally; they may be sexually dimorphic in direction (proclinate and almost parallel in males of the tachinid genus *Trafoia* Brauer & Bergenstamm, but inclined laterally in females); doubled, especially in bristly taxa; or absent and thus not differentiated from the hairs that are normally present on the tubercle.

ocellus (pl. **ocelli**) (Figs 3, 5): in most Diptera three ocelli, or simple eyes, are present on the ocellar triangle, arranged as one might expect, in a triangle. In some Mycetophilidae, however, the median ocellus is absent and the lateral ones are widely separated. Ocelli are absent in several nematocerous groups (all Culicomorpha, Psychodidae, Tipulidae and various taxa scattered among several other families, *e.g.*, many Cecidomyiidae), as well as some Brachycera (*e.g.*, often brachypterous and apterous species).

orbital plate (Fig. 41): in Schizophora, the upper part of the fronto-orbital plate, bearing the orbital setae (see **fronto-orbital plate**).

orbital seta (prevertical seta) (Figs 4, 41, 42): any seta arising from the orbital plate. They are usually reclinate in both sexes. In almost all females of Calyptratae and in some males as well, an additional pair, or two pairs, of proclinate orbital setae are present, lateral to the row of reclinate orbital setae.

outer vertical seta (**lateral vertical seta**) (Figs 4, 7, 41, 42): a paired, usually lateroclinate seta that is in line with, but usually distinctly larger than, the rest of the postocular setae; duplicated in some Psilidae; each seta is medially inclined in most Phoridae (see **inner vertical seta**).

paraclypeal sclerite (clypeal sclerite): sclerite, or pair of sclerites that arises in the frontoclypeal membrane between clypeus and lower facial, or genal margin in some Tachinidae, *e.g.*, *Clausicella* Rondani and *Ginglymia* Townsend.

parafacial (pl. **parafacials** or **parafacialia**) (Figs 5, 6, 42): that part of the face between the facial ridge and the eye in Schizophora. Dorsally, the parafacial is only arbitrarily separable from the frons, usually at the level of the insertion of the antenna, or at the position of the anteriormost frontal seta in Tachinidae. Ventrally, the parafacial is separated from the gena by the genal groove.

paravertical setae (Figs 7, 41, 42): a small pair, or two pairs of setae behind the postocellar setae and between the inner vertical setae.

peristomal seta, see **subvibrissal seta**.

postclypeus, see **clypeus**.

postcranium (Figs 5, 7): the entire back of the head according to McAlpine (1981: 16), who divided the postcranium into a dorsal portion, the occiput and a ventral part, the postgena. Merz & Haenni (2000: 29) regarded the terms postcranium and occiput to be synonymous and used occiput and postgena to describe the dorsal and ventral portions of the back of the head.

posterior tentorial pit, see **tentorium**.

postgena (Figs 5, 7): the ventral part of the back of the head, continuous with the gena laterally. In some primitive nematocerous families (*e.g.*, Tanyderidae), the postgenae are separated medially by a membrane; in most Diptera, however, they meet one another medially, or else the membrane between them has become sclerotised, to form the bottom portion of the postcranium (see **postcranium**).

postocellar setae (postvertical seta) (Figs 4, 7, 41, 42): a pair of small setae arising directly posterior to the ocellar triangle. In a few taxa these setae are doubled and are then distinguished as the medial and lateral postocellar setae (Merz & Haenni 2000: 34).

postocular setae (Figs 4, 7, 41): a single erect row of hairs on either side of the head forming a fringe behind each eye, beginning dorsally just below the outer vertical seta and extending ventrally to the gena. The postocular setae also delineate the postcranium.

postvertical seta, see **postocellar seta**.

proboscis (Fig. 3): the specialised mouthparts of Diptera that are partially enclosed in a tubular labium. They are rigidly attached to the head capsule in nematocerous families, especially biting forms, slightly articulated, but essentially non-retractible in non-Cyclorrhapha and fully retractible in most Eremoneura (Empidoidea and Cyclorrhapha), unless exceptionally elongate, in which case the apex projects anteriorly (see also under Mouthparts).

ptilinal fissure (frontal suture, ptilinal suture) (Fig. 4): all that is visible of the **ptilinum** after it has been retracted, extending as an inverted U-shaped line from the genal groove, just behind the vibrissa, dorsally around the lunule to join the frontal vitta. The fissure delineates the face from the parafacial and the lunule from the frons. Often, an individual fails to retract the ptilinum fully, leaving a gap in the fissure, or a portion of the ptilinum protruding. Some tachinid parasites of hairy caterpillars occasionally get the barbed hairs of their host caught up in the ptilinum as they force their way out of the host cocoon, leaving these hairs protruding from the fissure (see Brooks 1945).

ptilinum (Fig. 4): one of the most characteristic synapomorphies of the Schizophora and the basis of the name (fly with fissure), the ptilinum is an inflatable sac-like part of the front of the head that can be protruded between the face and the frons to exert pressure on the anterior cap of the puparium to force it open. In the tachinid genus *Gonia* Meigen, the cuticle of the ptilinum is covered with small thorn-like spines for rasping the soil ahead of the escaping fly (Strickland 1953). As the adult fly hardens, the ptilinum is retracted inside the head, leaving only a faint line, the **ptilinal fissure**, as evidence of its existence.

rostrum (Fig. 40): in Tipulidae and a few genera in other families, the face, clypeus and genae are elongated, forming a tube-like extension of the front of the head, called the rostrum, which is sometimes prolonged apically into a projection referred to as the **nasus**.

stemmatic bulla (Fig. 8): a small rounded shiny tubercle behind the margin of the eye in some Simuliidae (often with reduced compound eyes) and a few Chironomidae (*e.g.*, *Oreadomyia albertae* Kevan & Cutten-Ali-Khan), that is believed to be a remnant of the larval eye. The bulla lacks the transparent cornea and internal organisation of an ocellus and is unlikely to be homologous to one.

subcallus: in Tabanidae, that part of the front of the head between frons, antennae and genae, sometimes swollen, or shiny, or both (see **callus**).

subcranial cavity (oral cavity): in Cyclorrhapha, especially among Schizophora, the proboscis can be retracted into the ventral area of the head capsule by muscles inserted along the lower margin of the face (epistoma). Among schizophorans living at high latitudes and altitudes, the lower facial margin is usually projected anteriorly, perhaps to give these muscles greater range of motion in cold conditions and/or to exploit nectar and pollen from the generally small-sized flowers found in these environments. Although the subcranial cavity is often referred to as the "mouth", or oral cavity, the true mouth is inside the proboscis (see above) and the mouthparts are outside the mouth, not within.

subgena, see under **gena**.

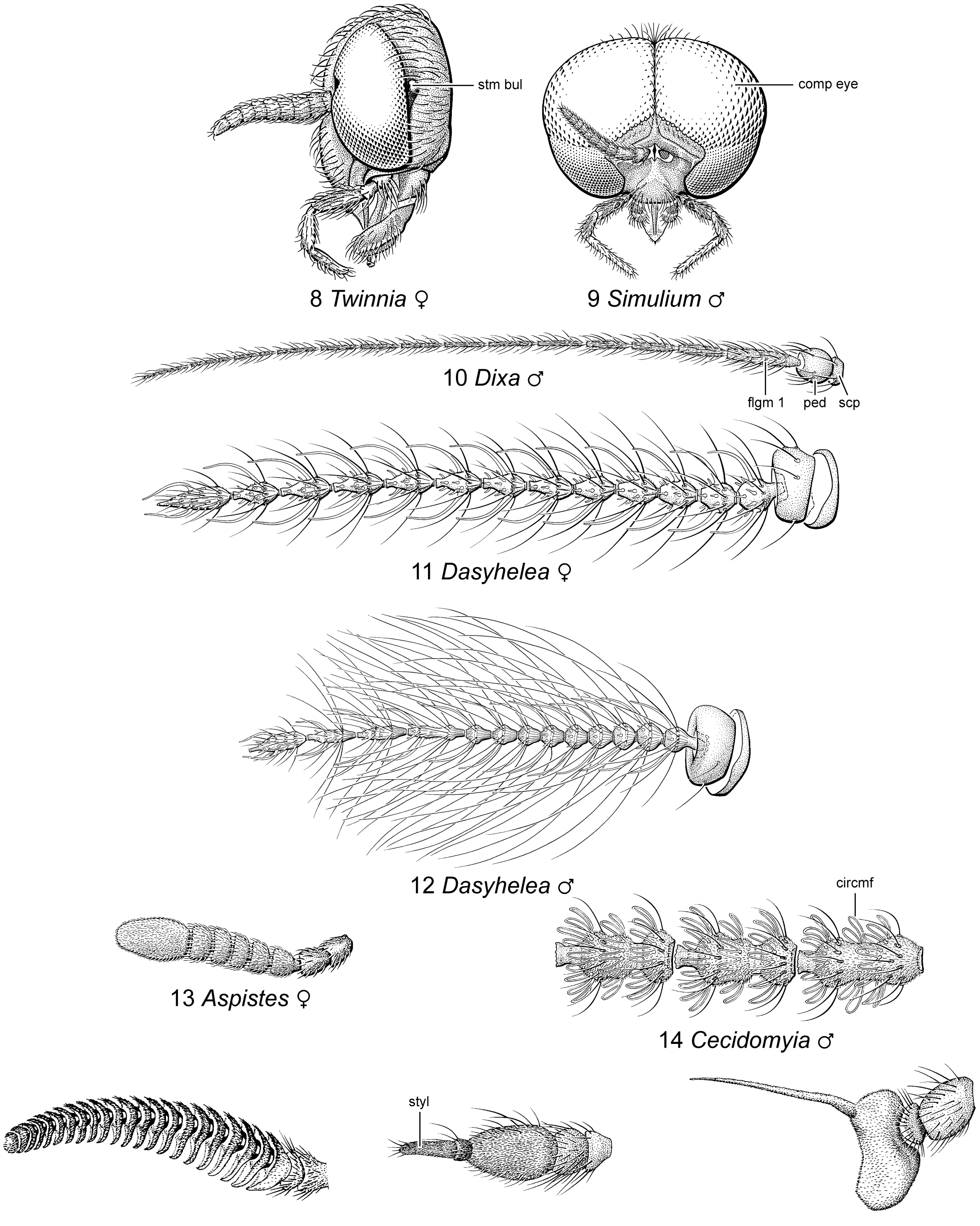
subvibrissal ridge: the lower cranial margin between the vibrissa and ventral margin of the gena in Schizophora.

subvibrissal seta (peristomal seta) (Figs 5, 42): large seta(e) on the subvibrissal ridge below the vibrissa. Usually only one or two setae are present, but in some Tachinidae there are more than four on each side, making the vibrissa appear raised above the ventral cranial margin.

supracervical setae, see under **median occipital sclerite**.

supravibrissal seta (Fig. 42): setae on the facial ridge above the vibrissa; taxonomically important in Calyptratae.

tentorium (Fig. 36): inner skeleton of the head capsule formed by paired sets of anterior, dorsal and posterior arms; the anterior and posterior arms arise, respectively, from externally visible **anterior tentorial pits** (frontoclypeal pits) (Fig. 36) and **posterior tentorial pits** (Fig. 7).



8 *Twinnia* ♀ 9 *Simulium* ♂ 10 *Dixa* ♂ 11 *Dasyhelea* ♀ 12 *Dasyhelea* ♂ 13 *Aspistes* ♀ 14 *Cecidomyia* ♂ 15 *Rachicerus* ♀ 16 *Bolbomyia* ♀ 17 *Symphoromyia* ♀

Figs 3.8–17. Heads and antennae of adult flies: (8) head of *Twinnia* sp. (Simuliidae), lateral view ♀; (9) same, *Simulium decorum* Walker (Simuliidae), anterior view (left antenna omitted) ♂; (10) antenna of *Dixa brevis* Garrett (Dixidae) ♂; (11) same, *Dasyhelea pseudoincisurata* Waugh & Wirth (Ceratopogonidae) ♀; (12) same ♂; (13) same, *Aspistes harti* Malloch (Scatopsidae) ♀; (14) same, *Cecidomyia resinicola* (Osten Sacken) (Cecidomyiidae) ♂; (15) same, *Rachicerus obscuripennis* Loew (Xylophagidae) ♀; (16) same, *Bolbomyia macgillisi* Chillcott (Rhagionidae) ♀; (17) same, *Symphoromyia inurbana* Aldrich (Rhagionidae) ♀ (all non-Afrotropical). Figs 8, 9 (after Peterson 1981, figs 2, 3), Figs 10–17 (after McAlpine 1981, figs 12, 13, 14, 21, 20, 22, 28, 29, respectively).

Abbreviations: circmf – circumfilum; comp eye – compound eye; flgm – flagellomere; ped – pedicel; scp – scape; stm bu – stemmatic bulla; styl – stylus.

vertex (Fig. 5): the uppermost portion of the head capsule, with no definite boundaries. In the keroplatid subfamily Macrocerinae, a separate defined plate that occupies all or most of the vertex and bears the ocelli, is referred to as the **cerebral sclerite** (Matile 1990).

vibrissa (Figs 5, 42): in Schizophora an exceptionally large anteromedially directed seta that occupies a prominent position on the vibrissal angle at the base of the facial ridge; it is especially well-developed in Calyptratae, but also robust in some acalyptrate families (Barraclough 1995). An important landmark, it may be above, below, or at the level of the lower facial margin and is continuous with the setae of the facial ridge (supravibrissal setae) and those of the subvibrissal ridge. The vibrissa is also usually flanked laterally by a few much smaller setae.

vibrissal angle: in Schizophora, the angle, when viewed in profile, on which the vibrissa arises, formed between the facial ridge above and the subvibrissal ridge below.

Compound eye

The compound eyes (Figs 6, 40, 42) usually occupy most of the side of the head, but may be so extensive, particularly in males, that they make up nearly all of the head (Fig. 9). The eyes of some members of the Diopsidae, Periscelididae, Platystomatidae, Richardiidae (non-Afrotropical), Tephritidae and Ulidiidae are located at the end of narrow stalks. In some groups, such as cavernicolous, termitophilous, or ectoparasitic forms, the eyes are considerably reduced, or absent. Eye colour is usually uniform reddish-brown to dark brown or black, but can appear bright metallic in certain taxa. In some families, such as Tabanidae, Syrphidae, Richardiidae and Tephritidae, a pattern of bands and patches is frequently evident in living specimens.

Glossary

dichoptic (Fig. 4): the condition in which the compound eyes do not meet between antennae and vertex (see **holoptic** below).

eye bridge: in Sciaridae and some Cecidomyiidae, the compound eyes are narrowly connected medially above the antennae to form an eye bridge; this narrow connection is just a specialised example of holopticism.

facet: the transparent cuticular covering, or cornea, of an individual **ommatidium**.

holoptic (Figs 6, 9): the condition in which the compound eyes meet in the midline between the antennae and vertex. Males of many families are holoptic and the ommatidia in the upper part of the eye of these males are often larger than those of the lower part (Fig. 9), sometimes strikingly so (*e.g.*, most Simuliidae and Bibionidae, some Tabanidae and Empididae, most Syrphidae). This phenomenon is associated with males that hover, or swarm while awaiting the arrival of females. Although not actually touching medially, the eyes of many male calyptrates and some acalyptrates (*e.g.*, Lonchaeidae, Milichiidae and Ctenostylidae), are closer together than those of their conspecific females (*cf*. Figs 4, 6) and again, it is assumed that this condition allows the male greater visual accuity to chase and capture females in the air. Both males and females of some Blephariceridae, Acroceridae and Hybotidae (*e.g.*, Hybotinae) are holoptic, again probably associated with greater visual powers while hunting for hosts or prey. In the tachinid genera *Phasia* Latreille and *Trichopoda* Berthold the eyes of the female, although not strictly holoptic, are more closely approximated medially than those of the male (see **dichoptic** above).

ommatidium (pl. **ommatidia**): a unit of the compound eye consisting of a corneal lens (seen externally as a single **facet** on the compound eye), crystalline cone, pigment cells, rhabdome and retinula cells, which together connect to nerve fibres. As mentioned above in the definition of **holoptic**, some ommatidia are larger than others, presumably to admit more light. Most enlarged ommatidia are found in the dorsal portion of male eyes (Fig. 9); however enlarged ommatidia may be found ventrally, as in males of the simuliid *Parasimulium* Malloch, the cecidomyiid *Trisopsis* Kieffer and the phorid *Auxanommatidia* Borgmeier. Some asilids have enlarged ommatidia in the central part of the compound eye, *e.g.*, *Holcocephala* Jaennicke.

ommatrichia (eye hairs): between some ommatidia fine straight hairs may arise that give the eye a pilose appearance; these hairs, referred to as ommatrichia, or eye hairs, may be long and easily visible, or so short as to require strong magnification to be seen. They may be dense, arising between every ommatidium, or sparse, arising only between every third or fourth ommatidium.

Antenna

Antennae vary extensively within Diptera and often exhibit marked sexual dimorphism. Each antenna is made up of three basic parts (or **antennomeres**), the basal segment, or **scape**, the second segment, or **pedicel** and the third segment referred to as the **flagellum**, which contains varying numbers of **flagellomeres** (the more terminal antennomeres) (Figs 10, 40).

Glossary

ascoids: translucent thin-walled sensoria found on the flagellomeres of many Psychodidae; they may be branched or unbranched and are variously shaped.

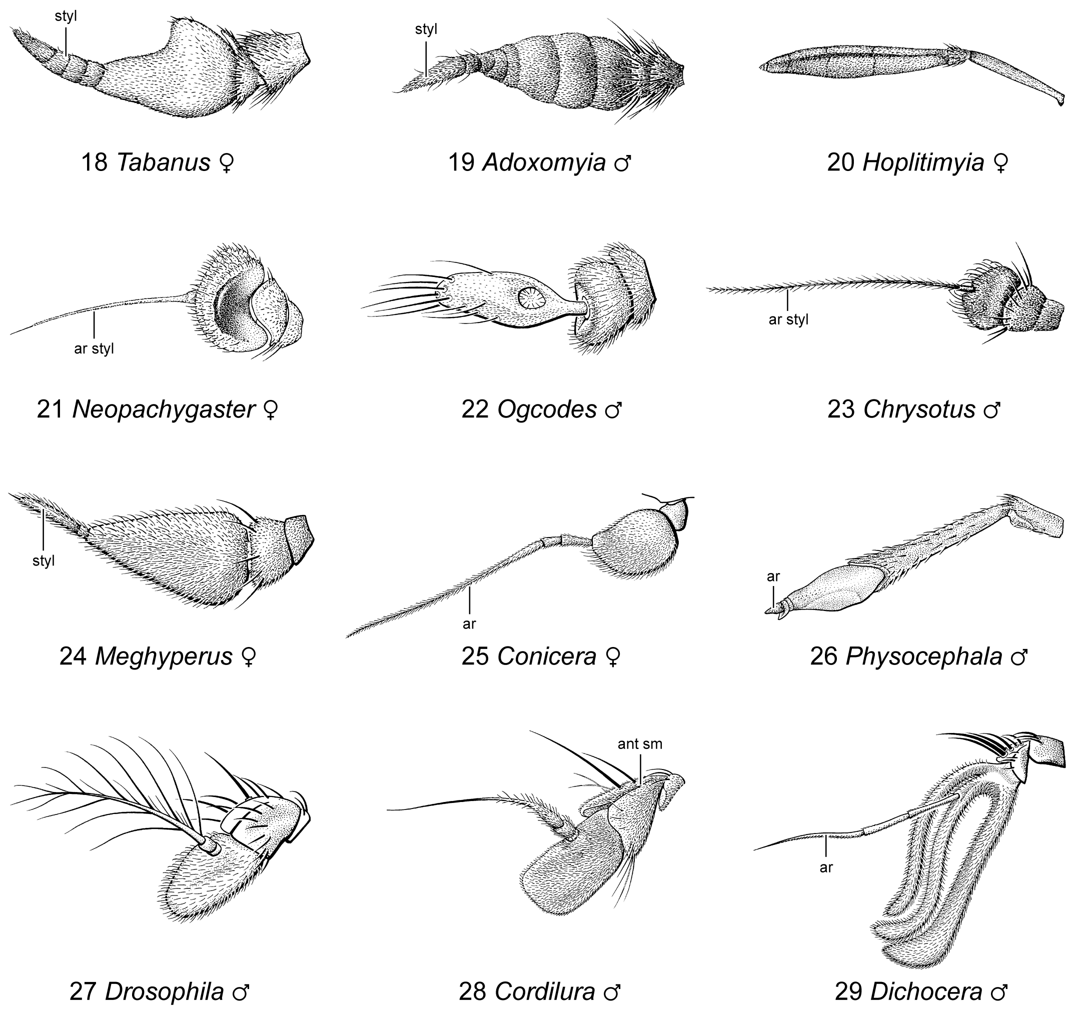
annular ridge, see **pedicel**.

antennal seam (pedicellar cleft, pedicellar seam) (Fig. 28): in Calyptratae and some acalyptrate families a longitudinal groove on the dorsolateral surface of the pedicel and corresponding apical notch. The seam is a useful character for recognising larger Calyptratae, but because of its occurrence in Tephritidae, Aulacigastridae, Periscelididae, Mormotomyiidae, some Platystomatidae and its slight manifestation in a few other acalyptrate families (*e.g.*, some Drosophilidae), this character is not very helpful for separating small calyptrates from acalyptrates. McAlpine (2011) gives a more complete account of the distribution of the antennal seam (as pedicellar cleft) in Schizophora.

antennal socket (Fig. 36): an opening in the frontal plate where the scape arises.

arista (Figs 4, 25, 26, 29, 41, 42): a term used for the last three articles of the flagellum (antennomeres 8–10, with 10 being the longest) in all Cyclorrhapha (Stuckenberg 1999), except the basal family Opetiidae (non-Afrotropical). These articles are generally slender and may arise either dorsally, or terminally on the postpedicel, but occasionally they are short (Fig. 26), or they may be absent altogether, as in males of the phorid genus *Abaristophora* Schmitz. Similar appearing apical whip-like flagellomeres occur in Athericidae and some Vermileonidae, Rhagionidae, Stratiomyidae and Empidoidea (Figs 21, 23). These apical flagellomeres are sometimes referred to as an arista, but because different antennomeres are involved (either 9–10, or 8–10 with 9 being the longest), they are best referred to as an arista-like stylus (Stuckenberg 1999) (see **stylus**). The arista of Cyclorrhapha is sometimes bare, or covered in a vestiture of microtrichia. The arista is referred to as **bare**, **micropubescent**, **pubescent**, **pectinate**, or **plumose** depending on the presence, or increasing length of the microtrichia. In pectinate, or plumose forms the individual microtrichia are usually referred to as **branches** (or rays).

aristomere (Fig. 25): one of three articles, or flagellomeres, that make up the arista in Cyclorrhapha. Usually, the basal aristomeres are very small and most of the arista is formed by the terminal article.



18 *Tabanus* ♀ 19 *Adoxomyia* ♂ 20 *Hoplitimyia* ♀

21 *Neopachygaster* ♀ 22 *Ogcodes* ♂ 23 *Chrysotus* ♂

24 *Meghyperus* ♀ 25 *Conicera* ♀ 26 *Physocephala* ♂

27 *Drosophila* ♂ 28 *Cordilura* ♂ 29 *Dichocera* ♂

Figs 3.18–29. Antennae of adult flies (lateral views): (18) *Tabanus sulcifrons* Macquart (Tabanidae) ♀; (19) *Adoxomyia rustica* (Osten Sacken) (Stratiomyidae) ♂; (20) *Hoplitimyia constans* (Loew) (Stratiomyidae) ♀; (21) *Neopachygaster maculicornis* (Hine) (Stratiomyidae) ♀; (22) *Ogcodes albiventris* Johnson (Acroceridae) ♂; (23) *Chrysotus pallipes* Loew (Dolichopodidae) ♂; (24) *Meghyperus* sp. (Atelestidae) ♀; (25) *Conicera dauci* (Meigen) (Phoridae) ♀; (26) *Physocephala furcillata* (Williston) (Conopidae) ♂; (27) *Drosophila colourata* Walker (Drosophilidae) ♂; (28) *Cordilura ustulata* Zetterstedt (Scathophagidae) ♂; (29) *Dichocera orientalis* Coquillett (Tachinidae) ♂ (all non-Afrotropical). Figs 18–29 (after McAlpine 1981, figs 30, 23, 25–27, 36, 33, 37, 38, 41, 43, 45 (as *D. tridens*), respectively).

Abbreviations: ant sm – antennal seam; ar – arista; ar styl – arista-like stylus; styl – stylus.

caestus (pl. **caesti**), see **pedicel**.

circumfila (sing. **circumfilum**) (Fig. 14): slender thread-like sensoria that encircle the flagellomeres of the antennae of some Cecidomyiidae and in certain species, particularly in males, form loops, or sinuous patterns.

conus: a narrow, thumb-like condyle, or conus of the pedicel that is inserted into the base of the first flagellomere. A conus is present in ceratomerine Empidoidea and several dolichopodid genera (*e.g.*, *Dolichopus* Latreille, *Tachytrechus* Haliday and *Syntormon* Loew) and a similar feature is present and appears to be a synapomorphy of almost all Cyclorrhapha, except the basal families Opetiidae (non-Afrotropical) and Platypezidae (Cumming *et al*. 1995: 143) (see **pedicel**).

first flagellomere (flagellomere 1, basal flagellomere, **postpedicel**, third antennal segment) (Figs 5, 10, 40, 42): the first article of the flagellum that is articulated to the apex of the pedicel. In nematocerous Diptera the first flagellomere is not strikingly differentiated from the following adjacent flagellomeres, but in Brachycera it is usually larger than the second and usually the largest portion of the antenna. Many exceptions occur, for example, in some Stratiomyidae, where the first three flagellomeres are similar to one another in size (Fig. 19) and, therefore, contrast with the remaining ones. In other Brachycera the flagellar base usually undergoes some degree of fusion, so that what is referred to as the first flagellomere is generally a compound structure. This enlargement and specialisation led Stuckenberg (1999) to propose that the flagellar base be termed the **postpedicel** (Figs 5, 42), irrespective of how many articles were fused together. In Cyclorrhapha, the first flagellomere, in contrast to the pedicel, is not setose, although it is usually finely pilose. The deep trichoid sensilla-containing invaginations, that each exit through a pore on the lateral surface of the first flagellomere of Ironomyiidae (non-Afrotropical), Syrphoidea and Schizophora, are termed **sacculi** (McAlpine 2011). These invaginations are not considered homologous with the **postpedicellar pouches** observed in the empidoid genus *Hormopeza* Zetterstedt and platypezid genus *Microsania* Zetterstedt (McAlpine 2011), which appear to be used to detect smoke that attracts these flies (Sinclair & Cumming 2006).

flagellomere (Figs 5, 10, 40, 42): any one of several articles constituting the flagellum. Flagellomeres are not true segments in that they are not individually musculated. According to Hennig (1973), the basal number of flagellomeres is 14 in nematocerous Diptera (although over 100 have been counted in an African psychodid), eight in the Lower Brachycera, three in the Asilomorpha and Empidoidea and four in Cyclorrhapha. Unfortunately, this number may not always be safely used to recognise all members of these taxa, for the number of flagellomeres varies widely in some nematocerous groups, depending on the species and is at times difficult to count (although most nematocerous Diptera with a reduced number of flagellomeres still have more than two palpal segments). For example, Simuliidae have 7–9 flagellomeres, Ceratopogonidae 6–13, Chironomidae 1–15, Scatopsidae 5–10, the cecidomyiid *Baeonotus* Byers has only six, while *Bibio* Geoffroy has seven. On the other hand, the xylophagid *Rachicerus* Walker has 20–36 flagellomeres (Fig. 15), no doubt secondarily subdivided (but it can be recognised as a brachyceran by its two-segmented palpus).

flagellum (Figs 5, 10, 40, 42): that part of the antenna beyond the pedicel and articulated to it; it is the third true segment of the antenna, divided into varying numbers of flagellomeres. The individual flagellomeres may bear long setae (**verticils**), especially among males of Culicomorpha (Fig. 12); in some taxa these long setae may be erected by hemolymph pressure during mating flights to make the antennae more receptive to wing beats of the female (see **pedicel**).

pedicel (Figs 5, 10, 40, 42): the second segment of the antenna. In male Culicomorpha (except Thaumaleidae, Simuliidae and some Ceratopogonidae), the pedicel is enlarged and globular (Fig. 30) and contains a sense organ (Johnston's organ), that is used for detecting wing-beat vibrations of the female. In some Conopidae, Pyrgotidae, Sciomyzidae and Ulidiidae the pedicel is extremely long, making up more than half the length of the antenna (Fig. 26) and in these families the antenna is porrect (*i.e.*, held extending forward). McAlpine (2011) described a number of useful taxonomic characters on the pedicel of higher Diptera, such as the **annular ridge** and paired **caesti**, which are modified raised surfaces that articulate with the first flagellomere (also see **conus**), and a recessed dome-like cuticular component of a chordotonal organ termed the **pedicellar button**.

pedicellar button, see **pedicel**.

postpedicel, see **first flagellomere**.

postpedicellar pouch, see **first flagellomere**.

sacculus (pl. **sacculi**), see **first flagellomere**.

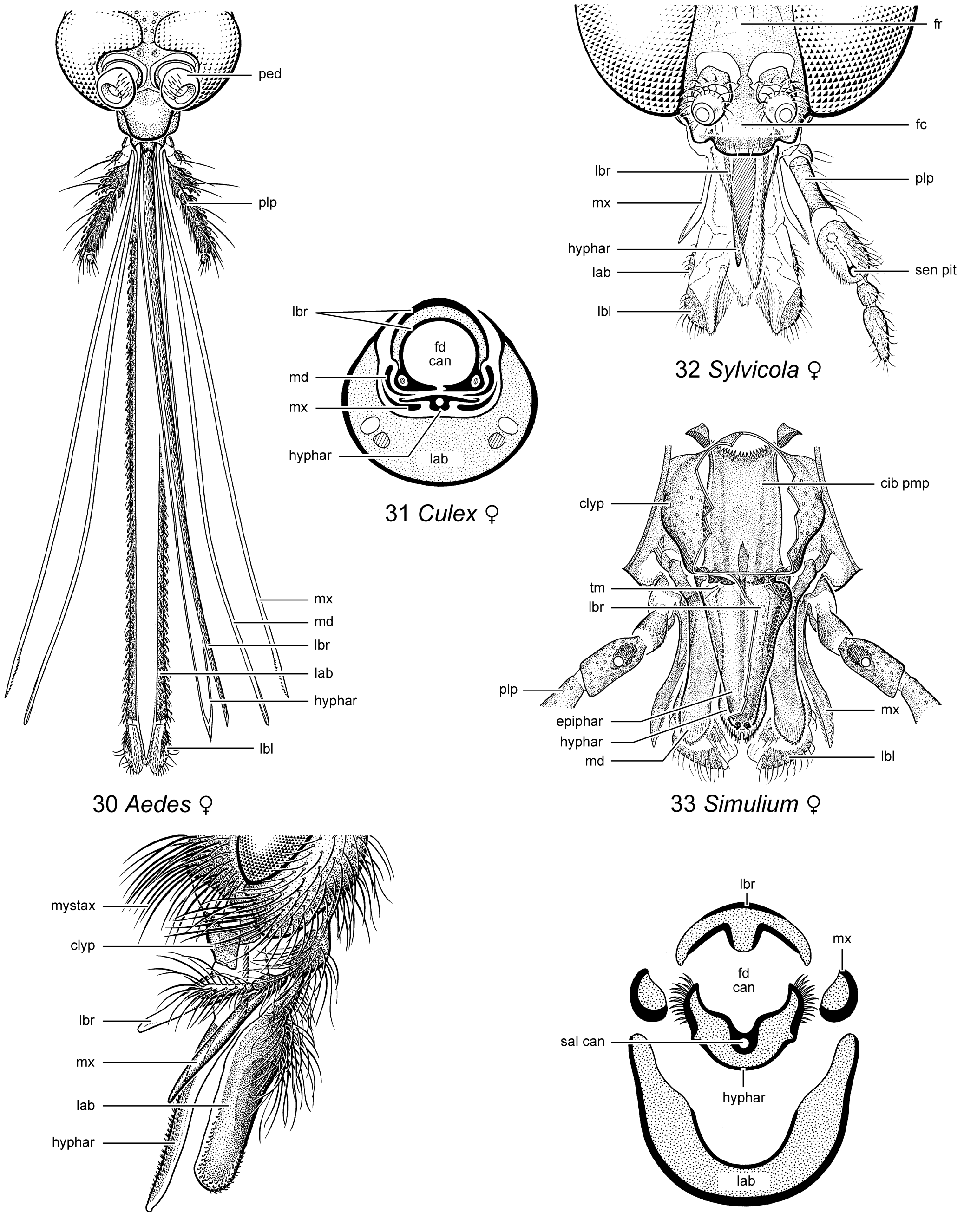
scape (Figs 10, 40): the first segment of the antenna, usually rather insignificant, except in the lower Brachycera, where it can be the longest segment of the antenna, as in the bombyliid genus *Lepidophora* Westwood. The scape is usually setose. In the tachinid genus *Microphthalma* Macquart, the apex of the scape extends as a flange over the pedicel.

stylus (style) (Figs 16, 18, 19, 21, 23, 24): the terminal flagellomeres, ending in antennomere 10 (flagellomere 8) in the orthorrhaphous Brachycera and Opetiidae (non-Afrotropical), that usually arise at the apex of the first flagellomere. The stylus is sometimes composed of as many as six terminal flagellomeres, but usually contains as few as one or two articles (Stuckenberg 1999). The bare hyaline process at the apex of the antenna in many asiloids and empidoids (actually antennomere 10 according to Stuckenberg (1999)), has also been referred to as the antennal style (Yeates 1994) (see **arista**).

verticil, see **flagellum**.

Mouthparts

Unless their mouthparts are non-functional (*e.g.*, some Oestridae), all Diptera have, at a minimum, a **labrum**, a **hypopharynx** and a **labium** (Fig. 32). The **mandibles** and/or **maxillae** are reduced in most flies, apart from females of blood-sucking (with few exceptions) nematocerous families (Figs 30, 33) and lower Brachycera, and are absent in many taxa.



30 *Aedes* ♀

31 *Culex* ♀

32 *Sylvicola* ♀

33 *Simulium* ♀

34 *Laphria* ♀

35 *Laphria* ♀

Figs 3.30–35. Heads and mouthparts of adult flies: (30) anterior view of lower part of head (antennae omitted) and mouthparts (individual stylets separated to show form and relationships) of *Aedes canadensis* (Theobald) (Culicidae) ♀; (31) cross-section through proboscis of *Culex pipiens* L. (Culicidae) ♀; (32) anterior view of lower part of head and mouthparts, with components separated, of *Sylvicola fenestralis* (Scopoli) (Anisopodidae) ♀; (33) anterior view of mouthparts and clypeus, cut away to show cibarium, of *Simulium vittatum* Zetterstedt (Simuliidae) ♀; (34) lateral view of lower part of head and mouthparts of *Laphria thoracica* F. (Asilidae) ♀; (35) same, cross-section through proboscis ♀ (all non-Afrotropical). Figs 30–32, 34, 35 (after McAlpine 1981, figs 46–48, 54, 53, respectively), Fig. 33 (after Peterson 1981, fig. 8).

Abbreviations: cib pmp – cibarial pump; clyp – clypeus; epiphar – epipharynx; fc – face; fd can – food canal; fr – frons; hyphar – hypopharynx; lab – labium; lbl – labellum; lbr – labrum; md – mandible; mx – maxilla; ped – pedicel; plp – palpus; sal can – salivary canal; sen pit – sensory pit; tm – torma.

Glossary

basiproboscis: a term used in Asilidae for the basal part of the proboscis that is enclosed by the base of the prementum. It is generally distinct from the more distal portion of the proboscis, which in asilids, is enclosed by the solidly fused apex of the prementum and the labella (see **distiproboscis**).

capitate proboscis, see **proboscis** below.

cardo (pl. **cardines**): the basal segment of the maxilla. It is scarcely detectable in most adult Diptera and is not used taxonomically, except in the larva.

cibarium (Figs 33, 36): the pump for drawing up liquid food; the internal sclerotised tube connected to and continuous with the food canal within the rolled labrum, derived from the posterior portion of the preoral cavity at the beginning of the pharynx. The cibarium is useful taxonomically in the Simuliidae. A small **hyoid sclerite** also occurs ventrally along the proximal margin of the cibarium in Calyptratae.

clypeal ridge (Fig. 36): a primarily internal ridge in Brachycera, that arises obliquely from the clypeus and articulates with the labrum and cibarium at the labrofulcral articulation point. It is derived from the clypeus, but is sometimes confused with the tormae that are derived from laterobasal processes of the labrum (see **torma** below).

clypeus (frontoclypeus) (Figs 4, 30, 33, 34, 36, 37, 39): really a part of the head capsule, rather than one of the mouthparts, but incorporated into the proboscis in Brachycera. In nematocerous families, the clypeus is a rounded convex sclerite between the labrum and the face and in blood-sucking flies it occupies most of the space between the antennae and mouthparts. Internally it supports the origins of the cibarial dilator muscles. In the Brachycera, exclusive of Tabanomorpha, the proboscis is more mobile and the clypeus has become reduced and is hinged at the **frontoclypeal suture**, the lower margin of the face. In Schizophora, the clypeus is even more widely separated from the face by the **frontoclypeal membrane** (Fig. 6) and the entire proboscis is capable of considerable extension and retraction (see also under Head).

distiproboscis: in Asilidae the labella are solidly fused to the apex of the prementum as part of the sheath through which the hypopharynx is driven into the prey (Fig. 34); this fused distal portion of the proboscis is generally distinct from the more basal part, which is enclosed by the base of the prementum (see **basiproboscis**).

epipharyngeal blades, see **labrum**.

epipharynx, see **labrum**.

geniculate proboscis, see **proboscis** below.

hyoid sclerite, see **cibarium**.

hypopharynx (lingua) (Figs 30–37, 39): the tongue, an unpaired median stylet-like extension of the posterior margin of the mouth, conveying the salivary canal. All flies that feed have a hypopharynx, if only for wetting dried honeydew so it can more easily be sucked up. The hypopharynx is of critical importance in blood-sucking flies for conducting anticlotting substances to the wound during feeding. In Asilidae, the hypopharynx is long and sharp (Fig. 34) and is the only mouth-part to enter the prey. Asilid saliva must be highly toxic as well as proteolytic, for asilids can subdue, in seconds, stinging prey larger than themselves, then later suck out the liquefied contents of the prey. When handled they can also inflict a painful bite.

labellum (pl. **labella**) (Figs 4, 5, 7, 30, 32, 33, 36–38, 40): homologous to the labial palpus, primitively two-segmented (as in Blephariceridae and Tanyderidae), but in most Diptera each palpus is reduced to a single, highly modified structure for sponging up fluids (see **pseudotracheae**). Although a paired structure, the two labella (**labellar lobes**), are fused medially into a single cupped structure at the end of the prementum, which is pressed onto the substrate during feeding. Channels on the ventral side, the pseudotracheae, all lead to the midline, from which point saliva can be pumped into them *via* the hypopharynx to wet the substrate and dissolve sugars or salts present there, or liquid food can be sucked up from them *via* the food canal in the labrum, aided by suction from the cibarial pump. The labella may be greatly reduced in some species, especially those with a long proboscis for taking nectar from tubular flowers (many Bombyliidae), or the labella themselves may also be greatly elongate for accomplishing the same task (*e.g.*, *Siphona* Meigen, in the Tachinidae). In the Asilidae (Fig. 34), the labella are fused to the apex of the prementum to form a solid sheath, through which the sharp hypopharynx is projected into the prey (see **distiproboscis**).

labium (Figs 30–35, 39): as in all mandibulate arthropods, the labium is homologous to the second maxillae, or most posterior pair of segmental head appendages. In Diptera these paired appendages are completely fused medially, to form a trough-like sheath surrounding the remaining mouthparts from behind and thus the labium is usually the most conspicuous part of the proboscis. The sheath itself is made up of the basal **postmentum** (mentum) and the apical **prementum**, terminating distally in the medially fused **labella** (**labellar lobes**). In most Diptera, the postmentum is insignificant, forming the ventral external closure of the head capsule, while the prementum and the labella are the predominant parts of the proboscis. The labium is hinged at its base and can be extended while feeding, or folded forward when at rest. In nematocerous Diptera and non-Schizophora this hinge is not very extensible and in blood-feeding forms it is even more closely associated with the head capsule, to provide stability to the mouthparts when they are inserted into the host. In Schizophora, however, the labium is particularly mobile, connected to the lower cranial margin by a substantial membranous cuticle that allows considerable extension so that the fly does not need to bend down to feed, but merely has to extend the proboscis. In blood-feeding Calyptratae, such as the stable flies, *Stomoxys* Geoffroy (Muscidae) (Figs 38, 39), *tsetse* (Glossinidae) and louse flies (Hippoboscidae), the entire proboscis is jabbed into the host with the help of recurved spines on the labella (see **prestomal teeth**).

labrum (Figs 4, 6, 30–37, 39): the upper lip, a triangular or elongate flap extending anteroventrally from the clypeus and hinged to it along the clypeolabral suture. Its ventral surface is grooved to form, along with the dorsal surface of the hypopharynx, the food canal. In most flies, the labrum is visible externally as a triangular, or elongate stylet between the encircling edges of the prementum, but it and the hypopharynx, can extend beyond the labella if the labium is withdrawn, which is apparently how predaceous Empidoidea stab their prey. In most Empidoidea the ventral wall of the labrum (**epipharynx**) is developed into apical tooth-like projections, referred to as **epipharyngeal blades** (or armature), that flank the median pointed labral tip (Bletchly 1954). These sharp blades are used for piercing and cutting tissue and are most heavily sclerotised in the empidoid family Dolichopodidae (Fig. 36).

lacinia (pl. **laciniae**) (galea) (Figs 30–36): the stylet of the maxilla in Diptera, misinterpreted by some authors as the galea, as indicated by McAlpine (1981: 20) and Wood & Borkent (1989: 1337). It is best developed in blood-feeding nematocerous and lower brachyceran families, as well as in some predaceous taxa; reduced, or vestigial in most other Diptera; absent in Cyclorrhapha. Set with retrorse teeth apically in blood-feeding groups and used to anchor the mouthparts in the skin of the host while the mandibles are cutting a hole, or in the case of mosquitoes, to gain purchase while the mandibles are inserted further (see **maxilla**).

mandible (Figs 30, 31, 33): a paired appendage of the head on either side of the mouth opening; a triangular or elongate stylet, which in blood-sucking forms is often set with saw-like teeth apically, for cutting the skin. In female members of Simuliidae (Fig. 33) and most Ceratopogonidae that blood-feed, the mandibles partially overlap one another and function as a pair of scissors, using as a fulcrum a tubercle on one mandible that fits into a depression on the other. Functional mandibles are also found in females of some Tanyderidae, most Blephariceridae, some Psychodidae (in several subfamilies), Culicidae, Corethrellidae, two genera of Chironomidae and many Tabanomorpha, all of which are apparently either predaceous, or blood-feeding.

maxilla (pl. **maxillae**) (Figs 30–36): a paired appendage of the head that arises behind the mandible and bears the palpus as its only external manifestation; it is hidden within the proboscis as a stylet, the lacinia. Well-developed in the blood-feeding forms mentioned under mandible, the lacinia is reduced, or vestigial in most Diptera and absent in Cyclorrhapha (see **cardo**, **lacinia**, **palpus** and **stipes**).

mentum, see **postmentum**.

palpifer: differentiated sclerotised region of the stipes that supports the palpus in certain taxa (*e.g.*, Hybotidae in the Empidoidea, as well as some Phoridae) (see **stipes**).

palpomere, see under **palpus**.

palpus (maxillary palpus, palp) (Figs 4, 5, 7, 30, 32, 33, 36, 37, 39, 40, 42): although part of the maxilla, this relationship is not readily apparent because the rest of the maxilla is enclosed in the labium and the palpus arises at, or near the base of the prementum. In nematocerous families the palpus is primitively divided into five segments (incorrectly referred to as palpomeres); although in many taxa there appear to be only four (probably because of great reduction of the basal segment). Further reductions in segment number occur in various nematocerous groups. The third segment of both sexes of most nematocerous families bears a sensory pit or vesicle (Lutz's organ), which is essentially an invagination that opens to the exterior *via* a pore. This pit is cavernous in females of many blood-sucking species and contains a cluster of club-shaped sensilla that are sensitive to carbon dioxide. The palpus in Brachycera is reduced to two segments in the lower Brachycera, even in blood-sucking forms belonging to the Tabanidae, Rhagionidae and Athericidae. Only one segment is present in the Eremoneura (Empidoidea and Cyclorrhapha); the apparent basal segment of the two-segmented palpus seen in some Phoridae (Brown 1992) is probably a palpifer (see above). Among several genera of Tachinidae, the single segment is reduced in size, or is lacking altogether.

postmentum (mentum): the basal sclerite of the labium retained in only a few nematocerous families, such as Blephariceridae, Tanyderidae, Anisopodidae, Psychodidae and Ceratopogonidae (Stuckenberg 2004).

prementum (haustellum, theca) (Figs 4, 5, 7, 36–38): the distal tubular portion of the labium forming the supporting sheath of the proboscis, terminating in the labella.

prestomal teeth (Fig. 38): bicuspid blades situated between the pseudotracheae at the base of the labella in Calyptratae; they are enlarged in predaceous groups (*e.g.*, coenosiine Muscidae, Scathophagidae) and are especially prominent in blood-feeding calyptrates (*e.g.*, stomoxyine Muscidae, Hippoboscoidea).

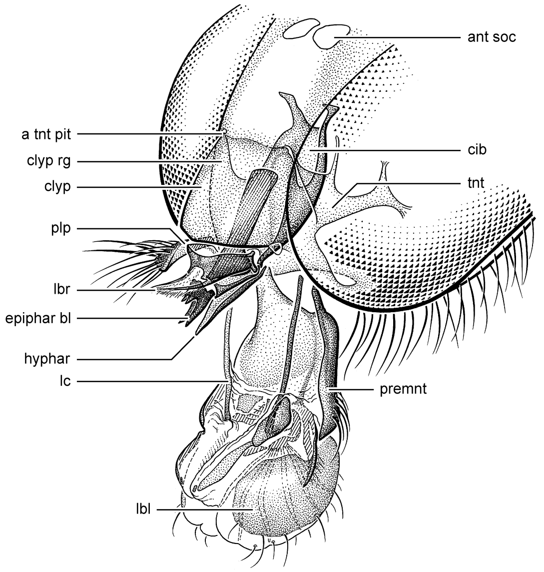
proboscis (Fig. 3): all of the mouthparts ensheathed in the labium extending from the subcranial cavity of the head capsule (often referred to as the "mouth"). In Schizophora the proboscis is capable of considerable extension and retraction, often being entirely withdrawn into the head capsule and the membrane joining it to the subcranial margin is correspondingly more extensive. When a proboscis is thin and bent with long labella, it is termed **geniculate**, whereas when it is thicker (*i.e.*, square to slightly rectangular), with short labella, it is termed **capitate** (see also under Head).

pseudotracheae (sing. **pseudotrachea**) (Fig. 37): interconnected channels on the ventral surface of the labella of many Brachycera that radiate out from the midline where the tips of the labrum and hypopharynx meet; they are reinforced with rings of chitin (hence the reference to tracheae) that are open ventrally.

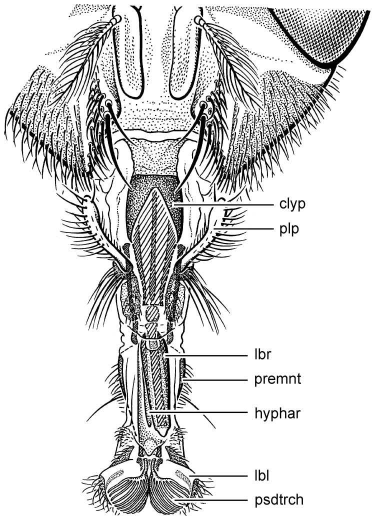
salivary canal (Fig. 35): the common salivary duct that in most Diptera extends the length of the hypopharynx to open at its apex. Saliva is used to wet the food so it can be dissolved and taken up by the pseudotracheae when present and to convey hemolytic enzymes to the host while blood-feeding to prevent clotting of the blood meal, or proteolytic enzymes in predaceous taxa to paralyse the prey and liquefy its tissues for consumption. Diptera cannot take solid food unless it is sufficiently finely divided (such as pollen grains), to be sucked up the food canal along with other liquids. Various pathogens (*e.g.*, viruses, bacteria and protozoa, such as *Plasmodium* spp. that cause malaria), take advantage of the salivary canal to enter new hosts while an infected fly is blood-feeding.

stipes: the distal segment of the maxilla, bearing the lacinia and the palpus (see **palpifer**).

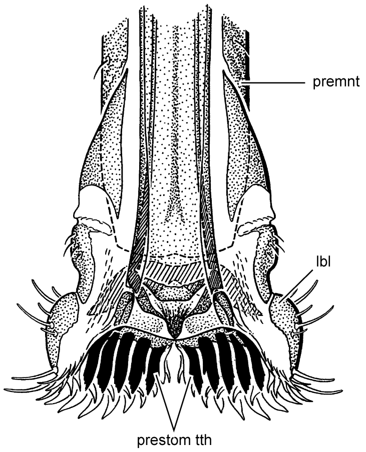
syntrophium (fascicle) (Figs 31, 35): term proposed by Jobling (1976) for the complex of mouthparts that functionally enclose the food and salivary canals, namely the labrum and



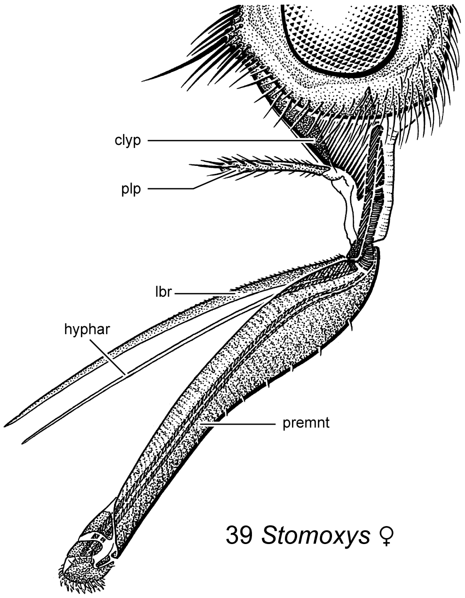
36 *Condylostylus* ♀



37 *Calliphora* ♀



38 *Stomoxys* ♀



39 *Stomoxys* ♀

Figs 3.36–39. Mouthparts (displayed to show form and relationships): (36) anterolateral view of proboscis with cibarium and tentorium of *Condylostylus sipho* (Say) (Dolichopodidae) ♀ (non-Afrotropical); (37) anterior view of proboscis and lower part of head of *Calliphora vomitoria* (L.) (Calliphoridae) ♀ (non-Afrotropical); (38) anterior view of enlarged apex of proboscis showing prestomal teeth of *Stomoxys calcitrans* (L.) (Muscidae) ♀; (39) same, lateral view of proboscis and lower part of head. Figs 36–39 (after McAlpine 1981, figs 51, 58, 57, 55, respectively).

Abbreviations: a tnt pit – anterior tentorial pit; ant soc – antennal socket; cib – cibarium; clyp – clypeus; clyp rg – clypeal ridge; epiphar bl – epipharyngeal blade; hyphar – hypopharynx; lbl – labellum; lbr – labrum; lc – lacinia; plp – palpus; premnt – prementum; prestom tth – prestomal teeth; psdtrch – pseudotrachea; tnt – tentorium.

hypopharynx, as well as the mandibles and maxillary laciniae when present, but not the labium.

torma (pl. **tormae**) (Fig. 33): a small laterobasal sclerite of the labrum situated on each side of the base of the epipharynx near the clypeolabral suture; tormae are best developed in those nematocerous families and orthorrhaphous Brachycera that possess piercing mouthparts (see also **clypeal ridge** above).

Thorax

In Diptera, the three thoracic segments, the **prothorax**, **mesothorax** and **metathorax**, are intimately fused together into a single spheroidal, or rectangular capsule, consisting almost entirely of the mesothorax, with its associated wing and leg muscles, while the prothorax and metathorax are reduced to a minimum, enough to support the leg musculature of the first and third pairs of legs and in the metathorax, the halter (Figs 40–42). Each segment is divided into a dorsal tergal region, the **notum** (pl. **nota**), a small ventral plate, the **sternum** (pl. **sterna**), which in the mesothorax and metathorax may be largely, or entirely internal and thus invisible externally and on each side of the thorax a lateral plate, the **pleuron** (pl. **pleura**).

The notum of the prothorax, the **pronotum**, is divided transversely into an anterior **antepronotum** and a posterior **postpronotum**, which appears to bear the **anterior thoracic spiracle** (mesothoracic spiracle). In nematocerous families the antepronotum is well-developed, while the postpronotum is reduced to a narrow band. The reverse is true in the Brachycera, in which the antepronotum is insignificant, while the postpronotum is expanded laterally to form the anterolateral corners of the thorax, sometimes bearing several setae of taxonomic importance. The notum of the mesothorax, the **mesonotum** (Fig. 2), occupying most of the dorsal surface of the thorax, is divided transversely into four areas, the **prescutum**, **scutum**, **scutellum** and **postnotum**. The prescutum is a rather vaguely defined anterior portion of the mesonotum, best seen in some nematocerous Diptera and is delineated laterally by the **prescutal pit**, whose position on each anterolateral corner of the scutum marks the former position of the pupal respiratory organ.

The most extensive area of the mesonotum, the scutum, is itself divided by the **transverse suture** into a **presutural area** and a **postsutural area** in most taxa. The presutural area in nematocerous families is bordered laterally by a narrow sclerite referred to as the **paratergite**. In nematocerous Diptera and most orthorrhaphous Brachycera the scutum is generally clothed in fine hairs or, in some Bombyliidae, scale-like hairs, while in Asilidae, Therevidae and Empidoidea, as well as in most Cyclorrhapha, some of the setae are stout and bristle-like. In the Eremoneura (Empidoidea and Cyclorrhapha) and particularly the Calyptratae, these setae tend to be arranged in four paired groups of longitudinal rows interspersed with much smaller erect, or recumbent setae; the **acrostichal setae** constitute the median row(s), flanked by **dorsocentral setae**, then by **intra-alar setae** and, just above the wing base, the **supra-alar setae**. The relative size and arrangement of these setae is of great taxonomic importance. The number of presutural *versus* postsutural setae in each row (Fig. 41) is sometimes denoted as a formula, with the presutural and postsutural setae separated by a "+" symbol (*e.g.*, **dc 3 + 4** denotes three presutural *versus* four postsutural dorsocentrals and **acr 4 + 2–3** denotes four presutural *versus* two to three postsutural acrostichals). Lateral to the transverse suture in Cyclorrhapha and some Empidoidea (*e.g.*, Dolichopodidae), is a small diamond-shaped, or triangular sclerite, the **notopleuron**, typically bearing one or two setae, while in the posterolateral corner of the scutum is the **postalar callus**, also bearing two or three setae. Laterally, above the calypter, the edge of the scutum turns down to form the **postalar wall**. A triangular part of this wall, just behind the wing base, the **tympanal fossa** or **tympanic pit**, bears setae in some Calliphoridae and Tachinidae (Fig. 46).

The scutellum is sharply delineated from the scutum by the **scutoscutellar suture**; typically the scutellum bears one or two pairs of marginal setae, a basal pair and an apical pair. Additional marginal setae, including one or more pairs of lateral setae as well as subapical setae and additional pairs, the discal scutellar setae, may be present on its surface.

The postnotum (formerly sometimes considered to be the notum of the metathorax), may be subdivided by a pair of grooves into a medial portion, the **mediotergite** and a lateral portion, the **laterotergite**; the laterotergite may be further divided by a horizontal groove into a dorsal **anatergite** and a ventral **katatergite**. In some Cyclorrhapha, particularly in Tachinidae, the mediotergite may be bordered dorsally by a transverse convex bulge, the **subscutellum**. The notum of the metathorax, the **metanotum**, connects the postnotum to the first abdominal tergite and usually is barely visible externally.

The side of the thorax, the pleuron, is separated from the scutum by the **lateral parapsidal suture**. It is considered derived from basal elements of the subcoxal region of the leg of the same segment that have come to occupy the lateral parts of the thorax, between the notum and sternum. In the dipteran thorax almost all of the side of the thorax is made up of the various components of the mesopleuron and the names of these components, for simplicity, are not preceded by the prefix meso-, while those corresponding parts of the prothorax and metathorax are prefixed by pro- and meta- accordingly.

The wing-bearing segment, the mesothorax, is reinforced by an invaginated strut extending from wing base to leg base, the **pleural suture**, a synapomorphy found in all winged insects, even those that have secondarily become wingless, including wingless adult Diptera. This suture separates the mesopleuron into an anterior episternum and a posterior epimeron. Each of these plates is further divided horizontally by the **anapleural suture** into a dorsal **anepisternum** (mesopleuron, of older terminology) and a ventral **katepisternum** (sternopleuron), in front of the pleural suture and a dorsal **anepimeron** (pteropleuron) and a ventral **katepimeron** (barette) behind the suture. The anepisternum, in Calyptratae and some other Schizophora, typically bears a vertical row of strong setae, as well as associated finer setulae, in front of the base of the wing, the anepisternal setae, while the anepimeron has a small tuft of hair, sometimes with a very large associated seta in some genera, the anepimeral (or pteropleural) seta, just below the wing base. Beneath the katepimeron and between the mid coxa and the posterior thoracic spiracle is the **meron** (hypopleuron), a sclerite derived from the mid coxa.

The **propleuron** and **metapleuron** are each, like their corresponding nota, greatly reduced relative to the mesopleuron.

The propleuron is indistinctly subdivided into an anterior **proepisternum** and a posterior **proepimeron**, although the pleural suture is indistinct (as there is no associated wing). The metapleuron is also subdivided into an anterior **metepisternum** and a posterior **metepimeron** by the rather indistinct **metapleural suture**. The metepisternum is indistinctly subdivided horizontally into a dorsal **metanepisternum** and a ventral **metakatepisternum**, directly behind the meron; these pleurites may be greatly reduced in some taxa and thus difficult to identify.

The sternal region of the thorax is much less extensive than the notal and pleural regions. The most extensive sternal sclerite is the **prosternum**, which is sometimes divided into an anterior **presternum** and a posterior **basisternum**. In some groups the prosternum fuses laterally with the proepisternum to form a sclerotised **precoxal bridge**. The **mesosternum** is mostly invaginated in Diptera, as a narrow internal phragma and is usually reduced externally. Similarly the **metasternum** is almost entirely invaginated.

Glossary

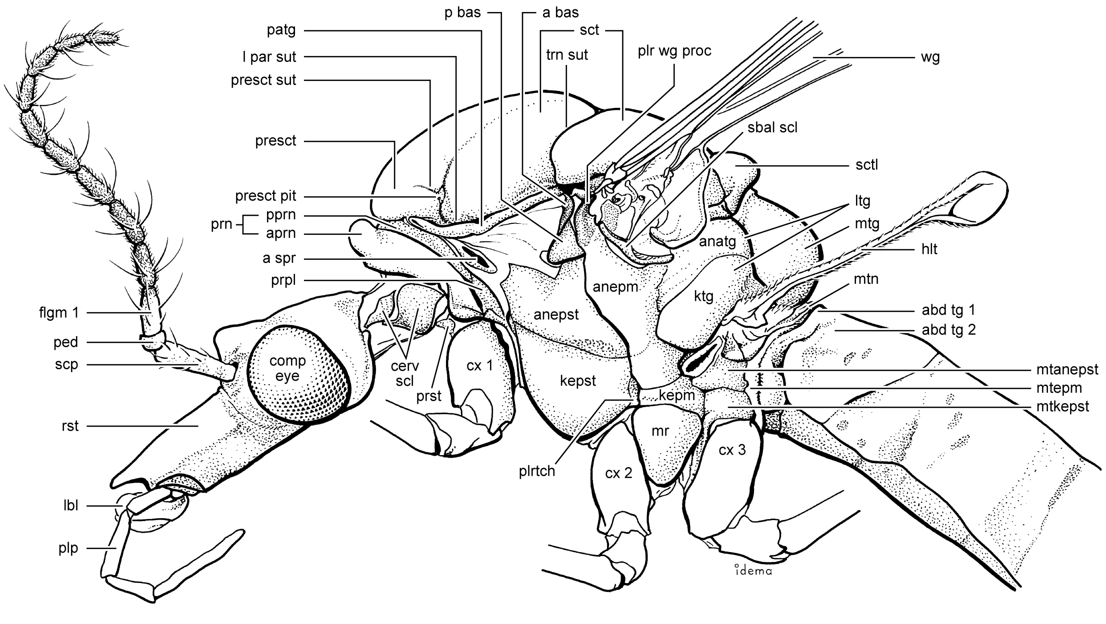
acrostichal setae (Fig. 41): the most medially placed longitudinal rows of setae on the scutum, generally referred to only in Eremoneura (Empidoidea and Cyclorrhapha), but occasionally used in other groups (*e.g.*, Chironomidae). Acrostichals vary from a single median row (uniserial, *e.g.*, most Platypezidae), to a pair of rows (biserial), or occasionally to two pairs of rows (*e.g.*, certain Empidoidea). In acalyptrates, they are usually reduced to a single pair of rows anterior to the scutoscutellar suture, but are more extensive in Calyptratae.

anapleural suture, see under **episternum**.

anatergite (Figs 40, 42): the dorsal portion of the laterotergite, dorsal to the katatergite; in Brachycera it has come to occupy a position behind rather than above the katatergite and thus is the intermediate portion of the postnotum, usually appearing as a flat, or concave area between the calypter and the halter. It may bear tiny setae (**infrasquamal setulae**) under the lower calypter in some Calyptratae (see **laterotergite**).

anepimeral setae (pteropleural setae) (Fig. 42): a tuft of setae, sometimes including also a large seta, arising from a small area below the wing base.

anepimeron (pteropleuron) (Figs 40, 42): the sclerite, or area of the mesopleuron below the wing base, between the



40 *Tipula* ♀

Fig. 3.40. Lateral view of head, thorax and base of abdomen of *Tipula trivittata* Say (Tipulidae) ♀ (non-Afrotropical). Fig. 40 (after McAlpine 1981, fig. 64).

Abbreviations: a bas – anterior basalare; a spr – anterior spiracle; abd tg – abdominal tergite; anatg – anatergite; anepm – anepimeron; anepst – anepisternum; aprn – antepronotum; cerv scl – cervical sclerite; comp eye – compound eye; cx – coxa; flgm – flagellomere; hlt – halter; kepm – katepimeron; kepst – katepisternum; ktg – katatergite; l par sut – lateral parapsidal suture; lbl – labellum; ltg – laterotergite; mr – meron; mtanepst – metanepisternum; mtepm – metepimeron; mtg – mediotergite; mtkepst – metakatepisternum; mtn – metanotum; p bas – posterior basalare; patg – paratergite; ped – pedicel; plp – palpus; plr wg proc – pleural wing process; plrtrch – pleurotrochantin; pprn – postpronotum; presct – prescutum; presct pit – prescutal pit; presct sut – prescutal suture; prn – pronotum; prpl – propleuron; prst – prosternum; rst – rostrum; sbal scl – subalar sclerite; scp – scape; sct – scutum; sctl – scutellum; trn sut – transverse suture; wg – wing.

pleural suture in front and the laterotergite behind, usually bearing setae only in the anterodorsal corner, below the base of the wing (see **epimeron**).

anepisternal cleft (pleural membrane) (Fig. 40): a U- or V-shaped membranous area on the dorsal part of the anepisternum.

anepisternal setae (mesopleural setae) (Fig. 42): setae on the anepisternum, which in Calyptratae and some other Schizophora form a vertical row, or band of setae, including a row of stout appressed setae, arising in front of the pleural suture and curving back over the base of the wing. Anterodorsally placed anepisternal setae directly above and behind the anterior thoracic spiracle are referred to as **poststigmatal setae** (*e.g.*, in the lonchaeid genus *Dasiops*). Anepisternal setae that occur behind the anterior thoracic spiracle in certain Culicidae are referred to as **postspiracular setae**.

anepisternum (mesopleuron) (Figs 40, 42): the part of the mesopleuron in front of the wing base, between the anterior thoracic spiracle and the pleural suture, and bounded ventrally by the katepisternum; secondarily divided in some Diptera (*e.g.*, metopinine Phoridae) (see **episternum**).

antepronotum (Fig. 40): the anteriormost subdivision of the pronotum, distinct in nematocerous families and virtually obsolete in Cyclorrhapha.

anterior lappet, see under **posterior spiracle**.

anterior spiracles (Fig. 40): a pair of spiracles on the thorax (mesothoracic spiracles), that appear associated with the prothorax (true prothoracic spiracles are absent). They are usually located behind the postpronotum and between it and the mesothorax; in some Phoridae and Hippoboscidae they open dorsally on top of the postpronotum.

basalare (Fig. 40): a vertical strut, or small sclerotised area at the base of the wing above the anepisternum, usually divided into an **anterior basalare** (dorsal basalare) and a **posterior basalare** (ventral basalare).

basisternum, see under **prosternum**.

cervix (Fig. 40): the neck; the primarily membranous area joining the head and thorax.

cervical sclerite (Fig. 40): one to three pairs of small sclerites in the membrane of the neck connecting the head and thorax (Michelsen 1996).

coxopleural streak (Fig. 42): the fissure separating the katepimeron from the meron in some calyptrates.

dorsocentral setae (Fig. 41): the paired rows of setae on the scutum lateral to the acrostichal setae and flanked by the intra-alar and/or supra-alar setae; they are generally referred to only in Eremoneura (Empidoidea and Cyclorrhapha), but are occasionally used in other groups (*e.g.*, Chironomidae). In Empidoidea and many acalyptrates, dorsocentrals are the most prominent scutal setae. In Calyptratae they are usually present on both the presutural and postsutural areas of the scutum, but their occurrence on these areas is more varied in the remainder of the Schizophora.

epimeron (Figs 40, 42): that part of the pleuron behind the pleural suture, divided by the **transepimeral suture** into an upper part, the anepimeron and a lower part, the katepimeron.

episternum (Figs 40, 42): that part of the pleuron in front of the pleural suture, divided by the **anapleural suture** into an upper part, the anepisternum and a lower part, the katepisternum.

greater ampulla (infra-alar bulla, subalar knob) (Fig. 42): a globular protuberance of the anepimeron below the base of the wing and in front of the anepimeral setae (arising from the basal portion of the pleural wing process), in many Syrphidae, certain acalyptrates (*e.g.*, Periscelididae, Ropalomeridae (non-Afrotropical), some Psilidae, some Sciomyzidae and most Tephritidae) and Calyptratae (see **pleural wing process**).

halter (pl. **halteres**) (Figs 2, 3, 40–42, 47): the highly modified wing of the metathorax in Diptera; it is a club-like structure consisting of a knob, or capitulum on a stalk, or stem, arising from its base in front of the posterior thoracic spiracle (see **prehalter**). Halteres function as balancing organs during flight.

humeral pit, see **prescutal pit**.

humeral setae, see **postpronotal setae**.

humerus, humeral callus, see **postpronotal lobe**.

hypopleural setae, see **meral setae**.

hypopleuron, see **meron**.

infrasquamal setulae: hairs on the anatergite just below the base of the lower calypter.

intra-alar setae (Fig. 41): on the scutum, the longitudinal row of setae lateral to the dorsocentral setae. In some Cyclorrhapha, particularly in Calyptratae, the first or anterior pair of presutural intra-alar setae, together with the first supra-alar seta, have been referred to as **posthumeral setae**.

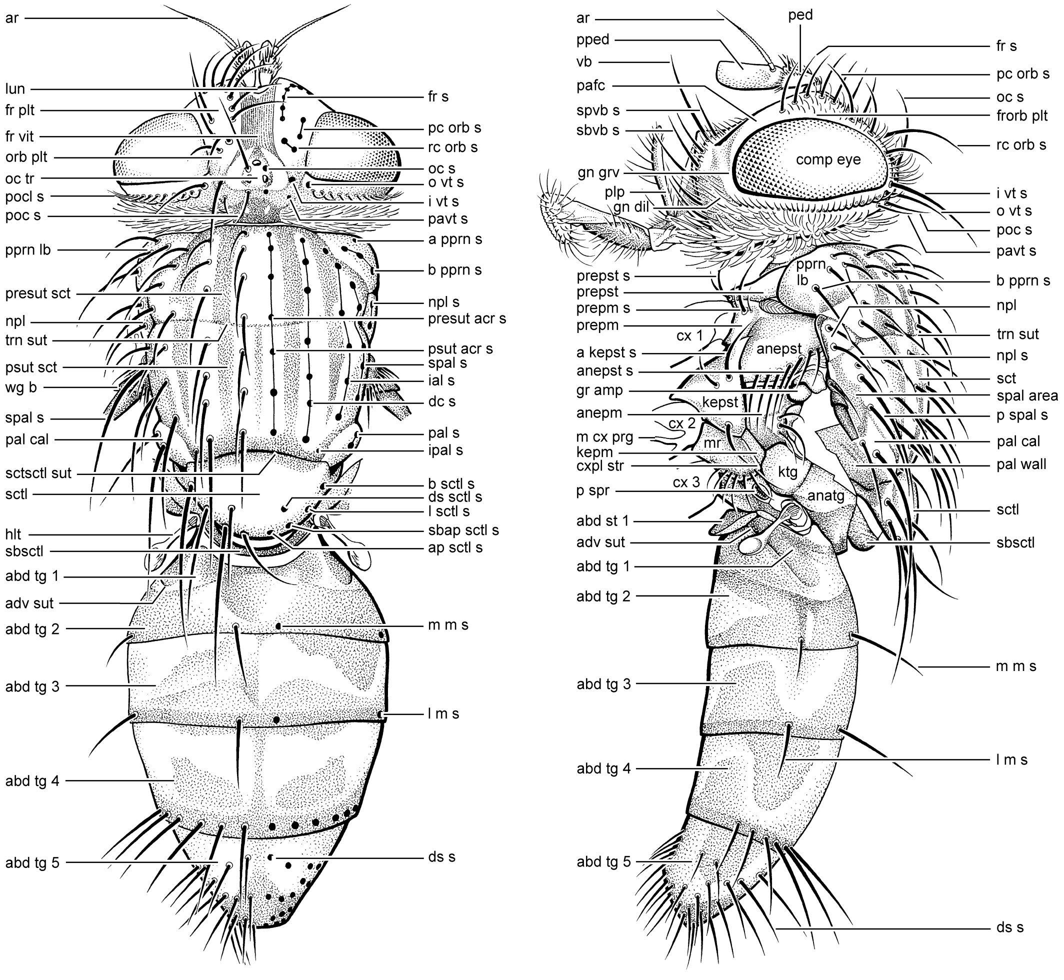
intrapostalar seta (Fig. 41): seta on the scutum near the postalar callus, considered by Merz & Haenni (2000, fig. 44) to be the posteriormost intra-alar seta.

katatergite (Figs 40, 42): the ventral (in nematocerous Diptera), or anterior (in Brachycera) portion of the laterotergite, appearing as a bulging sclerite just above the posterior spiracle, usually without setae, but in Asilidae bearing a vertical row, or patch of large setae (see **laterotergite**).

katepimeral setae: fine hairs on the katepimeron, or barette.

katepimeron (barette) (Figs 40, 42): the small sclerite between the anepimeron and the meron, below the anepimeron; in Schizophora reduced to a small rectangular band of cuticle that may bear one or more hairs. It may be scarcely recognisable in some acalyptrates (see **epimeron**).

katepisternal setae (sternopleural setae) (Fig. 42): in Schizophora one to four or more setae arising near the dorsal margin of the katepisternum; when three are present, they are usually arranged in a triangle, with the smallest seta being the most



41 *Exorista* ♀　　42 *Exorista* ♀

Figs 3.41–42. Head, thorax and abdomen of adult fly: (41) *Exorista larvarum* (L.) (Tachinidae), dorsal view ♀; (42) same, lateral view (non- Afrotropical). Figs 41, 42 (after McAlpine 1981, figs 65, 66).

Abbreviations: a kepst s – anterior katepisternal seta; a pprn s – anterior postpronotal seta; abd st – abdominal sternite; abd tg – abdominal tergite; acr s – acrostichal seta (indicated as presut and psut acr s); adv sut – adventitious suture; anatg – anatergite; anepm – anepimeron; anepst – anepisternum; anepst s – anepisternal seta; ap sctl s – apical scutellar seta; ar – arista; b pprn s – basal postpronotal seta; b sctl s – basal scutellar seta; comp eye – compound eye; cx – coxa; cxpl str – coxopleural streak; dc s – dorsocentral seta; ds s – discal seta; ds sctl s – discal scutellar seta; fr plt – frontal plate; fr s – frontal seta; fr vit – frontal vitta; frorb plt – fronto-orbital plate; gn dil – genal dilation; gn grv – genal groove; gr amp – greater ampulla; hlt – halter; i vt s – inner vertical seta; ial s – intra-alar seta; ipal s – intrapostalar seta; kepm – katepimeron; kepst – katepisternum; ktg – katatergite; l m s – lateral marginal seta; l sctl s – lateral scutellar seta; lun – lunule; m cx prg – mid coxal prong; m m s – median marginal seta; mr – meron; npl – notopleuron; npl s – notopleural seta; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; orb plt – orbital plate; p spal s – posterior supra-alar seta; p spr – posterior spiracle; pafc – parafacial; pal cal – postalar callus; pal s – postalar seta; pal wall – postalar wall; pavt s – paravertical seta; pc orb s – proclinate orbital seta; ped – pedicel; plp – palpus; poc s – postocellar seta; pocl s – postocular seta; pped – postpedicel; pprn lb – postpronotal lobe; prepm – proepimeron; prepm s – proepimeral seta; prepst – proepisternum; prepst s – proepisternal seta; presut acr s – presutural acrostichal seta; presut sct – presutural scutum; psut acr s – postsutural acrostichal seta; psut sct – postsutural scutum; rc orb s – reclinate orbital seta; sbap sctl s – subapical scutellar seta; sbsctl – subscutellum; sbvb s – subvibrissal seta; sct – scutum; sctl – scutellum; sctsctl sut – scutoscutellar suture; spal area – supra-alar area; spal s – supra-alar seta; spvb s – supravibrissal seta; trn sut – transverse suture; vb – vibrissa; wg b – wing base.

ventrally located. In other Diptera numerous setae or setulae are sometimes present on the katepisternum.

katepisternum (sternopleuron) (Figs 40, 42): the large bulging sclerite in front of the mid coxa, usually the largest sclerite on the ventral surface of the thorax (but greatly reduced in Asilidae because of forward movement of the mid coxa). The prothorax lacks a katepisternum, while that of the metathorax, the metakatepisternum, is a small sclerite just above the hind coxa. The katepisterna of the mesothorax meet each other mid-ventrally, enclosing the mesosternum, which is invaginated as a narrow internal phragma (see **episternum**).

lappets, see under **posterior spiracle**.

laterotergite (metapleuron, pleurotergite) (Figs 40, 42): the lateral extension of the **postnotum**, located between the wing base and the base of the halter, usually subdivided into **anatergite** and **katatergite** by an indistinct vertical groove. In orthorrhaphous Brachycera it usually bears pile or hairs and in asilids and some empidoids, a group of setae. It is usually bare in calyptrates and is arched over by the lower calypter, although the anatergite may support a small group of hairs near its dorsal edge (see **infrasquamal setulae**).

lesser ampulla, see **subalar sclerite**.

mediotergite (metatergite) (Fig. 40): often mistakenly called the postnotum, even though it is only the convex median portion of this sclerite, lying directly behind and beneath the scutellum. It is usually bare and in most Chironomidae is creased by a median longitudinal furrow (see **postnotum**).

meral setae (hypopleural setae) (Fig. 42): erect setae, usually forming a row of stout setae on the posterior edge of the meron in front of the posterior spiracle.

meron (hypopleuron) (Figs 40, 42): believed to be derived from the pleural part of the mid coxa, this sclerite lies behind the katepisternum, between the mid coxa and the posterior spiracle. It is usually bare, except in a number of families of calyptrates and is important taxonomically in separating the Muscoidea (Scathophagidae, Fanniidae, Anthomyiidae and Muscidae), in which it is bare, from the Oestroidea (Calliphoridae, Sarcophagidae, Rhinophoridae, Tachinidae and Oestridae), in which there is a vertical row, or patch of setae (see **meral setae**).

mesonotum (Figs 2, 41): the major part of the dorsum of the thorax, except for the narrow anterior band, the pronotum and the even narrower posterior band, the metanotum. It is divided into prescutum, scutum, scutellum and postnotum, with the scutum being by far the largest portion. In the past, the term mesonotum has often been applied to the scutum alone.

mesopleural setae, see **anepisternal setae**.

mesopleuron (see also **anepisternum**) (Figs 40, 42): the entire side of the mesothorax, which includes everything between the edge of the scutum above and the coxae below and between the anterior spiracle and the halter and posterior spiracle. Earlier authors used the term to apply only to the anepisternum of the mesothorax, the sclerite anterior to the pleural suture.

metakatepisternum (Fig. 40): the anteroventral portion of the metapleuron, between the metanepisternum above and the hind coxa below (see **metepisternum**).

metanepisternum (Fig. 40): the anterodorsal portion of the metapleuron, between the posterior spiracle and halter above and the metakatepisternum below (see **metepisternum**).

metanotum (Fig. 40): the sclerite forming the dorsum of the metathorax, between postnotum (mesothorax) and first abdominal segment; in most Diptera it is so narrow as to be scarcely recognisable, unless the abdomen is bent down out of the way.

metapleural suture (Fig. 40): an indistinct groove on the metathorax extending from the base of the halter to the hind coxa that divides the metepisternum from the metepimeron. The metapleural suture is equivalent to the mesopleural suture (see **pleural suture**) that extends between the wing base and the mid coxa.

metapleuron (Figs 40, 42): the side of the metathorax, always greatly reduced relative to the mesopleuron, extending from the halter to the hind coxa and between the meron and the abdomen; bearing the posterior spiracle.

metepimeron (Fig. 40): that part of the metapleuron behind the metapleural suture, fairly large in orthorrhaphous Brachycera and pilose on its upper part, but in Cyclorrhapha usually reduced to a sliver of bare cuticle.

metepisternum (Fig. 40): the sclerite in front of the metapleural suture, between the posterior spiracle and the hind coxa. It is usually indistinctly divided by a furrow into an upper part, the metanepisternum and a lower part, the metakatepisternum and seems to be without setae in all flies.

notopleural cleft: a depression on the anterior surface of the notopleuron of some Phoridae, often covered by a ridge of cuticle. It is associated with the opening of a **notopleural gland** (Disney 2004).

notopleural setae (Figs 41, 42): a pair of stout setae on the notopleuron in most Cyclorrhapha, as well as in some orthorrhaphous Brachycera (*e.g.*, Asilidae, Therevidae and Empidoidea), where the number of setae is variable. Sarcophaginae are unusual in having four notopleural setae, the usual large pair, interspersed by two smaller ones.

notopleuron (Figs 41, 42): a small triangular subdivision of the scutum just behind the postpronotum and in front of the transverse suture of the scutum, best delineated in Cyclorrhapha.

operculum, see under **posterior spiracle**.

paratergite (Fig. 40): a narrow triangular wedge of cuticle along the lateral edge of the scutum extending between the postpronotum and the wing base in many nematocerous families and orthorrhaphous Brachycera. Usually bare, it may be setose in some taxa (*e.g.*, certain Ceratopogonidae), or have scales in some Culicidae.

phragma: an invaginated internal fold of cuticle to strengthen the sclerite and serve as a point of muscle attachment.

pleural suture (Fig. 40): a furrow on the side of the thorax between the wing base and mid coxa, marking an inward folding of cuticle to provide rigidity to the mesopleuron.

pleural wing process (subalifer) (Fig. 40): a vertical extension of the anepimeron that articulates with the base of the wing (see **greater ampulla**).

pleurotergite, see **laterotergite**.

pleurotrochantin (Fig. 40): a small sclerite between the katepisternum and katepimeron that is present in a few nematocerous groups (*e.g.*, *Tipula* L., *Plecia* Wiedemann and Culicomorpha).

plumule (plumula), see under **subalar sclerite**.

postalar callus (Figs 41, 42): an oval portion of the posterolateral corner of the scutum, lateral to the scutellum. The postalar callus is weakly developed, or indistinct in acalyptrates; in the Cyclorrhapha it usually bears a pair of setae.

postalar seta (Fig. 41): one or two setae (more in some Tachinidae) on the postalar callus.

postalar wall (Fig. 42): the vertical surface of the thorax below the postalar callus.

posterior lappet, see under **posterior spiracle**.

posterior spiracle (Fig. 42): the spiracle of the metathorax, just below and slightly anterior to the base of the halter. The anterior, ventral and posterior edges of the posterior spiracle are usually fringed with fine hairs, leaving a small opening near the dorsal margin of the spiracle. These fringes of hairs are usually organised to form the **anterior** and **posterior lappets** and vary greatly in size, extent and colour; those hairs of the posterior lappet may be consolidated to form an **operculum** that covers most of the spiracular opening.

posthumeral setae, see presutural setae under **intra-alar setae** and/or **supra-alar setae**.

postmetacoxal bridge (postcoxal bridge): in some wasp-waisted Tachinidae (particularly some Phasiinae) and some Asilidae, the area enclosed by the metepimera, the hind coxae and the first abdominal sternite is sclerotised to form the postmetacoxal bridge. A postmetacoxal bridge is also present in some acalyptrate families, such as Syringogastridae, Somatiidae and Tanypezidae (all three non-Afrotropical), as well as in some genera of Richardiidae (non-Afrotropical), Platystomatidae and Tephritidae. In all these acalyptrate groups, however, the postmetacoxal bridge does not include the first abdominal sternite. The bridge may be darkly pigmented, thus easily recognised, or pale and similar to membrane, but then it is reinforced by parallel transverse ridges.

postnotum (mediotergite, mesophragma) (Fig. 40): the convex sclerite forming the posterior surface of the dorsal part of the thorax, behind and below the scutellum (as the **mediotergite**), extending laterally and anteriorly (as the **laterotergite**) between the calypter and the posterior spiracle.

postpronotal lobe (humeral callus, humerus) (Figs 41, 42): rather insignificant in nematocerous Diptera, the postpronotal lobe forms the anterolateral corner of the dorsum of the thorax in Brachycera.

postpronotal setae (humeral setae) (Figs 41, 42): setae on the postpronotal lobe that are universally present in calyptrates and also in some orthorrhaphous Brachycera and nematocerous families (*e.g.*, Culicidae). Their arrangement in certain groups, such as Tachinidae, is of considerable taxonomic value.

postpronotum (Figs 40–42): the posterior part of the dorsum of the pronotum, separated from the antepronotum by a transverse suture and better developed in Brachycera than in the nematocerous Diptera. In Brachycera the postpronotum and its enlarged lateral lobes are intimately associated with the scutum (see **postpronotal lobe**).

postscutellum, see **subscutellum**.

postspiracular scale: a small raised scale-like lobe found just behind the posterior spiracle in Athericidae and Tabanidae.

postspiracular setae, see **anepisternal setae**.

poststigmatal setae, see **anepisternal setae**.

postsutural: pertaining to the posterior part of the scutum behind the transverse suture.

prealar seta, see first postsutural supra-alar seta, under **supra-alar setae**.

precoxal bridge: a sclerotised connection between the prosternum and the proepisternum, in front of and above the fore coxae.

prehalter: a distinct lobe arising from the base of the halter in Ptychopteridae.

prescutal pit (humeral pit) (Fig. 40): a small depression on the anterolateral corner of the scutum, behind the postpronotal lobe, that marks the position of the base of the pupal respiratory organ.

prescutal suture (Fig. 40): an indistinct furrow extending medially from the prescutal pit, present in some nematocerous families; not to be confused with the transverse suture.

prescutellum (proscutellum): a small, transverse lens-shaped bulge found immediately in front of the scutellum (*e.g.*, in certain groups of Tabanomorpha and basal Phoridae).

prescutum (Fig. 40): the anteriormost portion of the mesonotum in front of the prescutal suture, evident in some nematocerous families.

presternum, see under **prosternum**.

presutural (Fig. 41): pertaining to the anterior part of the scutum in front of the transverse suture.

presutural seta, see presutural supra-alar setae under **supra-alar setae**.

proepimeral setae (prostigmatal setae, stigmatal setae) (Fig. 42): in Cyclorrhapha, setulae and setae that arise on the proepimeron, below the anterior spiracle and above the fore coxa and in front of the anepisternum and katepisternum of the mesothorax.

proepimeron (Fig. 42): that part of the prothoracic pleuron behind the propleural suture that extends from the anterior spiracle to the fore coxa. The posterior margin of the proepimeron usually blends in with the mesepisternum and is not readily distinguishable from it.

proepisternal setae (propleural setae) (Fig. 42): one or more setae at the ventral margin of the proepisternum and/or a patch of hairs on the midregion, the "disc of the propleuron".

proepisternum (Fig. 42): that part of the propleuron anterior to the propleural suture, above the prosternum and behind the cervical sclerites of the neck (also see **precoxal bridge**). In Cyclorrhapha it usually bears one or more setae, the proepisternal setae, at its ventral angle. In Tabanidae, the proepisternum is distinctly divided into an upper proanepisternum and a lower prokatepisternum; its upper portion is strongly inflated and covered with pile, while in Cyclorrhapha this region is usually concave and bare (pilose in most Calliphoridae and some Tachinidae).

pronotum (Figs 40–42): the dorsal part of the prothorax, divided transversely by an indistinct fissure into an antepronotum and a postpronotum that bears the postpronotal lobes. In nematocerous families the antepronotum is larger than the postpronotum, while the reverse tends to occur in Brachycera.

propleural setae, see **proepisternal setae**.

propleuron (Fig. 40): the side of the prothorax, between the pronotum dorsally and the fore coxa (see **proepimeron** and **proepisternum**).

proscutellum, see **prescutellum**.

prosternum (Fig. 40): a parallel-sided, or trapezoidal, concave sclerite between the fore coxae, sometimes with setae along its edges, or over its surface (also see **precoxal bridge**). The prosternum is often divided into an anterior more dorsal **presternum** and a posterior more ventral **basisternum** (*e.g.*, many nematocerous Diptera).

prostigmatal setae, see **proepimeral setae**.

pteropleural setae, see **anepimeral setae**.

pteropleuron, see **anepimeron**.

scutellar setae (Fig. 41): paired setae along the margin of the scutellum, the marginal setae, which in Schizophora are usually termed **basal**, **lateral**, **subapical** (preapical) and **apical scutellar setae**, depending on their position and **discal setae**, which arise from the midregion.

scutellum (Figs 40–42): the rounded, or triangular projection behind the scutum over the base of the abdomen, separated from the scutum by the scutoscutellar suture.

scutum (mesonotum) (Figs 40–42): essentially the dorsal surface of the mesothorax between the pronotum and the scutellum, separated into a small prescutum (in some nematocerous families) and the true scutum, which is in turn divided by the transverse suture into a presutural and a postsutural area.

sternopleural setae, see **katepisternal setae**.

sternopleuron, see **katepisternum**.

stigmatal setae, see **proepisternal setae**.

subalar knob, see **greater ampulla**.

subalar sclerite (subalar ridge, vallar ridge) (Fig. 40): a thin sclerite behind the pleural wing process, which is situated in the subalar membrane between the insertion of the wing and the dorsal margin of the anepimeron. In Syrphidae the posteroventral margin is usually extended and fringed with long hairs to form the **plumule**. In Schizophora the subalar sclerite is frequently dilated into one or more protuberances, with the anteriormost swollen portion often referred to as the **lesser ampulla** (see **greater ampulla**).

subscutellum (infrascutellum, postscutellum) (Figs 41, 42): a transverse bulge between the scutellum and the postnotum, particularly well-developed in some Tephritidae, Curtonotidae, some Calliphoridae, a few Oestridae and all Tachinidae.

supra-alar setae (Figs 41, 42): on the scutum, the longitudinal row of setae lateral to the intra-alar setae and above the base of the wing. In some Cyclorrhapha, particularly in Calyptratae, the first (anterior) presutural supra-alar seta and the first or anterior pair of presutural intra-alar setae have jointly been referred to as **posthumeral setae**, while the posterior presutural supra-alar seta has been referred to as the **presutural seta**. The first (anterior) postsutural supra-alar seta has also sometimes been termed the **prealar seta** in Calyptratae.

suprasquamal ridge (Fig. 46): a narrow oval sclerite, usually bare, or with a tuft or tufts of erect hairs, running anteroventrally along the medial edge of the lower calypter between the upper calypter and the anterolateral corner of the scutellum and hidden by the wing membrane unless the wing is bent downwards.

transepimeral suture, see under **epimeron**.

transverse suture (Figs 40, 42): a furrow across the scutum that divides it into a presutural and postsutural area; of particular importance in Calyptratae with reference to position of setae.

tympanal fossa (Fig. 46): membrane between the suprasquamal ridge and postalar wall strengthened by a rib-like sclerite, the **tympanal ridge**; the lowermost membranous portion that opens towards the wing base in Calyptratae is referred to as the **tympanic pit**.

tympanic pit, see **tympanal fossa**.

Wing

Only the front or mesothoracic pair of wings is developed for flight in Diptera (Figs 2, 3, 43a, 43b, 45a, 45b). Each wing is attached to the mesothoracic segment through the **axillary area**, which consists of a series of articulated **axillary sclerites** linked along the posterior margin by several membranous lobes (*i.e.*, **anal lobe**, **alula**, **upper calypter** and **lower calypter**), that may, or may not, be present depending on the group (Figs 44a, 44b).

The venation of the wing varies greatly throughout the order and is of tremendous taxonomic value. The stalk contains the bases of the six main longitudinal veins, the **costal** (***C***), **subcostal** (***Sc***), **radial** (***R***), **medial** (***M***), **cubital** (***Cu***) and **anal** (***A***) veins. In the most generalised condition each of the longitudinal veins consists of two main branches, a convex anterior branch and a concave posterior branch (Figs 44a, 44b), except for the costa and subcosta, which are unbranched. The longitudinal veins are sometimes connected by **crossveins**, which together delimit portions of wing membrane called **cells**, named after the vein anterior to them. Following the convention consistently adopted by McAlpine (1981), but contrary to Merz & Haenni (2000), longitudinal veins are designated by uppercase abbreviations and crossveins and cells are designated by lowercase abbreviations. Cells and crossvein abbreviations are not easily confused, because crossvein abbreviations can be recognised by the inclusion of a hyphen (*e.g.*, *r–m*) in their formation; the only exception being the humeral crossvein (*h*) for which no associated cell is named.

There are two wing venation systems currently in use in Diptera; the widely used traditional system outlined by McAlpine (1981) and Merz & Haenni (2000) (Figs 43b, 44b, 45b) and the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006). Both systems were discussed by Cumming & Wood (2009), but only the traditional system was figured. The alternative system is based on a better homologised Diptera and Mecoptera fore wing base and has been adopted as the standard, for use throughout this *Manual*. It has also been corroborated in a comparative study of wing structure of primitive Mesozoic fossil Diptera by Shcherbakov *et al*. (1995). Under this system, the Diptera wing vein A_1 (as used in McAlpine 1981) is homologised with the Mecoptera vein *CuP*, CuA_1 (*sensu* McAlpine 1981) is considered M_4, whereas CuA_2 is *CuA* and the posterior cubital cell (*cup*) is cell *cua* (Figs 43a, 44a, 45a). The faint vein paralleling *CuA* (*CuP sensu* McAlpine 1981; Fig. 43b) is interpreted as a pseudovein in the new alternative system.

The veins may be bare, or covered with various types of macrotrichia, whereas the membrane is either bare and shiny, or more or less dull owing to a covering of microtrichia. In Blephariceridae and the north temperate Deuterophlebiidae (non-Afrotropical), a secondary net-like pattern of fine folds is also present on the membrane. The wing is often tinted with colour and sometimes patterned. Clear wings are referred to as **hyaline**, whereas darkened wings are referred to as **fumose** or **infuscated**.

Functional (**macropterous**) wings are more or less elongate-oval in shape, with rounded, or somewhat pointed apices. Partial or total reduction (**stenoptery** – narrowed, but complete wings, **brachyptery** – wings reduced in length, or **aptery** – wings absent) may occur, often only in one sex, in connection with peculiar habits or niches (*e.g.*, ectoparasitism, cave- and litter-dwellers, high mountain species).

Glossary

alula (axillary lobe) (Figs 44a, 44b, 45a, 45b): a lobe of the wing membrane at the base of vein *A* between the calypter and anal lobe, not to be confused with a calypter.

alular incision (axillary incision) (Figs 44a, 44b, 45a, 45b): a cleft in the posterior wing margin near the base, separating the alula from the anal lobe.

anal cells (Figs 43a, 43b): each of the cells behind the anal vein or veins, vein A_1 and vein A_2. Using the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) there are two anal cells, **cell** $\boldsymbol{a_1}$ and **cell** $\boldsymbol{a_2}$ in Tipulidae and Trichoceridae (non-Afrotropical) (Fig. 43b), whereas other Diptera have at most only one anal cell, **cell** $\boldsymbol{a_1}$; in Eremoneura (Empidoidea and Cyclorrhapha) at least, the first anal vein is fused with the apex of vein CuA_2 and the cell behind this vein (cell *cup* or *cua*) has also been referred to as the anal cell (see **cubital cells**). The alternative system of Wootton & Ennos (1989) and Saigusa (2006) recognises only one anal cell (**cell** $\boldsymbol{a_1}$; Fig. 43a) in the groundplan of the Diptera (see **anal vein**).

anal lobe (Figs 43a–45b): that part of the wing membrane along the hind margin near the base, usually rounded, distal to the alula.

anal vein (Figs 43a–45b): the last veins of the series behind the cubital vein, generally present in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) as two veins, $\boldsymbol{A_1}$ and $\boldsymbol{A_2}$ (Fig. 43b). In Tipulidae and Trichoceridae (non-Afrotropical), both these veins reach the margin independently, while in most other Diptera A_2 appears to be extremely shortened or absent (Starý 2008). Wootton & Ennos (1989) and Saigusa (2006) interpret A_1 in the traditional system as vein *CuP*, while they consider the *CuP* to be a pseudovein (Figs 43a–45a). Therefore in their alternative system, Wootton & Ennos (1989) and Saigusa (2006) essentially recognise only one anal vein (A_1) in the groundplan of Diptera, which is equivalent to vein A_2 in the traditional system. Veins in the anal area of the wing fuse together in Brachycera, so that the traditional first anal vein is actually CuA_2+A_1 (Fig. 45b), or $CuA+CuP$ (Fig. 45a) in the alternative system (see **cubital vein**).

anterior cubital cell, see **cubital cells**, ***cua***.

arculus, see **medial vein**, anterior branch (***MA***).

axillary incision, see **alular incision**.

axillary lobe, see **alula**.

axillary sclerites (axillary plates) (Figs 44a, 44b): three or four irregularly shaped plates behind the base of vein *R* and between the bases of veins *M*, *Cu* and *A* and the thorax.

basal costal cell, ***bc*** (Figs 43a–45b): a small cell between vein *C* and the subcosta (*Sc*) at the base of the wing, closed distally by the humeral crossvein.

basal medial cell, ***bm*** (second basal cell) (Figs 43a–45b): a small cell near the base of the wing that is closed distally by the *bm–cu* crossvein in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45), or by the *bm–m* crossvein in the alternative system of Wootton & Ennos (1989) and Saigusa (2006).

basal medial crossvein, ***bm–m*** (Fig. 45a), see **basal medial–cubital crossvein**.

basal medial–cubital crossvein, ***bm–cu*** (*tb*) (Fig. 45b): the crossvein between the base of vein *M* (M_1 or M_{1+2}) and CuA_1, closing the basal medial cell apically in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45). Crossvein *bm–cu* is actually the same as crossvein *m–cu* including the base of M_3, but the designation "*b*" is used to distinguish crossvein *bm–cu* from crossvein *dm–cu* when both occur (see **discal medial–cubital crossvein**, ***dm–cu*** **and medial–cubital crossvein**, ***m–cu***). Crossvein *bm–cu* is equivalent to ***bm–m***, or the base of M_4 (Fig. 45b), in the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006).

basal radial cell, ***br*** (cell *r*, first basal cell) (Figs 43a–45b): a small cell near the base of the wing between the radial vein and vein *M*, closed distally by the *r–m* crossvein.

basicosta (**basicostale**, humeral plate) (Figs 44a, 44b, 45a, 45b): a scale-like sclerite between the tegula and the base of the costa. Saigusa (2006) considers the basicosta of Calyptratae (Figs 44a, 44b) as interpreted by McAlpine (1981: 28), to be homologous with the basisubcostale (basisubcosta) of Mecoptera.

calypter (pl. **calypteres**) (squama) (Figs 44a, 45a, 44b, 45b, 46): one of two rounded lobes at the base of the wing, between the alula and thoracic wall in many Diptera (*e.g.*, Acroceridae, Tabanidae, Calyptratae); when the wing is at rest the smaller **upper calypter**, the more anterior of the two, folds over the larger **lower calypter**, which forms a cup-like hood over the halter in Cyclorrhapha.

cell: any part of the wing membrane delineated by veins, crossveins and/or the wing margin.

costa, see **costal vein**.

costagial break (Figs 45a, 45b): a point of weakness in the costa near the base, proximal to the humeral crossvein, occurring infrequently in some families of Schizophora.

costal breaks (Figs 45a, 45b): a series of three points of weakness, or flexure in the costa of taxonomic importance in Schizophora (see **costagial break**, **humeral break** and **subcostal break**).

costal cell (Figs 43a–45b): the wing membrane between the costal (C) and subcostal (*Sc*) veins distal to the humeral crossvein (*h*), often closed apically by the subcosta terminating in the costa.

costal margin: the anterior margin of the wing, usually delimited by the costa.

costal section (costal sector): pertaining to the relative lengths of four sections of the costa that are delimited by points of termination of crossvein *h* and of veins R_1, R_{2+3}, R_{4+5} and M_1; section 1 is between *h* and R_1, section 2 is between R_1 and R_{2+3}, section 3 is between R_{2+3} and R_{4+5} and section 4 is between R_{4+5} and M_1. The relative lengths of the costal sections are important taxonomically in certain families of Eremoneura (Empidoidea and Cyclorrhapha).

costal spine: one or two short stout setae arising from the front of vein *C* in some families of Schizophora, usually at the level of the subcostal break.

costal vein, or **costa**, ***C*** (Figs 43a–45b): the sclerotised thickened anterior edge of the wing, extending around the wing tip in some families, but ending at the apex of vein R_{4+5}, or *M* in most Diptera.

crossband: a transverse band of colour on the wing, especially important taxonomically in Tephritoidea; White *et al*. (1999: fig. 33.3) defined nine types of crossbands in Tephritidae based on their position on the wing membrane, namely the **humeral band** (over the humeral crossvein), **subbasal band** (over the humeral crossvein and cells *br*, *bm* and *cua*), **subcostal band** (over cells *sc*, *br*, *bm* and *cua*), **discal band** (over the pterostigma, cell *dm* and *r–m* crossvein), **accessory costal band** (between the discal and subapical bands), **radial-medial band** (over at least the *r–m* crossvein, but not the pterostigma), **subapical band** (over at least the *dm–m* crossvein), **anterior apical band** (from cell r_1 along the apex of wing), **posterior apical band** (between the subapical and anterior apical bands).

crossvein (transverse vein): any short vein, usually at a strong angle to the major longitudinal veins, connecting two of them and therefore enclosing a cell.

cubital cells, **cua_1** (**cell M_4**, fifth posterior cell), ***cua*** and ***cup*** (anal cell, basal cubital cell) (Figs 43a–45b): in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) the **anterior cubital cell**, **cell cua_1**, is enclosed by the cubital fork, formed by veins CuA_1 and CuA_2; the posterior cubital cell, **cell *cup***, is behind it, between veins *CuP* and A_1 (in older terminology it is also called the anal cell) (Figs 43b–45b). In the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006), where vein *CuP* is regarded as a pseudovein, the latter cell is formed by veins *CuA* and *CuP* and is referred to as the **anterior cubital cell**, or **cell *cua*** (Figs 43a–45a); it has also been referred by Steyskal (1984) and White *et al*. (1999: 884), as the basal cubital cell, or cell *bcu*). In the alternative system, **cell *cup***, when present, occupies the anterior portion of the anal area of the wing and is open at the costal margin.

cubital fork (Figs 43b, 45b): the branching of veins CuA_1 and CuA_2 in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45), enclosing **cell cua_1** (referred to as the fifth posterior cell in older terminology), or **cell m_4** in the alternative system of Wootton & Ennos (1989) and Saigusa (2006) (Figs 43a, 45a).

cubital vein or **cubitus**, ***Cu*** (Figs 43a–45b): the fifth vein of the wing, behind the media, vein *M*. It branches into an anterior branch, **vein *CuA*** and a posterior branch, **vein *CuP***. In the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) vein *CuA* (*Cu*) further branches into **CuA_1** (Cu_1) and **CuA_2** (Cu_2) (Figs 43b, 45b); CuA_1, along with the crossvein at its base, has also been interpreted as **vein M_4** (Byers 1989; Wootton & Ennos 1989; Saigusa 2006) (Figs 43a, 45a) (see **medial vein**).

cubitus, see **cubital vein**.

discal cell, ***d*** (Figs 43a, 43b): the wing membrane between veins M_1 and M_3, closed apically by the base of vein M_2 and the *m–m* crossvein.

discal medial cell, ***dm*** (*d–m*) (Figs 45a, 45b): in Cyclorrhapha vein *M* is unbranched and in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) the *dm* cell lies between *M* and vein CuA_1. It is closed apically by the discal medial-cubital crossvein, *dm–cu*. Cell *dm* also occurs in some groups of orthorrhaphous Brachycera (*e.g.*, Bombyliidae, Scenopinidae, Empidoidea). In the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006), the *dm* cell lies between veins M_1 and M_4, and is closed apically by crossvein *dm–m*.

discal medial crossvein, ***dm–m*** (Fig. 45b), see **discal medial–cubital crossvein**.

discal medial–cubital crossvein, ***dm–cu*** (posterior crossvein, *tp*) (Fig. 45b): the crossvein between vein *M* (M_1 or M_{1+2}) and CuA_1 closing the discal medial cell apically in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) (see **basal medial–cubital crossvein**, ***bm–cu***); it is equivalent to ***dm–m*** (Fig. 45a) in the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006).

false vein: vein-like thickenings in the membrane of certain groups of nematocerous Diptera that resemble veins, perhaps as a result of folding in the pupal stage (see **pseudovein** and **spurious vein**).

humeral break (Figs 45a, 45b): a weakness, or point of flexure in the costa just beyond the level of the humeral crossvein.

humeral crossvein, ***h*** (Figs 43a–45b): a short crossvein between the costa and subcosta, separating the basal costal cell from the costal cell proper.

humeral plate, see **basicosta**.

jugum (neala): a triangular prolongation at the base of the wing in some Psychodidae (*e.g.*, Psychodinae); not homologous with the jugum or neala of the fore wing of higher insects.

longitudinal vein, see above under Wing and also below under **radial vein**.

lower calypter (lower squama, squamula thoracica) (Figs 44a–46): in most Diptera a fringed flap of membrane at the base of the wing attached to the thoracic wall; in Cyclorrhapha it is usually quite conspicuous, evenly convex dorsally and sometimes even somewhat transparent, forming a hood over the halter.

lower squama, see **lower calypter**.

marginal cell, see **cell** $\boldsymbol{r_1}$ under **radial cells**.

media, see **medial vein**.

medial cells (Figs 43a, 43b): **cell** $\boldsymbol{m_1}$ (second posterior cell in older terminology) is behind vein M_1, **cell** $\boldsymbol{m_2}$ (third posterior cell) is behind vein M_2 and **cell** $\boldsymbol{m_3}$ (fourth posterior cell) is behind vein M_3. Wootton & Ennos (1989) and Saigusa (2006) consider vein CuA_1 to be vein M_4 (Figs 43a, 45a) and the cell behind this as **cell** $\boldsymbol{m_4}$ (fifth posterior cell), but in the traditional terminology adopted by McAlpine (1981: 31) and Merz & Haenni (2000: fig. 47) this cell is termed **cell** $\boldsymbol{cua_1}$, the anterior cubital cell.

medial crossvein, ***m–m*** (*mm*) (Figs 43a, 43b): a crossvein in some nematocerous Diptera that connects veins M_2 and M_3 to close the discal cell; the apparent crossvein between veins M_1 and M_2 that partially closes the discal, or discal medial cell in some orthorrhaphous Brachycera, is interpreted as the base of M_2.

medial–cubital crossvein, ***m–cu*** (*mcu*) (Fig. 43b): the crossvein between vein M_3 and CuA_1 in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) that closes the basal medial cell apically in some nematocerous and orthorrhaphous Brachycera families; Wootton & Ennos (1989) and Saigusa (2006) interpret this vein as the base of M_4 and not as a crossvein; the actual *m–cu* crossvein in their system is positioned more posteriorly between M_4 and *CuA* (Fig. 43a) (see **basal medial–cubital crossvein**, ***bm–cu***).

medial vein, or **media**, ***M*** (Figs 43a–45b): literally the middle vein, between the radius, vein *R* and cubitus, vein *Cu*. Made up primarily of the posterior branch(es) of the media. Although it is unbranched in Schizophora and various other taxa, many non-schizophorans have two branches, $\boldsymbol{M_1}$ and $\boldsymbol{M_2}$ and some (certain nematocerous groups and lower Brachycera) have $\boldsymbol{M_3}$, associated with a discal cell. When M_2 and M_3 are absent, the single branch is referred to as M_1 or M_{1+2}. Byers (1989), Wootton & Ennos (1989), Shcherbakov *et al.* (1995) and Saigusa (2006) have convincingly argued for the interpretation of CuA_1 as $\boldsymbol{M_4}$ (see **cubital vein**) (Figs 43a–45a) on the basis of homology with the fore wing base of Mecoptera. The anterior branch of the media (***MA***) (**arculus**) is reduced to a short transverse vein near the base of the wing (Figs 43b, 44b); Saigusa (2006) considers the true *MA* to be absent in Diptera.

node: the junction of the radial sector with R_1, sometimes enlarged, often pigmented in species with patterned wings and usually bearing setae, at least in Cyclorrhapha.

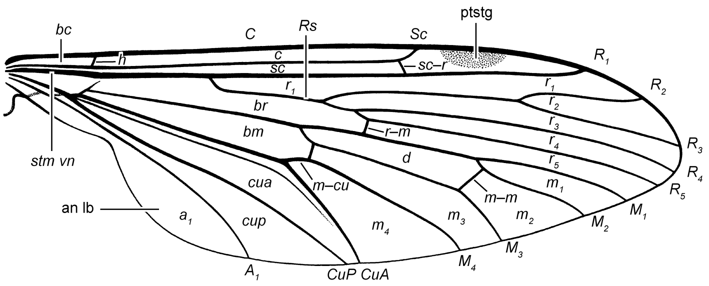
petiole: an ambiguous term, either a stem vein, at or near the base of the wing, or the fusion of the apices of two adjacent veins at, or near the wing margin, *e.g.*, R_{4+5} and M_1 in many calyptrates do not end separately in the margin, but fuse to produce a "closed" cell r_{4+5}. In many orthorrhaphous Brachycera, medial and cubital cells as well as radial cells may be "closed and petiolate" at the margin by anastomosis of the apices of veins.

posterior cell, see either **cell** $\boldsymbol{r_{4+5}}$ or **cell** $\boldsymbol{r_5}$ (first posterior cell) under **radial cells**, or **cells** $\boldsymbol{m_1}$, $\boldsymbol{m_2}$, $\boldsymbol{m_3}$, $\boldsymbol{m_4}$ ($\boldsymbol{cua_1}$) (second, third, fourth and fifth posterior cells) under **medial cells**.

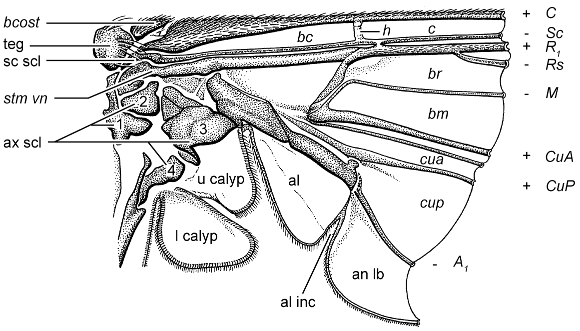
posterior crossvein, see **discal medial–cubital crossvein**, ***dm–cu***.

posterior cubital cell, see **cubital cells**, ***cup***.

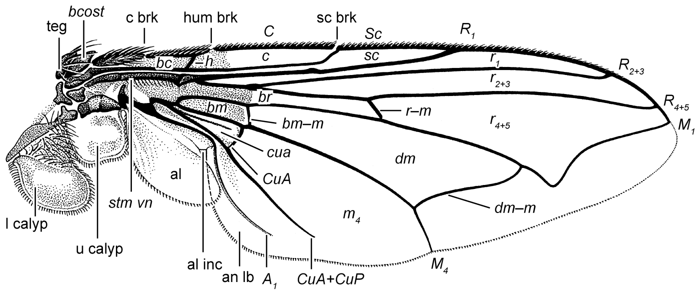
pseudovein: a thickening in the membrane resembling a true vein, but without enclosed tracheal trunk. See **false vein** and **spurious vein**.



43a Ground-plan of Diptera wing



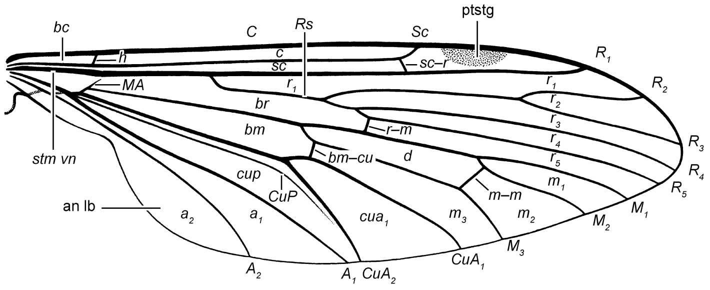
44a *Tabanus* ♀



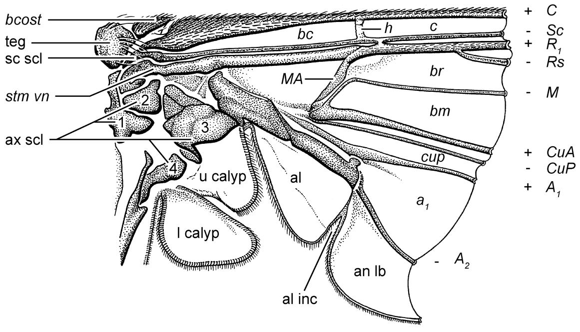
45a *Compsomyiops* ♀

Figs 3.43a–45a. Wings (dorsal views) outlining alternative venation system of Wootton & Ennos (1989) and Saigusa (2006): (43a) hypothetical groundplan of a basal dipteran; (44a) wing base, showing axillary sclerites of *Tabanus americanus* Forster (Tabanidae) ♀; (45a) complete wing, with calypteres of *Compsomyiops callipes* (Bigot) (Calliphoridae) ♀ (both non-Afrotropical). Figs 43a–45a (after McAlpine 1981, figs 67, 68, 69 (as *Paralucilia wheeleri*)).

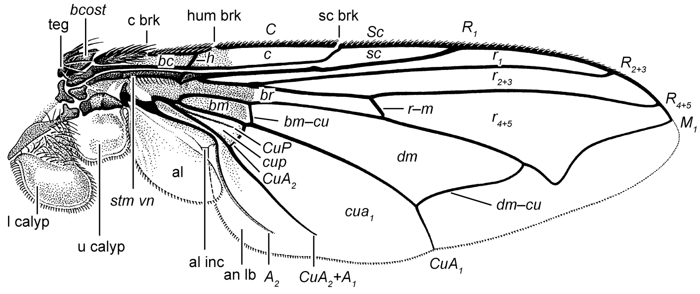
Abbreviations: A_1 – first branch of anal vein; a_1 – first anal cell; al – alula; al inc – alular incision; an lb – anal lobe; ax scl – axillary sclerites; *bc* – basal costal cell; *bcost* – basicosta; *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *c* – costal cell; c brk – costagial break; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; *h* – humeral crossvein; hum brk – humeral break; l calyp – lower calypter; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; r_2 – second radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_4 – upper branch of third branch of radius; r_4 – fourth radial cell; R_{4+5} – third branch of radius; r_{4+5} – fourth + fifth radial cell; R_5 – lower branch of third branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein; sc brk – subcostal break; *sc–r* – subcostal–radial crossvein; sc scl – subcostal sclerite; *stm vn* – stem vein; teg – tegula; u calyp – upper calypter.



43b Ground-plan of Diptera wing



44b *Tabanus* ♀



45b *Compsomyiops* ♀

Figs 3.43b–45b. Wings (dorsal views) outlining traditional venation system: (43b) hypothetical groundplan of a basal dipteran; (44b) wing base, showing axillary sclerites of *Tabanus americanus* Forster (Tabanidae) ♀; (45b) complete wing, with calypteres of *Compsomyiops callipes* (Bigot) (Calliphoridae) ♀ (both non-Afrotropical). Figs 43b–45b (after McAlpine 1981, figs 67, 68, 69 (as *Paralucilia wheeleri*)).

Abbreviations: A_1 – first branch of anal vein; a_1 – first anal cell; A_2 – second branch of anal vein; a_2 – second anal cell; al – alula; al inc – alular incision; an lb – anal lobe; ax scl – axillary sclerites; *bc* – basal costal cell; *bcost* – basicosta; *bm* – basal medial cell; *bm–cu* – basal medial–cubital crossvein; *br* – basal radial cell; *C* – costal vein; *c* – costal cell; c brk – costagial break; *CuA* – basal part of anterior branch of cubital vein; CuA_1 – first branch of anterior branch of cubital vein; cua_1 – anterior cubital cell; CuA_2 – second branch of anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *dm* – discal medial cell; *dm–cu* – discal medial–cubital crossvein; *h* – humeral crossvein; hum brk – humeral break; l calyp – lower calypter; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; *MA* – anterior branch of media; *m–m* – medial crossvein; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; r_2 – second radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_4 – upper branch of third branch of radius; r_4 – fourth radial cell; R_{4+5} – third branch of radius; r_{4+5} – fourth + fifth radial cell; R_5 – lower branch of third branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein; sc brk – subcostal break; *sc–r* – subcostal–radial crossvein; sc scl – subcostal sclerite; *stm vn* – stem vein; teg – tegula; u calyp – upper calypter.

pterostigma (stigma) (Fig. 43a, 43b): a darkened part of the membrane at the apex of cell *sc*, often ending before the apex of vein R_1, but sometimes extending into cell r_1.

radial cells (Figs 43a, 43b, 45a, 45b): each of the cells behind one of the branches of the radial vein; as such, **cell r_1** (marginal cell in older terminology) lies behind vein R_1, **cell r_{2+3}** (first submarginal cell) lies behind vein R_{2+3}, **cell r_2** lies behind vein R_2, **cell r_3** lies behind vein R_3 and **cell r_4** (second submarginal cell) and **cell r_{4+5}** or **cell r_5** (first posterior cell in older terminology) lie behind veins R_4 and R_{4+5} or R_5.

radial–medial crossvein, ***r–m*** (anterior crossvein, *rm*, *ta*) (Figs 43a, 43b, 45a, 45b): an important landmark in all Diptera, except those with reduced wing venation, the crossvein connecting the most posterior branch of the radius and the media, closing the basal radial cell. Many species with patterned wings have a dark macula (spot) around crossvein *r–m*. In Acroceridae a second radial-medial crossvein (***r–m2***) (plus rarely a third) is sometimes present towards the apex of the wing.

radial sector, ***Rs*** (Figs 43a–44b): the posterior branch of the radius, vein *R*, arising from R_1 at the node; the node and the first part of *Rs* usually bear setae in Cyclorrhapha.

radial vein or **radius**, ***R*** (first, second and third longitudinal veins) (Figs 43a–45b): the main and largest, vein of the wing, usually subdivided into two main branches, the anterior branch R_1 (first longitudinal vein) and the posterior branch, or radial sector ***Rs***, comprising R_{2+3} (second longitudinal vein), which is again often subdivided into R_2 and R_3, especially in nematocerous Diptera and R_{4+5} (third longitudinal vein), also usually subdivided in nematocerous and orthorrhaphous brachyceran families into R_4 (upper branch of third longitudinal vein) and R_5 (lower branch of third longitudinal vein). Auxiliary crossveins occur between some radial veins in a few groups, such as certain genera of Bombyliidae and Empididae.

radius, see **radial vein**.

remigium, see **stem vein** and **subcostal sclerite** *sensu* Hall (1948).

spurious vein: in Syrphidae, a longitudinal vein-like thickening in the membrane between veins *R* and *M*, bisecting crossvein *r–m* and ending in cell r_{4+5}.

squama, see **calypter**.

squamula alaris, see **upper calypter**.

squamula thoracica, see **lower calypter**.

stem vein (remigium) (Figs 43a–44b): the thickened base of vein *R* between the wing base and base of vein *M*. It may be setose or bare. In some calliphorids it bears an even row of fine setae along its posterior edge, dorsally (in Chrysomyinae) and also ventrally (in Toxotarsinae).

stigma, see **pterostigma**.

subcosta, see **subcostal vein**.

subcostal break (Figs 45a, 45b): a weakness, or point of flexure in the costa just before or at the level of the apex of the subcosta.

subcostal cell, ***sc*** (Figs 43a, 43b, 45a, 45b): the membrane between the subcosta and radius, closed distally either by vein R_1, or by the *sc–r* crossvein.

subcostal–radial crossvein, ***sc–r*** (Figs 43a, 43b): a crossvein between the subcosta and radius; it is located near the apex of the subcosta in some primitive nematocerous families, but is placed much more basally in various groups of orthorrhaphous Brachycera (Stuckenberg 2001). The *sc–r* crossvein is absent in Cyclorrhapha, except in most Syrphidae and some Conopidae.

subcostal sclerite (remigium *sensu* Hall (1948)) (Figs 44a, 44b): a narrow triangular sclerite on the underside of the wing at the base of vein *R*, bearing a few setae in some calyptrates, *e.g.*, *Lucilia* subgenus *Lucilia* Robineau-Desvoidy.

subcostal vein or **subcosta**, ***Sc*** (Figs 43a–45b): a slender vein between costa and radius that may end blindly in the membrane, or terminate in the costa. In a few groups the subcosta terminates in R_1 (e.g., most Dolichopodidae), or appears to fuse with it.

submarginal cells, see **cells r_{2+3}** and **r_4** under **radial cells**.

supernumerary crossvein: any additional crossvein between longitudinal veins present in certain genera of some families (e.g., Nemestrinidae, some Asilidae and Curtonotidae).

tegula (Figs 44a–45b): scale-like sclerite at the base of the wing, adjacent to the basicosta, usually bearing setae along its distal margin.

transverse vein, see **crossvein**.

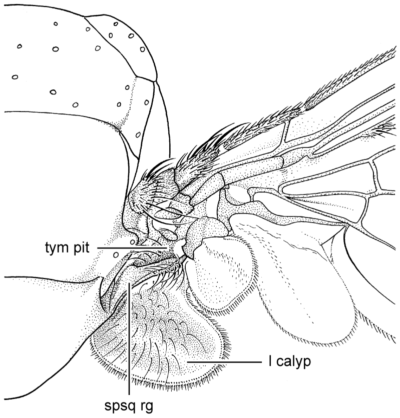
upper calypter (squamula alaris, upper squama) (Figs 44a–45b): a lobe at the base of the wing along its posterior edge, between lower calypter and alula. When the wing is at rest, it is usually folded over the lower calypter.

upper squama, see **upper calypter**.

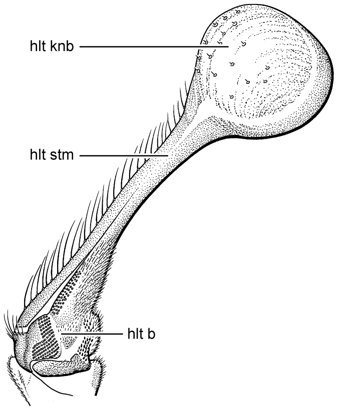
vein: thickened, sclerotised reinforcements of the wing, arising as outgrowths of the tracheal system.

Legs

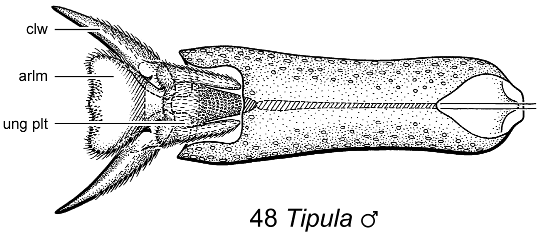
The three pairs of walking legs, namely the **fore leg**, **mid leg** and **hind leg** are each made up of a **coxa** (pl. **coxae**), **trochanter**, **femur** (pl. **femora**), **tibia** (pl. **tibiae**) and **tarsus** (pl. **tarsi**) (Figs 2, 3). Each of the legs may show conspicuous modifications related to prey-catching, predator avoidance, digging and cleaning behaviour. Secondary sexual features associated with courtship and copulation may also be apparent on the legs. The position of these modifications on the different leg surfaces is determined by assuming that each leg is fully extended laterally at a right angle from the main axis of the body (Fig. 1), so that it has an anterior (a), dorsal (d), posterior (p) and ventral (v) surface. Intermediate surfaces are described as



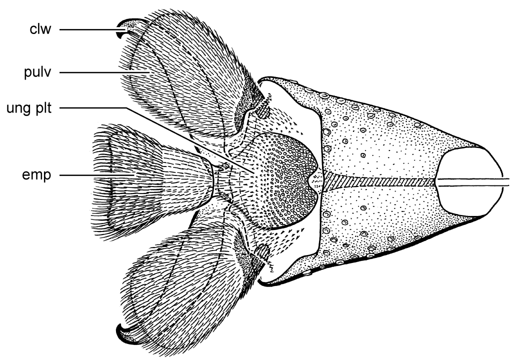
46 *Calliphora* ♀



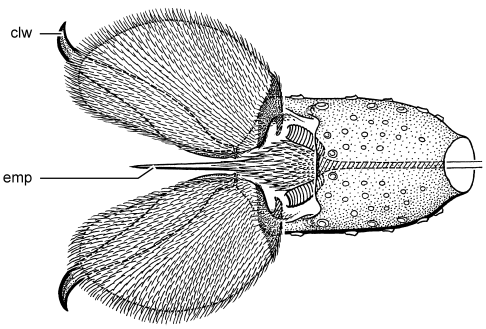
47 *Bibio* ♂



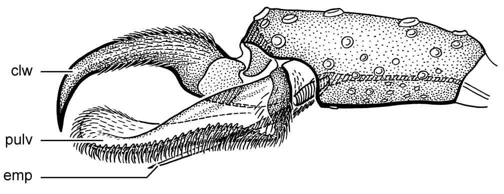
48 *Tipula* ♂



49 *Stratiomys* ♂



50 *Musca* ♂



51 *Musca* ♂

Figs 3.46–51. Wing base, halter and fifth tarsomeres: (46) base of wing of *Calliphora* sp. (Calliphoridae) ♀ (non-Afrotropical); (47) halter of *Bibio* sp. (Bibionidae) ♂ (non-Afrotropical); (48) ventral view of acropod and fifth tarsomere of *Tipula dorsimacula* Walker (Tipulidae) ♂ (non-Afrotropical); (49) same, *Stratiomys badia* Walker (Stratiomyidae) ♂ (non-Afrotropical); (50) acropod and fifth tarsomere of *Musca autumnalis* De Geer (Muscidae), ventral view ♂; (51) same, lateral view. Fig. 46 (after Shewell 1987, fig. 12), Figs 47–51 (after McAlpine 1981, figs 70, 73, 75, 78, 77, respectively).

Abbreviations: arlm – arolium; clw – claw; emp – empodium; hlt b – halter base; hlt knb – halter knob; hlt stm – halter stem; l calyp – lower calypter; pulv – pulvillus; spsq rg – suprasquamal ridge; tym pit – tympanic pit; ung plt – unguitractor plate.

anterodorsal (ad), posterodorsal (pd), posteroventral (pv) and anteroventral (av).

Glossary

acropod (posttarsus) (Figs 48–51): small terminal sclerite closely associated with the fifth tarsomere bearing the unguitractor plate ventrally and the claws, pulvilli and arolium distally.

apical comb: a row of fine setulae at the apex of the tibiae in some families of Diptera, apparently used for grooming various body parts.

arolium (Fig. 48): median protrusion at the distal end of the acropod that is associated with the fifth tarsomere, usually bearing a median process (*i.e.*, empodium or mediolobus).

basitarsus, see **first tarsomere** under **tarsomere**.

calcar: a large distinctive posterodorsal bristle-like seta on the hind tibia of some Calyptratae.

calcipala: a flange-like lobe that extends distally from the inner surface of the first tarsomere of the hind leg of some Simuliidae; its edge is serrated suggesting a grooming function (Adler *et al*. 2004: 41).

claw (tarsal claw, unguis) (Figs 48–51): one of a pair of hook-like structures that arise from the dorsolateral surface of the acropod.

coxa (Fig. 3): the basal segment of each leg that articulates with the thorax.

ctenidium (pecten): comb-like row (or rows) of stout setae, on the anteroventral surface of the apical portion of the fore femur in several families of Diptera, but on the dorsal surface of the tibiae in some Phoridae; frequently one bristle-like seta on the fore femur, referred to as a **ctenidial spine**, is distinctively larger than the other setae.

empodium (Figs 49–51): median process of the acropod found in most Diptera that arises from the ventral surface of the arolium; when present it is generally referred to as either **pulvilliform** (*i.e.*, flap-like and similar in shape to pulvilli) (Fig. 49), or **setiform** (Figs 50, 51). However, Röder (1984, 1986) considers both forms as non-homologous structures. He interprets the setiform median process as an outgrowth of the unguitractor plate, which he refers to as the empodium, whereas the pulvilliform median lobe (termed the **mediolobus**) is derived from the membranous area distal to the unguitractor plate.

femur (pl. **femora**) (Figs 2, 3): the most substantial subbasal segment of the leg between the trochanter and tibia.

mediolobus, see pulvilliform under **empodium**.

metatarsus, see **first tarsomere** under **tarsomere**.

pecten, see **ctenidium**.

pedisulcus: an acute or blunt notch-like indentation on the dorsal surface of the second tarsomere of the hind leg in both sexes of some Simuliidae.

posttarsus, see **acropod**.

preapical seta: a dorsal, or anterodorsal seta near the apex of the femora or tibiae; presence or absence of preapical setae is taxonomically important in the Dolichopodidae and at the family level in acalyptrates.

pulvilli (sing. **pulvillus**) (Figs 49, 51): paired flap-like processes of the acropod found in most Diptera; the pulvilli, in combination with the empodium (or mediolobus) act to grip the substrate.

setal palisade: longitudinal rows of enlarged setae on the dorsal surface of the tibiae in some Phoridae.

spur: an enlarged spine often present at the apex of the tibia; true spurs are articulated and may be single, or paired, whereas unarticulated spurs are actually processes of the distal tibial margin and are not homologous to true spurs.

tarsomere (Figs 2, 3): each tarsus is subdivided into five tarsomeres in almost all Diptera, namely the **first** (basitarsus, metatarsus), **second**, **third**, **fourth** and **fifth** (distitarsus) **tarsomeres**; the fifth tarsomere is associated distally with the claw-bearing acropod. The number of tarsomeres is reduced in only a few Cecidomyiidae and Phoridae.

tarsus (pl. **tarsi**) (Fig. 3): the distal segment of the leg, subdivided with few exceptions into five tarsomeres. A few authors (*e.g.*, Adler *et al*. 2004: 41) consider the first tarsomere (basitarsus) to be a true segment distinct from the remaining tarsomeres, but this interpretation is not followed here.

tibia (Figs 2, 3): the middle segment of the leg between the femur and the tarsus, generally not as stout as the femur.

trochanter (Fig. 3): a small immovable segment between the coxa and the femur that is usually fused with the femur.

unguis (pl. ungues), see **claw**.

unguitractor plate (Figs 48, 49): ventral sclerite of the acropod.

Abdomen

In the dipteran groundplan the abdomen is composed of 10 segments, plus the **proctiger** that bears a pair of **cerci** and the **anus**. The basal segments that are anterior to the modified genital segments are collectively referred to as the **preabdomen**. The remaining complex of modified genital and anal segments, including any adjacent segments that are modified for copulation and oviposition, are referred to as the **terminalia** (postabdomen) (Figs 2, 3, 52, 66).

Glossary

abdominal plaques (Fig. 59): circular patches along the anterior margin of the preabdominal tergites and sternites of nematocerous Diptera and orthorrhaphous Brachycera. These patches represent external remnants of attachment sites of muscles in the pupa (Stoffolano *et al*. 1988) and are absent in Cyclorrhapha, because the pupa is immobile and contained inside a puparium.

abdominal spiracles (stigmata) (Fig. 56): the external openings of the tracheae on the abdominal segments; in what is assumed to be the primitive condition, each abdominal segment has one pair of spiracles, with each spiracle located laterally in the pleural membrane of the segment. In Diptera there are no more than eight pairs in the female, seven in males, but this number is frequently reduced in various taxa across the order, especially in Cyclorrhapha, where the spiracles can also become incorporated into the lateral margins of the tergites.

adventitious suture, see under **syntergite**.

anus (Figs 70, 87): posterior opening of the digestive tract, positioned at the apex of the abdomen between the cerci (see **proctiger**).

cercus (pl. **cerci**) (Figs 52, 56, 59, 71, 72, 88): one of a pair of terminal appendages on either side of the anus that are derived from the proctiger; in the female groundplan they are composed of two segments, but are reduced to a single segment in most higher Diptera; in males the cerci consist of only one segment. In some taxa the cerci are fused together, or are reduced and indistinguishable from other components of the proctiger.

cingulum: structure of unknown function that protrudes between abdominal segments 4 and 5 in certain male hydrophorine Dolichopodidae (*e.g.*, *Hydatostega* Philippi and *Scellus* Loew); the cingulum usually terminates in a pair of flag-like appendages that are often haired and/or are brightly coloured.

discal setae: setae found on the disk of the preadominal tergites in many Calyptratae, referred to as median, or lateral depending on their position (see **marginal setae**).

marginal setae: setae found along the posterior margin of the preadominal tergites in many Calyptratae; referred to as median, or lateral depending on their position (see **discal setae**).

preabdomen: basal segments anterior to the modified genital segments or terminalia. The preabdomen generally consists of segments 1–7 in the nematocerous Diptera and orthorrhaphous Brachycera, segments 1–6 in female Cyclorrhapha and segments 1–5 in male Cyclorrhapha.

proctiger (anal segment) (Figs 70, 87): in a strict sense the anus-bearing region posterior to (or arising from) segment 10, but generally used for all associated structures behind segment 9 (**cerci**, **epiproct**, **hypoproct**, **paraprocts**) in male Diptera (Wood 1991) and in females of at least Cyclorrhapha.

rectal papillae (Fig. 60): prominent ovoid structures on the wall of the rectum that appear to reabsorb water passing through the gut. Most Diptera have four rectal papillae, but some Asilidae have five and Apioceridae and Mydidae, which are among the most dry-adapted flies, have many more (14–80 papillae) (Woodley 1989: 1387).

stigmata (sing. stigma), see **abdominal spiracles**.

syntergite: in Cyclorrhapha and some orthorrhaphous Brachycera, the fused tergites of the first two abdominal segments are referred to as syntergite 1 + 2. A line of fusion, the **adventitious suture**, is usually recognisable, but is seldom distinct. Only tergites 1 and 2 are affected; the sternites usually remain separate and distinct, although in Tabanidae, Pyrgotidae and Ctenostylidae they may be fused into a **synsternite** (or one may be absent).

terminalia (postabdomen) (Figs 2, 3): complex of genital and anal segments, including any adjacent segments that are modified for copulation and oviposition. The terminalia generally consist of segments 8–10 (including the proctiger) in the nematocerous Diptera and orthorrhaphous Brachycera, segments 7–10 (including the proctiger) in female Cyclorrhapha, and segments 6–10 (including the proctiger) in male Cyclorrhapha.

Female terminalia

The terminalia of the female include the genital and anal segments of the abdomen posterior to the preabdomen that are modified for oviposition and copulation (Figs 52–65). The segments involved vary depending on the group, but generally consist of segments 8–10 (including the proctiger) in the nematocerous Diptera and orthorrhaphous Brachycera, as well as segment 7 in the Cyclorrhapha. The definitions presented here for the female postabdomen incorporate terminology adopted by Kotrba (2000) and focus primarily on external structures, but also include certain internal structures of ectodermal origin, which are more or less sclerotised, or pigmented and are useful for diagnosing certain groups.

Glossary

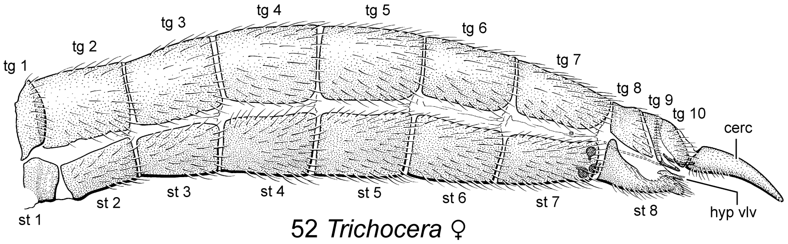
acanthophorites (Figs 57, 58, 60, 61): spine-bearing hemitergites found in many orthorrhaphous Brachycera that are derived from tergite 10 (see **pseudacanthophorites**); **acanthophorite spines** are innervated and project from alveoli; they are therefore a type of macrotrichia. In some groups of Empidoidea (*e.g.*, *Microphor* Macquart) acanthophorite spines are reduced to **acanthophorite setae**.

accessory glands (appendicular glands, colleterial glands, parovaria) (Fig. 63): paired glandular organs of ectodermal origin that are derived from segment 9; they are unpaired in a few groups. In the viviparous Pupipara (Glossinidae and Hippoboscidae), the accessory glands produce nutrient for the developing larvae and are referred to as **milk glands**; the "milk glands" of the viviparous Mesembrinellinae (Calliphoridae), however, are derived from the spermathecae (Kotrba 2000: 80).

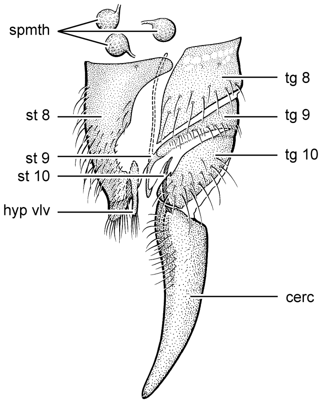
aculeus (ovipositor blade) (Fig. 63): the piercing part of the ovipositor in Tephritoidea that is generally retracted with the eversible ovipositor membrane inside the oviscape; the aculeus consists of an elongate tergite and sternite 8, in addition to the proctiger, which in Tephritidae is usually fused with tergite 8 beyond the cloacal opening and sternite 8 to form a piercing **aculeus tip** (see **cloaca**).

adanal plates: small paired sclerites ventrolateral of, or fused to, the cerci in nycteribiine Hippoboscidae.

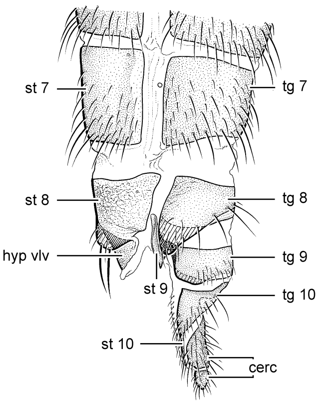
anal lobe: a ventrally directed extension of segment 10 found in many Simuliidae, not to be confused with the anal lobe of the wing.



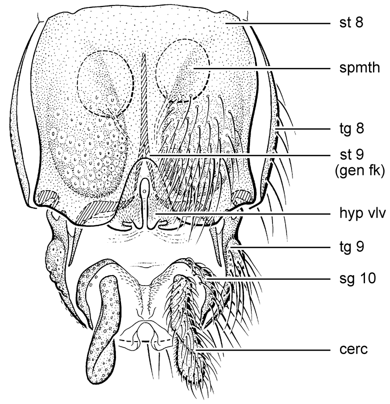
52 *Trichocera* ♀



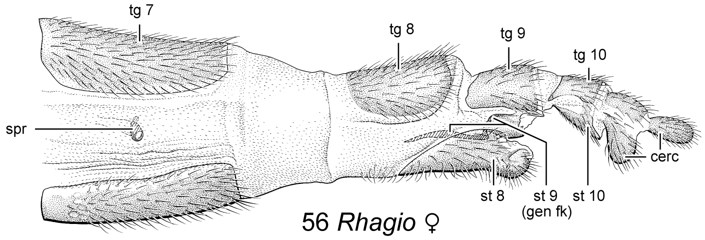
53 *Trichocera* ♀



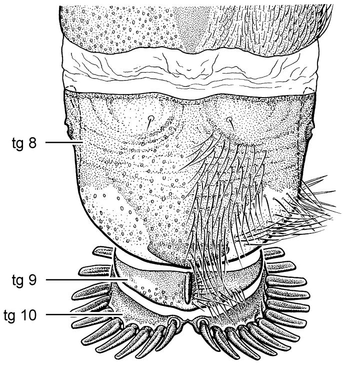
54 *Boletina* ♀



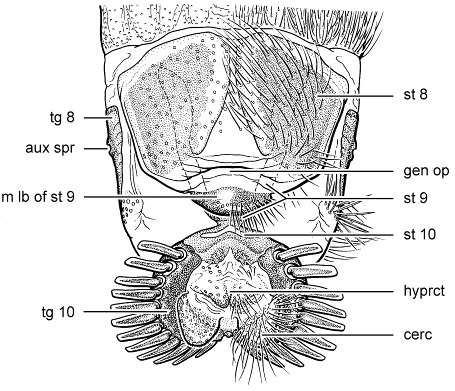
55 *Chironomus* ♀



56 *Rhagio* ♀



57 *Rhaphiomidas* ♀



58 *Rhaphiomidas* ♀

Figs 3.52–58. Female abdomens and terminalia: (52) lateral view of entire abdomen of *Trichocera columbiana* Alexander (Trichoceridae – non-Afrotropical); (53) same, enlarged view of terminalia; (54) lateral view of terminalia of *Boletina* sp. (Mycetophilidae); (55) ventral view of terminalia of *Chironomus plumosus* (L.) (Chironomidae); (56) lateral view of terminal segments of abdomen of *Rhagio mystaceus* (Macquart) (Rhagionidae); (57) terminal segments of abdomen of *Rhaphiomidas acton* Coquillett (Mydidae), dorsal view; (58) same, ventral view (all non-Afrotropical). Figs 52–58 (after McAlpine 1981, figs 79, 80, 83, 86, 94, 99, 100).

Abbreviations: aux spr – spiracle; cerc – cercus; gen fk – genital fork; gen op – genital opening; hyp vlv – hypogynial valve; hyprct – hypoproct; m lb – median lobe; sg – segment; spmth – spermatheca; spr – spiracle; st – sternite; tg – tergite.

basicercus (Figs 54, 56): basal segment of the two-segmented cercus found in some female nematocerous Diptera and orthorrhaphous Brachycera.

bursa (bursa copulatrix): general term for a pouch of various homologies in the genital chamber, which during mating receives a spermatophore, or male genitalia and/or sperm (see **ventral receptacle**). The **bursa inseminalis** is a posterodorsal pouch of the genital chamber found in certain nematocerous groups; it receives sperm during copulation.

cercus (pl. **cerci**) (Figs 53–56, 58–65): one of a pair of terminal appendages on either side of the anus derived from the proctiger. The cerci are composed of two segments in the female groundplan, but are reduced to a single segment in many nematocerous Diptera and orthorrhaphous Brachycera, as well as in all Eremoneura (Empidoidea and Cyclorrhapha) (see **basicercus**).

cloaca (Fig. 63): in Tephritidae, the terminal portion of the vagina and rectum fuse to form a cloaca, which has a single external opening, the **cloacal opening**, between the divided sclerites of sternite 8.

epigynium: tergite 8 of the female terminalia.

epiproct (supra-anal plate, tergite 10) (Fig. 64): the dorsal sclerite of the proctiger.

eversible ovipositor membrane (eversible membrane, eversible ovipositor sheath, inversion membrane, ovipositubus, oviprovector) (Figs 62, 63): the elongate membranous area of the ovipositor in various acalyptrate Diptera (*e.g.*, Agromyzidae and Tephritoidea), between syntergosternite 7 (oviscape) and segment 8 (aculeus), which is inverted for retraction of the tip of the ovipositor inside the oviscape. The eversible ovipositor membrane usually bears minute cuticular denticles (previously referred to, collectively, as the rasper), as well as paired dorsal and ventral sclerites basally, termed taeniae (see **taeniae**).

fertilisation chamber: in Schizophora an unpaired evagination arising from the anteroventral portion of the vagina where eggs are fertilised during oviposition; it is further developed as the ventral receptacle (Fig. 63) in most acalyptrate Schizophora (see **ventral receptacle**).

furca, see **genital fork**.

genital chamber: ectodermal invagination leading anteriorly toward the common oviduct from the genital opening behind sternite 8; in Cyclorrhapha the genital chamber forms a tubular organ termed the vagina. The **primary gonopore** is generally positioned at the anterior end of the genital chamber, where the spermathecal ducts and accessory glands open on the chamber's dorsal wall (see **vagina**).

genital fork (furca, sternite 9, vaginal apodeme) (Figs 55, 56, 61): an internalised sclerite of the dorsal wall of the genital chamber derived from sternite 9, absent or unrecognisable in most Cyclorrhapha (see **sternite 9**).

genital opening (secondary gonopore, vulva) (Fig. 58): external opening of the genital chamber, or vagina, located medially behind sternite 8 (see **cloaca**).

hypogynial valve (gonapophysis, hypovalve, ovipositor lobe, ovipositor valve, sternal valve) (Figs 52–55): one of a pair of lateral processes arising from sternite 8.

hypogynium (subgenital plate): sternite 8 of the female terminalia.

hypoproct (anal sclerite in nycteribiine Hippoboscidae, intra-anal plates in Tipulidae, sternite 10, subanal plate) (Fig. 65): the ventral sclerite of the proctiger.

insula: median sclerite derived from sternite 8 or 9 in Culicidae and clothed with microtrichia or macrotrichia.

milk glands, see **accessory glands**.

morula gland, see **ventral receptacle**.

ovipositor (intersegment 6/7 and 7/8, ovicauda, oviscapt): the parts of the terminalia that are modified for oviposition, involving different segments and structures in different groups.

ovisac, see **uterus**.

oviscape (ovipositor sheath, oviscapt) (Figs 62, 63): the basal conical or tubular segment of the ovipositor that is usually formed by fusion of tergite and sternite 7 into **syntergosternite 7.** The oviscape forms a tubular sheath that generally receives the retracted apical components of the ovipositor (*e.g.*, as in Tephritoidea).

paraproct (Fig. 55, sg 10): one of a pair of lateral sclerites arising from the proctiger.

primary gonopore, see under **genital chamber**.

proctiger, see above under Abdomen.

pseudacanthophorites: spine-bearing cerci found in some species of tethinine Canacidae (Freidberg & Beschoski 1996), which like acanthophorites are used for digging during oviposition. Similar spine-bearing cerci are also present in some Tephritidae and Curtonotidae.

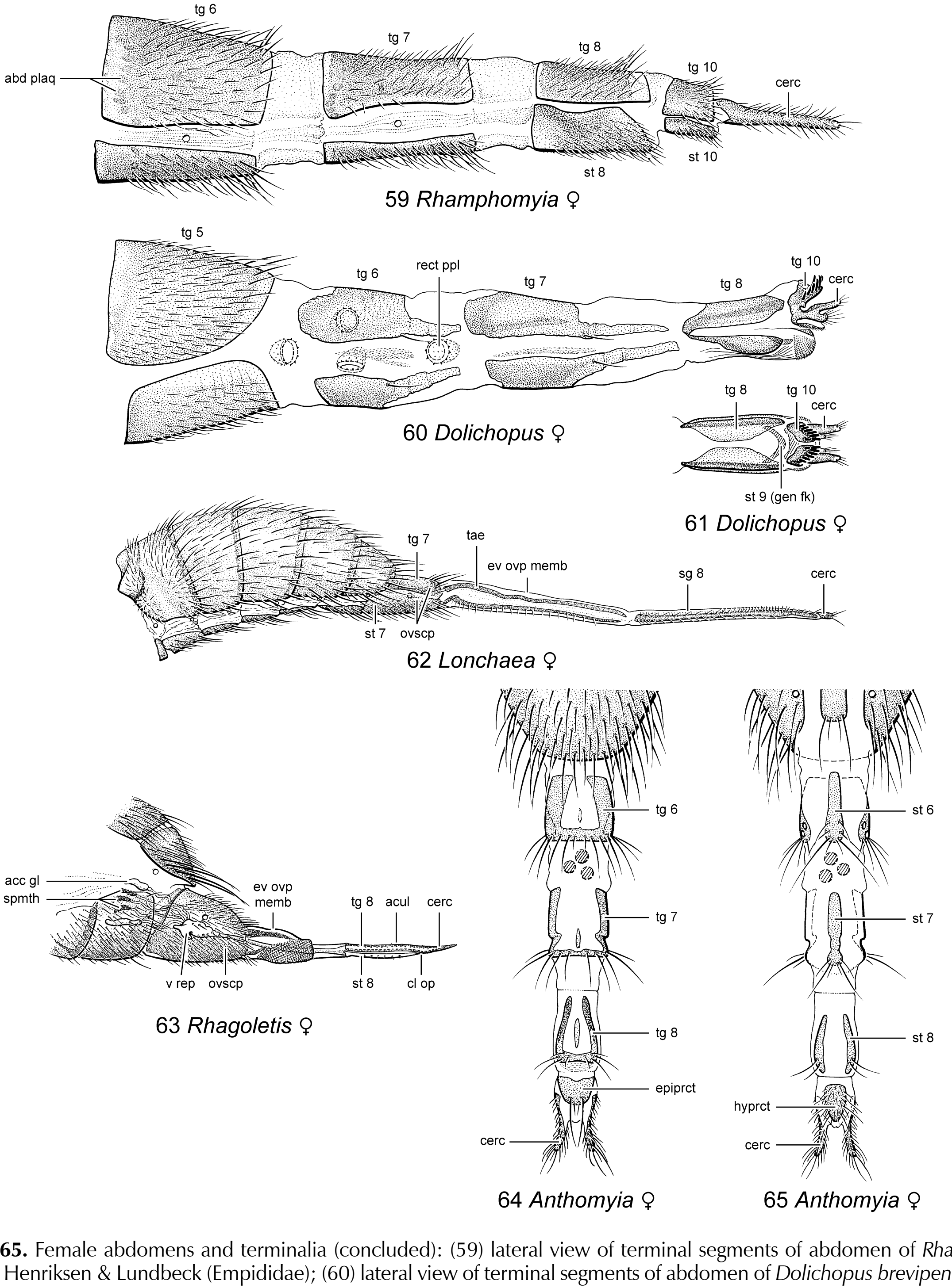
sand chamber: haired invagination of segment 8 found in most Bombyliidae that is used as a receptacle where the eggs are coated with sand. A similar structure is found in a few Asilidae.

secondary gonopore, see **genital opening**.

sperm pump: musculated section of a spermathecal duct found in many orthorrhaphous Brachycera and a few Cyclorrhapha (*e.g.*, *Stylogaster* Macquart in Conopidae), not to be confused with the sperm pump of males.

spermatheca (pl. **spermathecae**) (sperm receptacle, receptaculum seminis) (Figs 53, 55, 63): sperm-storage organ derived from segment 8, generally more or less heavily sclerotised and usually spherical, or cylindrical; most Diptera possess three spermathecae, but the number may vary from zero to four depending on the group (some Diptera considered to lack spermathecae possess membranous spermathecal capsules that are difficult to discern).

spermathecal duct (spermiduct): a sclerotised duct that leads from each spermatheca to the dorsal wall of the genital chamber (or genital fork), where it opens near the primary



59 *Rhamphomyia* ♀

60 *Dolichopus* ♀

61 *Dolichopus* ♀

62 *Lonchaea* ♀

63 *Rhagoletis* ♀

64 *Anthomyia* ♀

65 *Anthomyia* ♀

Figs 3.59–65. Female abdomens and terminalia (concluded): (59) lateral view of terminal segments of abdomen of *Rhamphomyia filicauda* Henriksen & Lundbeck (Empididae); (60) lateral view of terminal segments of abdomen of *Dolichopus brevipennis* Meigen (Dolichopodidae); (61) same, ventral view of last four segments; (62) lateral view of entire abdomen of *Lonchaea polita* Say (Lonchaeidae); (63) lateral view of terminal segments of abdomen of *Rhagoletis pomonella* (Walsh) (Tephritidae); (64) extended terminal segments of abdomen of *Anthomyia pluvialis* (L.) (Anthomyiidae), dorsal view; (65) same, ventral view (all non-Afrotropical). Figs 59–62, 64, 65 (after McAlpine 1981, figs 101–103, 110, 105, 106, respectively), Fig. 63 (after Foote & Steyskal 1987, fig. 43).

Abbreviations: abd plaq – abdominal plaque; acc gl – accessory gland; acul – aculeus; cerc – cercus; cl op – cloacal opening; epiprct – epiproct; ev ovp memb – eversible ovipositor membrane; gen fk – genital fork; hyprct – hypoproct; ovscp – oviscape; rect ppl – rectal papilla; sg – segment; spmth – spermatheca; st – sternite; tae – taenia; tg – tergite; v rep – ventral receptacle.

gonopore; in many Diptera with three spermathecae, two of the three ducts unite before connecting to the genital chamber.

spermathecal sac: sac-like structure associated with the spermathecae in Therevidae, Scenopinidae, Apsilocephalidae and Evocoidae (the last two named non-Afrotropical); in Therevidae the sacs vary greatly in size and shape, depending on the species involved and range in number from zero to three (but not two). Their function is unknown, but they may act as intermediate storage organs for sperm and nutrients prior to transfer of sperm to the spermathecae (Winterton *et al*. 1999).

sternite 9 (preatrial and postatrial sclerites in Culicidae) (Figs 53–56, 58, 61): present, but generally reduced in female Diptera, often internalised as a sclerite of the dorsal wall of the genital chamber and indistinguishable, or absent in most Cyclorrhapha (see **genital fork**).

syntergosternite 7, see **oviscape**.

taeniae (sing. **taenia**) (Fig. 62): in many Tephritoidea paired strip-like dorsal and ventral sclerites on the basal portion of the eversible ovipositor membrane (see **eversible ovipositor membrane**).

theca (ventral genital plate): the ventral prolongation of the sternal portion of segment 5 found in certain Conopidae (most Conopinae and Myopinae), presumably as an aid in clasping the aculeate hymenopteran host during oviposition.

uterus (incubation pouch, ovisac): the anterior portion of the vagina, which tends to be enlarged and possesses an increased tracheal supply in various viviparous and ovolarviparous Cyclorrhapha for the retention of developing eggs.

vagina: the tubular extension of the genital chamber in Cyclorrhapha that stretches from the common oviduct to the genital opening located behind sternite 8 (see **genital chamber**).

ventral receptacle (morula, morula gland) (Fig. 63): in most acalyptrate Diptera an unpaired organ that arises from the anteroventral part of the vagina, which is derived from the fertilisation chamber found in Schizophora (see **fertilisation chamber**). It functions as a chamber for fertilisation and/or as a sperm reservoir and when enlarged is often correlated with reduced spermathecae (Kotrba 2000: 82). The ventral receptacle is extremely diverse in shape and sclerotisation; when it is multi-chambered (*e.g.*, most Tephritoidea and Diopsidae), it has been referred to as a morula, or morula gland.

vulva, see **genital opening**.

Male terminalia

The main components of the male terminalia consist of the copulatory structures of the primary genital segment (segment 9), as well as the proctiger, which together form the **hypopygium**. The basic components of the hypopygium are the **epandrium** (tergite 9), the **hypandrium** (sternite 9), paired two-segmented **gonopods** derived from appendages of segment 9, a median tubular **aedeagus**, **parameres** and the **proctiger**. The **terminalia** (male postabdomen, protandrium) are also considered to include modified adjoining anterior sclerites, such as segment 8 in many nematocerous families and orthorrhaphous Brachycera and segments 6–8 in many Cyclorrhapha (Figs 66–88). Structures of the male terminalia follow the uniform set of terms for the entire Diptera that were presented in a series papers by Wood (1991), Sinclair *et al*. (1994) and Cumming *et al*. (1995), as modified by Sinclair (2000) and subsequently reviewed by Sinclair *et al*. (2013). Alternate views on the homology of structures of the male terminalia, particularly those concerning the Eremoneura (Empidoidea and Cyclorrhapha), are summarised by Sinclair (2000, table 1).

In Diptera the apical portion of the male abdomen and terminalia may be bent or flexed forward ventrally and may also be rotated facultatively, or obligatorily through 45° to 360° (*e.g.*, 180° rotation shown in Figs 68, 70). Modifications involving **flexion** and **rotation**, including the 360° **circumversion** that characterises Cyclorrhapha, are adaptations for protecting the genitalia when at rest and for allowing an upright mating position (see Sinclair *et al*. 2013). McAlpine (1981: 56) summarised the occurrence of flexion and rotation throughout the Diptera, while Cumming *et al*. (1995) reviewed the condition in Eremoneura.

Glossary

accessory glands, see **ejaculatory duct**.

acrophallus (Fig. 88): the distinctive region of the distiphallus that surrounds the phallotrema or external genital opening in Calyptratae, often bearing small denticles (see **distiphallus**).

adminiculum, see **ventral plate**.

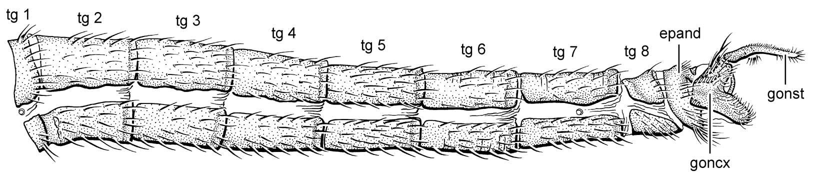
aedeagal apodeme, see **ejaculatory apodeme** and **phallapodeme**.

aedeagal guide, see **phallic guide**.

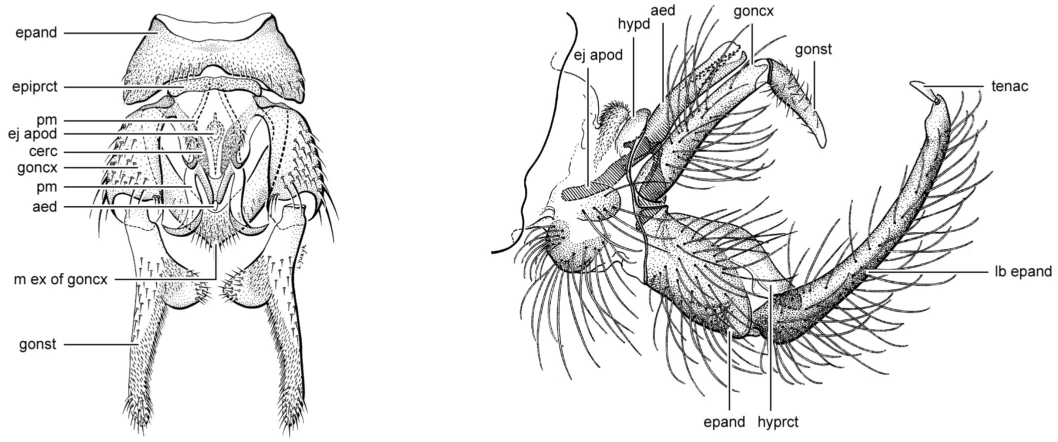
aedeagal tines (endophallic tines) (Fig. 72): elongate, slender sickle-shaped filaments within the sperm sac of Athericidae, Tabanidae and the tabanomorph genus *Bolbomyia* Loew, which arise from the base of the endoaedeagal process; possible precursors of aedeagal tines have also been noted in *Rhagio* F. (Rhagionidae) by Sinclair *et al*. (1994). The tines are pushed posteriorly along with the endoaedeagal process beyond the parameral sheath and functional gonopore, by contraction of the muscles of the ejaculatory apodeme (Bonhag 1951).

aedeagus (penis, phallosome) (Figs 67–70): tubular intromittent organ generally possessing a single external opening (phallotrema), although a tripartite aedeagus is present in several families. In the groundplan of the Brachycera the aedeagus is mostly membranous and largely enclosed in a parameral sheath; in Stratiomyomorpha and Muscomorpha *sensu* Woodley (1989: 1373) the aedeagus is indistinguishably fused to the parameral sheath to form the phallus (see **phallus**). The aedeagus is also reduced to a membranous sac in Culicomorpha (Sinclair 2000: 65 ; Sinclair et al. 2007), presumably correlated with the transfer of preformed spermatophores in many of the included families (*e.g.*, in Ceratopogonidae, see **ventral plate**).

annulus, see **syntergosternum**.

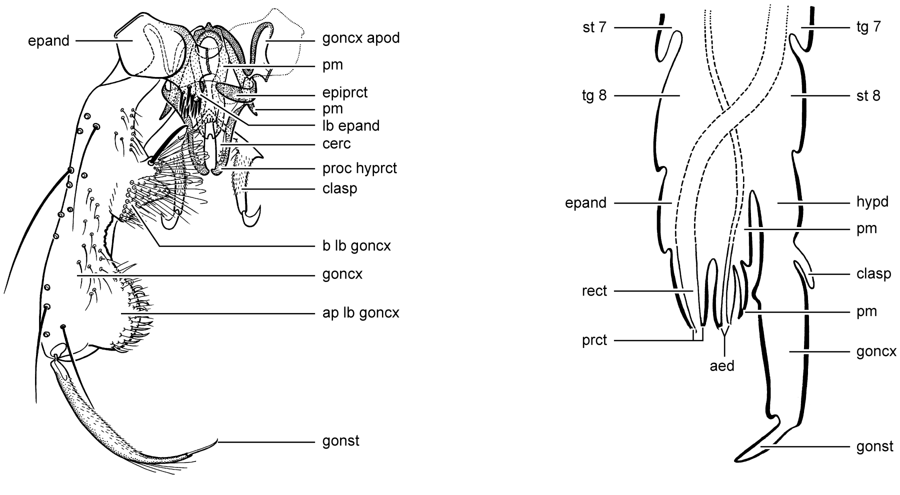


66 *Trichocera* ♂



67 *Trichocera* ♂

68 *Psychoda* ♂



69 *Aedes* ♂

70 *Aedes* ♂

Figs 3.66–70. Male abdomen and terminalia: (66) lateral view of entire abdomen of *Trichocera garretti* (Alexander) (Trichoceridae – non-Afrotropical); (67) same, dorsal view of terminalia; (68) lateral view of terminalia in post-emergence position, subsequent to 180° rotation, of *Psychoda phalaenoides* (L.) (Psychodidae); (69) dorsal view of terminalia of *Aedes hexodontus* Dyar (Culicidae); (70) longitudinal section through terminal segments of abdomen, subsequent to 180° rotation of terminalia shortly after emergence, of *Aedes* sp. (Culicidae) (all non-Afrotropical). Figs 66, 67, 69, 70 (after McAlpine 1981, figs 111, 115, 116, 120), Fig. 68 (after Quate & Vockeroth 1981, fig. 18).

Abbreviations: aed – aedeagus; ap lb goncx – apical lobe of gonocoxite; b lb goncx – basal lobe of gonocoxite; cerc – cercus; clasp – claspette; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; hyprct – hypoproct; lb epand – lobe of epandrium; m ex – median extension; pm – paramere; prct – proctiger; proc hyprct – process of hypoproct; rect – rectum; st – sternite; tenac – tenaculum; tg – tergite.

bacilliform sclerite (processus longus) (Figs 81–84, 88): one of a pair of rod-like thickenings of the subepandrial sclerite that extend from the anterodorsal surface of the phallus to the posterolateral corner of the epandrium, or to the base of the surstylus, in Eremoneura (Empidoidea and Cyclorrhapha) and the non-Afrotropical families Apystomyiidae and Apsilocephalidae. In most Schizophora the bacilliform sclerites are the main component of the subepandrial sclerite and articulate with the hypandrial arms near the base of the phallus, although in some acalyptrates the bacilliform sclerites are secondarily reduced and do not extend to the surstyli (see **subepandrial sclerite**).

basiphallus (phallobase): the main proximal portion of the phallus in Cyclorrhapha that is continuous with the apical **distiphallus**. In many Cyclorrhapha the basiphallus bears a distinct dorsal lobe termed the **epiphallus** (Fig. 88).

cercus (pl. **cerci**) (forceps, mesolobus, superior forceps, syncercus, valvula medialis) (Figs 66–69, 71, 72, 74–85, 87, 88): one of a pair of single-segmented terminal appendages on either side of the anus derived from the proctiger. In many taxa the cerci are reduced and indistinguishable from other components of the proctiger, but in some groups the cerci are enlarged and clasper-like, or are fused together (syncercus or mesolobus).

claspette, see **ventral plate**.

distiphallus (hypophallus, mesophallus, ventrolateral process) (Figs 85, 88): the main apical portion of the phallus in Cyclorrhapha that arises from the proximal **basiphallus**; in Calyptratae the distinctive region of the distiphallus that surrounds the phallotrema (genital opening) is referred to as the **acrophallus**. The distiphallus is subdivided into various structures (some listed as synonyms in brackets above) in different groups of Schizophora, such as the taxonomically important basolateral paired **paraphallus** in many Agromyzidae and Clusiidae (Lonsdale & Marshall 2012; Nowakowski 1973), the swollen apical **glans** in Tephritoidea, the basal membranous **saccus** and more slender terminal sclerotised **filum** in Anthomyzidae (Roháček & Barber 2005), and the diverse terminal processes (*e.g.*, **vesica**, **harpes**, **juxta** and **stylus)** of certain Sarcophagidae (Giroux *et al*. 2010; Roback 1954).

ejaculatory apodeme (aedeagal apodeme *sensu* McAlpine (1981: 53) concerning lower Diptera, ejacapodeme, endophallus apodeme) (Figs 67, 68, 71–73, 82, 84, 85, 87, 88): unpaired apodeme of the sperm pump inserted at the base of the sperm sac; the ejaculatory apodeme supports muscles that assist in compressing the pump (see **sperm pump**). The ejaculatory apodeme is absent in all Culicomorpha (Sinclair 2000: 69; Wood 1991).

ejaculatory duct (Fig. 87): duct or ducts of ectodermal origin that run from the mostly endodermal **vasa deferentia** (at the point where the **accessory glands** connect), to the base of the endophallus (usually at the sperm pump) (see **sperm pump**).

endoaedeagal process (endoaedeagus, endophallus, posterior part of aedeagus) (Fig. 72): in Brachycera a slender sclerotised posterior extension, that arises from the apex of the ejaculatory apodeme in most Xylophagomorpha, Tabanomorpha, some Nemestrinidae, Asilidae and possibly Bombyliidae (Sinclair *et al*. 1994); the endoaedeagal process is absent in Stratiomyomorpha and Eremoneura (Empidoidea and Cyclorrhapha).

endoaedeagal tube (Ductusrohr, endoaedeagus): slender, inconspicuous membranous tube within the sperm sac of many Asiloidea and some Bombyliidae; the endoaedeagal tube appears to be a posterior extension of the ejaculatory duct; it is perforated with pores and often covered in spinules, granules, or platelets (Sinclair 2000: 69).

endophallus: inner seminal duct of the aedeagus, or phallus extending from the sperm sac.

epandrium (dorsal sclerite, periandrium, tergite 9) (Figs 67–80, 82–85, 87, 88): tergite 9 of the male genital segment, fused to the hypandrium (sternite 9) to form a ring in the dipteran groundplan (Wood 1991), but secondarily separated in some nematocerous groups and almost all Brachycera (see **hypandrium**). The epandrium is a subrectangular sclerite in most nematocerous Diptera and basal orthorrhaphous Brachycera, but is deeply cleft posteriorly, or completely divided in many asiloids and Eremoneura (Empidoidea and Cyclorrhapha), associated with its involvement in clasping (see **surstylus**). Many Psychodidae also have clasper-like epandrial lobes (see Sinclair *et al*. 2013) that have been referred to as cerci (= cercopodia) or surstyli.

epiphallus (Fig. 88): a distinct lobe in many Cyclorrhapha that arises from the dorsomedial surface of the basiphallus. The enlarged dorsal portion of the parameral sheath of the phallus that is found in many Bombyliidae has also been referred to as the epiphallus (Yeates 1994).

epiproct (tergite 10) (Figs 67, 69): the middorsal sclerite of the proctiger, positioned between the lateral cerci; it is lost in males of Acroceridae and all Heterodactyla (Bombyliidae, Asiloidea, Eremoneura) (Sinclair 2000: 72).

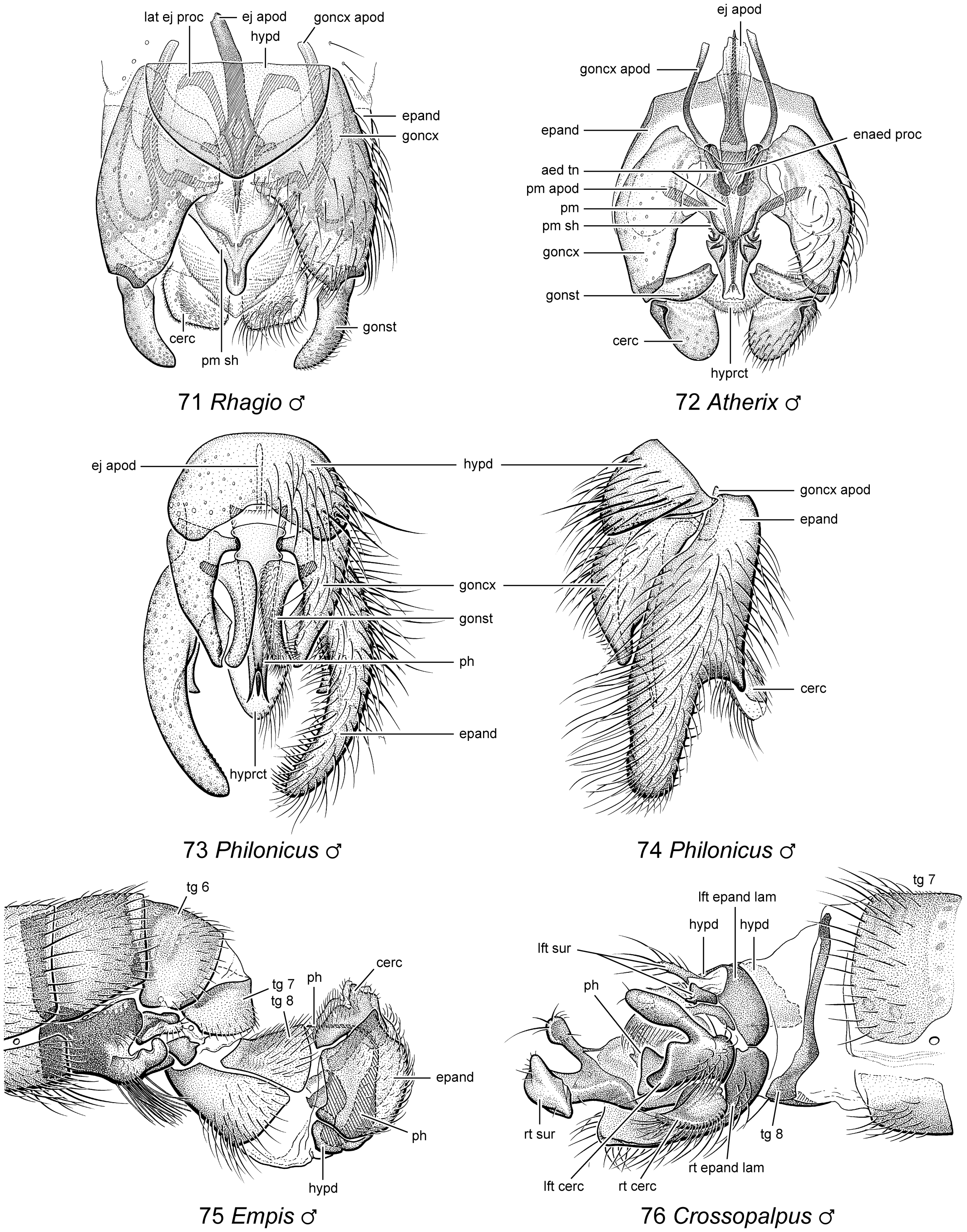
filum, see **distiphallus**.

glans (pl. **glandes**) (aedeagal glans) (Fig. 85): swollen expandable apical portion of the distiphallus in many Tephritoidea.

gonocoxal apodeme (basal piece in Culicidae, basimeral apodeme, dorso-inner anterior process, sternapodeme) (Figs 69, 71, 72, 74): a process that projects anteriorly from each gonocoxite, or the gonocoxal region of the composite hypandrial sclerite (see **hypandrium**). The gonocoxal apodemes (as a pair) indicate the position of the medially attached parameres in the nematocerous Diptera, or the parameral sheath in Brachycera (see **phallus**). Gonocoxal apodemes are inconspicuous in many nematocerous families. They are greatly reduced and do not project beyond the hypandrium in those Empidoidea with permanent male genitalic rotation, as well as in all Cyclorrhapha (Cumming *et al*. 1995).

gonocoxal plate, see **ventral plate**.

gonocoxite (basimere, basistyle, coxite, gonocoxa) (Figs 66–74): basal component of the two-segmented clasping gonopod. The gonocoxites are assumed by Wood (1991) and Sinclair *et al*. (1994) to be separate from each other in the dipteran groundplan, although Griffiths (1996) has questioned



71 *Rhagio* ♂ 72 *Atherix* ♂

73 *Philonicus* ♂ 74 *Philonicus* ♂

75 *Empis* ♂ 76 *Crossopalpus* ♂

Figs 3.71–76. Male terminalia (continued): (71) ventral view of *Rhagio vertebratus* (Say) (Rhagionidae); (72) same, *Atherix lantha* Webb (Athericidae); (73) ventral view of *Philonicus* sp. (Asilidae); (74) same, left lateral view; (75) lateral view of terminal abdominal segments and terminalia of *Empis browni* Curran (Empididae); (76) right lateral view of *Crossopalpus armata* (Melander) (Hybotidae) (all non-Afrotropical). Fig. 71 (after James & Turner 1981, fig. 14), Fig. 72 (after Webb 1981, fig. 6), Figs 73, 74 (after Wood 1981, figs 74, 75), Figs 75, 76 (after Steyskal & Knutson 1981, figs 52, 51 (as *Drapetis*), respectively).

Abbreviations: aed tn – aedeagal tine; cerc – cercus; ej apod – ejaculatory apodeme; enaed proc – endoaedeagal process; epand – epandrium; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; hyprct – hypoproct; lat ej proc – lateral ejaculatory process; lft cerc – left cercus; lft epand lam – left epandrial lamella; lft sur – left surstylus; ph – phallus; pm – paramere; pm apod – parameral apodeme; pm sh – parameral sheath; rt cerc – right cercus; rt epand lam – right epandrial lamella; rt sur – right surstylus; tg – tergite.

this polarity. Gonocoxites are fused together midventrally, generally with the hypandrium, in some nematocerous and lower brachyceran groups, as well as in all Eremoneura (Empidoidea and Cyclorrhapha) (see **gonopod**).

gonopod: one of a pair of two-segmented claspers that are composed of a proximal gonocoxite and a distal gonostylus; in the dipteran groundplan the gonopods remain separate from each other and from the hypandrium, but fusion of the gonocoxal portions with each other and often with the hypandrium, appears to have occurred independently numerous times within the order (Wood 1991) (see **gonocoxite** and **gonostylus**).

gonostylus (clasper, distimere, dististyle, telomere, stylus) (Figs 66–73): the distal articulated clasping lobe of the two-segmented gonopod, usually positioned on the apical margin of the goncoxite, but retracted to a subapical position in Asiloidea *sensu* Sinclair *et al*. (1994). It is subdivided into two branches in most Tipulidae (Ribeiro 2006) and sometimes bears thickened setae (rostral spines) basally. Gonostyli are hypothesised by Sinclair (2000: 54) and Sinclair & Cumming (2006) to be absent in Eremoneura (Empidoidea and Cyclorrhapha) (see **postgonite** concerning use of gonostylus in Cyclorrhapha).

harpes, see **distiphallus**.

hypandrial arms (gonocoxal arms) (Figs 83, 84): dorsal extensions of the hypandrium (composite gonocoxal-hypandrial sclerite) in Schizophora, which articulate with the base of the bacilliform sclerites.

hypandrium (sternite 9, ventral sclerite) (Figs 68, 70, 71, 73–85, 88): sternite 9 of the male genital segment; fused laterally with the epandrium (tergite 9) and separate from the gonopods (gonocoxites) in the groundplan of Diptera (Wood 1991). In some orthorrhaphous Brachycera and all Eremoneura (Empidoidea and Cyclorrhapha), the hypandrium and gonocoxites are indistinguishably fused together; in these groups this entire ventral composite structure is referred to as the hypandrium following Sinclair *et al*. (1994) and Cumming *et al*. (1995).

hypophallus, see **distiphallus**.

hypoproct (decasternum, opisthophallus, paraproct, sternite 10) (Figs 68, 69, 72, 73, 79, 80, 83, 84): the midventral sclerite of the proctiger, positioned between the lateral cerci and continuous with the subepandrial membrane anteriorly (see **subepandrial membrane** and **subepandrial sclerite**).

hypopygium: the male genital capsule, made up of the copulatory structures of the primary genital segment (segment 9) and the proctiger; not to be confused with the terminalia that may also include modified adjoining anterior sclerites.

interbase, see **paramere**.

juxta, see **distiphallus**.

lateral ejaculatory process (aedeagal dorso-anterior sclerite, external ejaculatory sclerite, lateral aedeagal apodeme) (Fig. 71): one of a pair of sclerites of the brachyceran sperm pump, inserted laterally on the anterodorsal wall of the sperm sac; each lateral ejaculatory process supports a muscle that assists in compressing the pump (see **sperm pump**). Lateral ejaculatory processes are absent in most Stratiomyomorpha, Hilarimorphidae (non-Afrotropical), Apystomyiidae (non-Afrotropical) and Eremoneura (Empidoidea and Cyclorrhapha) (Sinclair *et al*. 2013).

median sclerite (aedeagus in Simuliidae): strap-like dorsal extension of the ventral plate that supports the floor of the membranous aedeagal sac in Simuliidae (see **ventral plate**).

mesophallus, see **distiphallus**.

parameral sheath, see **paramere** and **phallus**.

paramere (aedeagus in Culicidae, dorsal plate, paraphysis, phallus *sensu* Belkin (1968) in Dixidae, penis valve in Chaoboridae, tegmen in Blephariceridae) (Figs 67, 69, 71, 72): one of a pair of posteriorly directed processes each attached to a gonocoxal apodeme; in many groups parameres are fused to each other medially over the aedeagus to form a single plate. In Tipuloidea the dorsolateral portion of the paramere that connects to the gonocoxal apodeme is referred to as the **interbase**. The parameres in Brachycera form a covering termed the **parameral sheath** that partially surrounds the apex of the aedeagus (Figs 71, 72); in the Muscomorpha *sensu* Woodley (1989) and most Stratiomyomorpha this sheath is fused to the aedeagus to form a modified composite intromittent organ referred to as the phallus (see **phallus**).

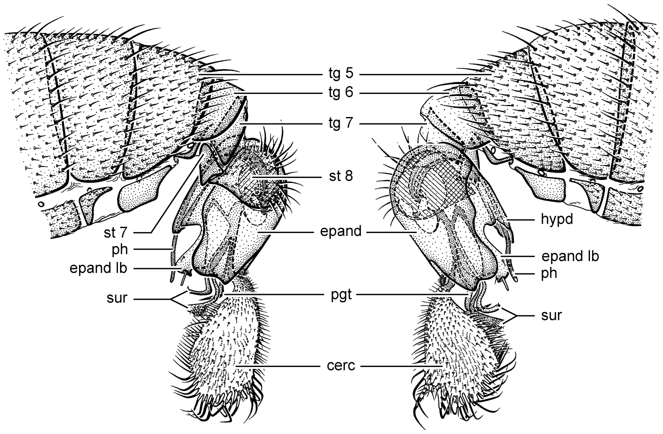
paraphallus, see **distiphallus**.

phallapodeme (aedeagal apodeme *sensu* authors concerning Cyclorrhapha) (Figs 80–83, 85, 88): novel structure in the Cyclorrhapha found in every major lineage, except Opetiidae (non-Afrotropical), which is derived from a median longitudinal invagination of the hypandrium (composite gonocoxal-hypandrial sclerite). In the basal cyclorrhaphan lineages the phallapodeme tends to surround and support the base of the phallus while remaining broadly connected to the hypandrium (*e.g.*, as in the platypezid *Microsania*); in Syrphoidea and Schizophora the phallapodeme is no longer extensively connected to the hypandrium and is typically a rod-like lever that assists in moving the base of the phallus and the postgonites; occasionally in some schizophoran families (*e.g.*, Diopsidae, most Tephritoidea), the anterior portion of the phallapodeme becomes secondarily fused to the hypandrium (see **phallic guide**).

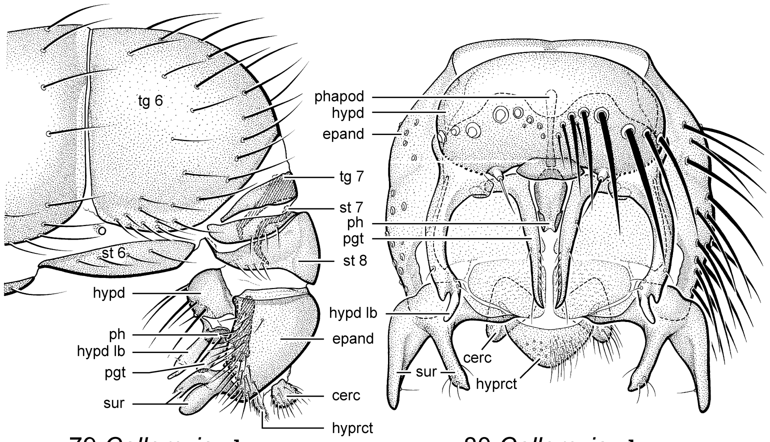
phallic guide (aedeagal guide, fulcrum *sensu* Roháček & Barber (2005) in Anthomyzidae, intermedium) (Figs 82, 85): general term for any ventromedial posteriorly directed lobe that is derived from the gonocoxites; in Cyclorrhapha it arises from the gonocoxal portion of the hypandrium and connects to the phallapodeme, or appears simply as a ventral extension of the phallapodeme.

phallic plate (aedeagal dorsal sclerite, ventral proctiger sclerite, "y" sclerite): in Eremoneura (Empidoidea and Cyclorrhapha), a short to long sclerotised extension of the base of the phallus towards the base of the subepandrial sclerite (or bacilliform sclerites) and the hypandrial arms; the phallic plate is extremely long in Neriidae and Micropezidae.

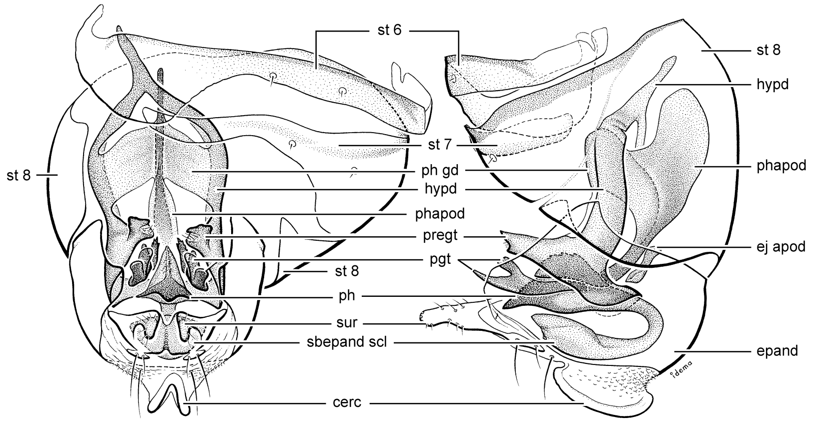
phallotrema (pl. **phallotremata**) (genital opening, secondary gonopore): external genital opening at the apex of the



77 *Dolichopus* ♂ 78 *Dolichopus* ♂



79 *Callomyia* ♂ 80 *Callomyia* ♂



81 *Neopiophila* ♂ 82 *Neopiophila* ♂

Figs 3.77–82. Male terminalia (continued): (77) left lateral view of *Dolichopus brevipennis* Meigen (Dolichopodidae); (78) same, right lateral view; (79) left lateral view of terminal segments of abdomen of *Callomyia* sp. (Platypezidae); (80) same, ventral view of terminalia; (81) ventral view of *Neopiophila setaluna* McAlpine (Piophilidae); (82) same, lateral view (all non-Afrotropical). Figs 77–82 (after McAlpine 1981, figs 128, 129, 132, 133, 135, 136).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epand lb – epandrial lobe; hypd – hypandrium; hypd lb – hypandrial lobe; hyprct – hypoproct; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; sbepand scl – subepandrial sclerite; st – sternite; sur – surstylus; tg – tergite.

aedeagus or phallus, as opposed to the **primary gonopore**, which opens into the sperm pump.

phallus (aedeagus *sensu* authors concerning Stratiomyomorpha and Muscomorpha *sensu* Woodley (1989)) (Figs 73, 75–85, 87, 88): the modified intromittent organ in the brachyceran lineages Stratiomyomorpha and Muscomorpha *sensu* Woodley (1989); the phallus is formed by the fusion of the parameral sheath and the aedeagus it encircles to produce a composite structure. In Cyclorrhapha the phallus is often subdivided into specialised regions referred to as the **basiphallus**, **epiphallus**, **distiphallus** and **acrophallus**.

postgonal apodeme (basal piece, Gelenkfortsatz, gonostylar apodeme): small subdivided sclerite at the base of the postgonite in most oestroid Calyptratae.

postgonite (gonostylus *sensu* Cumming *et al*. (1995) concerning Cyclorrhapha, opisthoparamer, paramere *sensu* McAlpine (1981: 53) concerning Eremoneura, paraphysis) (Figs 77–84, 87, 88): one of a pair of processes located near the base of the phallus in Eremoneura (Empidoidea and Cyclorrhapha), that are derived from the gonocoxal portion of the hypandrium (Sinclair 2000: 61; Sinclair & Cumming 2006); they are movably articulated at their base in Cyclorrhapha (except Opetiidae – non-Afrotropical), but partially fused to the hypandrium in most Empidoidea (for review of homology interpretations, see Sinclair 2000, table 1).

pregonite (proparamer, suspensory sclerite) (Figs 81, 82, 87, 88): one of a pair of lobes derived from the hypandrium (composite gonocoxal-hypandrial sclerite), in many Schizophora, positioned anteroventrally to the postgonites.

prensisetae (Fig. 85): short, stout teeth-like setae on the distal margin of the surstyli in certain acalyptrate groups, such as Drosophilidae and Tephritoidea.

primary gonopore, see under **phallotrema**.

proctiger, see above under Abdomen.

prosophallus, see **ventral plate**.

pseudocercus (pl. **pseudocerci**) (ventral epandrial lobe): apical subdivision of the epandrium found in some acalyptrate taxa (*e.g.*, some Sphaeroceridae) (see also **surstylus**).

rostral spine, see **gonostylus**.

saccus, see **distiphallus**.

sperm duct, see **sperm pump**.

sperm pump (genital vesica) (Figs 67, 68, 71–73, 82, 84, 85, 87, 88): in the groundplan of Diptera composed primarily of the **ejaculatory apodeme** (with its associated muscles) and the **sperm sac**; it is located between the ejaculatory duct(s) and the endophallus. In Cyclorrhapha (including Opetiidae – non-Afrotropical) and a few other non-cyclorrhaphan groups, the sperm pump is separated from the base of the phallus by a long **sperm duct** (Figs 85, 87, 88). The sperm pump is lost in Culicomorpha (Sinclair 2000: 71), correlated presumably with the transfer of preformed spermatophores in many of the included families.

sperm sac (endophallus *sensu* Bonhag (1951)) (Figs 85, 87): the membranous reservoir of the sperm pump.

stylus, see **distiphallus**.

subepandrial membrane: the membranous roof of the deeply invaginated pouch that separates the epandrium and proctiger from the gonopods and hypandrium; this intersegmental membrane extends from the hypoproct anteriorly to the anterodorsal margin of the paramere or parameral sheath (the Dorsal-Brücke *sensu* Hennig (1976)). An extensive sclerite, or pair of sclerites, develops in the subepandrial membrane in numerous families of lower Brachycera and all Eremoneura (Empidoidea and Cyclorrhapha) (see **subepandrial sclerite**).

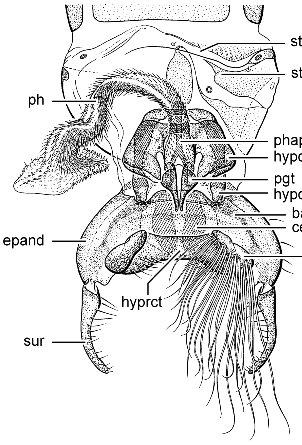
subepandrial sclerite (decasternum, mediandrium, sternite 10, ventral epandrial sclerite) (Figs 81–84, 88): the extensive sclerite, or pair of sclerites, that develop in the subepandrial membrane of many Brachycera. In the Eremoneura (Empidoidea and Cyclorrhapha) and the non-Afrotropical families Apsilocephalidae and Apystomyiidae, the subepandrial membrane is sclerotised along its entire length, so that the subepandrial sclerite articulates with the anterodorsal surface of the phallus; in these groups this sclerite contains a pair of rod-like extensions, termed bacilliform sclerites, that extend to the posterolateral corners of the epandrium, or to the base of the surstyli (see **bacilliform sclerite**).

surstylus (pl. **surstyli**) (außerer Forceps, gonostylus *sensu* Zatwarnicki (1996) concerning Eremoneura, inferior forceps, paralobe, paralobus, telomere *sensu* Griffiths (1972: 31) concerning Cyclorrhapha, valvula lateralis) (Figs 76–85, 87, 88): apical clasping lobe derived from a posterolateral outgrowth of the epandrium; the external surface of each surstylus is formed by the epandrium, whereas the inner surface is formed basally by the bacilliform sclerite. In some taxa each surstylus is divided into more than one lobe described by their position on the epandrium (*e.g.*, **lateral** *versus* **medial**, **outer** *versus* **inner**, **dorsal** *versus* **ventral**). Unlike other apical lobes of the epandrium (*e.g.*, pseudocercus, ventral epandrial lobe), each surstylus is abducted by the lever-like action of the bacilliform sclerite and adducted by a single muscle (Cumming *et al*. 1995). Although somewhat similar looking epandrial processes occur in a few nematocerous families (*e.g.*, Ptychopteridae, Psychodidae and Canthyloscelidae (non-Afrotropical)), true surstyli occur only in Eremoneura (Empidoidea and Cyclorrhapha) and in the non-Afrotropical families Apsilocephalidae and Apystomyiidae. They are usually clearly articulated lobes as in almost all Cyclorrhapha, but are only weakly articulated in some basal groups of Empidoidea and Apystomyiidae.

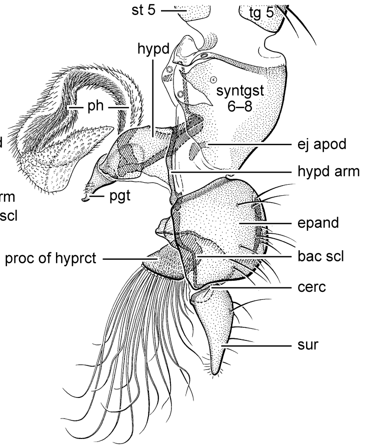
syncercus, see **cercus**.

syntergosternum (Fig. 86): a more or less symmetrical ring located between segments 5 and 9, or 6 and 9 in most Cyclorrhapha as a result of circumversion (*i.e.*, 360° genitalic rotation), composed of the distorted remnants of segments 6–8, or 7–8. The asymmetrical ring formed by the fusion of sternites 6–8 in many Schizophora, is referred to as the **annulus** (Lonsdale *et al*. 2010).

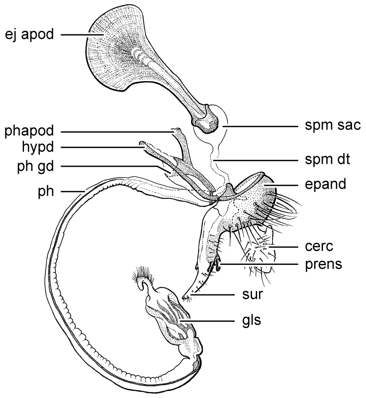
tegmen, see **paramere** and **ventral plate**.



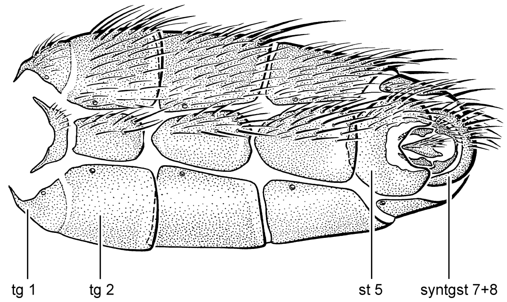
83 *Meoneura* ♂



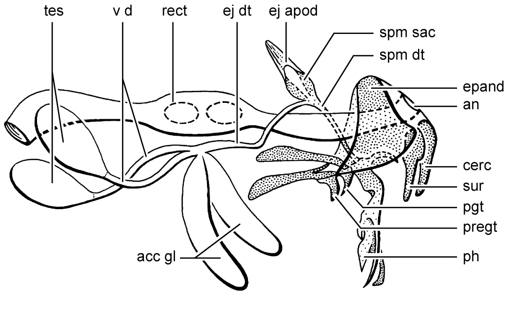
84 *Meoneura* ♂



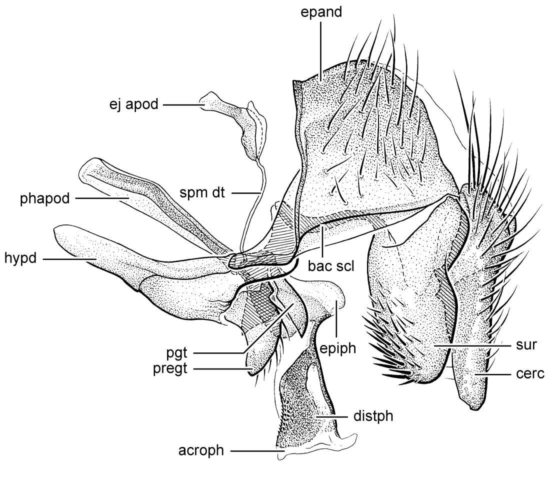
85 *Rhagoletis* ♂



86 *Melanophora* ♂



87 *Phormia* ♂



88 *Masistylum* ♂

Figs 3.83–88. Male abdomen and terminalia (concluded): (83) terminalia of *Meoneura obscurella* (Fallén) (Carnidae), ventral view; (84) same, lateral view; (85) terminalia of *Rhagoletis pomonella* (Walsh) (Tephritidae), lateral view; (86) abdomen of *Melanophora roralis* (L.) (Rhinophoridae), ventral view; (87) diagrammatic longitudinal section through genitalia and terminalia of *Phormia regina* (Meigen) (Calliphoridae); (88) terminalia of *Masistylum arcuatum* (Mik) (Tachinidae), lateral view (all non-Afrotropical). Figs 83, 84, (after Sabrosky 1987, figs 7, 8), Fig. 85 (after Foote & Steyskal 1987, fig. 41), Figs 86–88 (after McAlpine 1981, figs 137, 138, 141).

Abbreviations: acc gl – accessory gland; acroph – acrophallus; an – anus; bac scl – bacilliform sclerite; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; ej dt – ejaculatory duct; epand – epandrium; epiph – epiphallus; gls – glans; hypd – hypandrium; hypd arm – hypandrial arm; hyprct – hypoproct; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; prens – prensiseta; proc – process; rect – rectum; spm dt – sperm duct; spm sac – sperm sac; st – sternite; sur – surstylus; syntgst – syntergosternite; tes – testis; tg – tergite; v d – vas deferens.

tenacula (sing. **tenaculum**) (retinacula) (Fig. 68): stiff flattened setae on the inner apical surface of the clasper-like epandrium (see Sinclair *et al*. 2013) of many Psychodidae.

vas deferens (pl. **vasa deferentia**), see **ejaculatory duct**.

ventral appendage, see **ventral plate**.

ventral epandrial lobe, see **pseudocercus**.

ventral plate (aedeagus in Ceratopogonidae, **adminiculum** in Tipulidae, **claspettes** in Culicidae, prosophallus in Dixidae, tegmen, ventral appendage or **gonocoxal plate** in Thaumaleidae, volsellae in Chironomidae) (Fig. 69): medial ventral structure in Culicomorpha that is derived from the gonocoxites; often a single medial plate, but clearly divided and furnished with hooks in some taxa (Culicidae and most Chironomidae); absent in Corethrellidae and Chaoboridae. The ventral plate is articulated in the Chironomoidea (exclusive of Thaumaleidae), when present, where it assists to enlarge the female genital chamber, prior to the transfer of a preformed spermatophore (Wood & Borkent 1989). A similar structure sometimes referred to as the tegmen occurs in Sciaridae.

vesica, see **distiphallus**.

volsella, see **ventral plate**.

Literature cited

Adler, P.H., Currie, D.C. & Wood, D.M. 2004. *The black flies (Simuliidae) of North America*. New York: Cornell University Press, Ithaca.

Barraclough, D.A. 1995. An illlustrated identification key to the acalyptrate fly families (Diptera: Schizophora) occurring in southern Africa. *Annals of the Natal Museum* **36**: 97–133.

Belkin, J.N. 1968. Mosquito studies (Diptera, Culicidae). VII. The Culicidae of New Zealand. *Contributions of the American Entomological Institute* **3**: 1–182.

Bletchly, J.D. 1954. The mouthparts of the dance fly, *Empis livida* L. (Diptera, Empididae). *Proceedings of the Zoological Society of London* **124**: 317–334.

Bonhag, P.F. 1951. The skeleto-muscular mechanism of the head and abdomen of the adult horsefly (Diptera: Tabanidae). *Transactions of the American Entomological Society* **77**: 131–202.

Brooks, A.R. 1945. The genus *Girschneria* Townsend (Diptera, Tachinidae). *The Canadian Entomologist* **77**: 184–185.

Brown, B.V. 1992. Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridea). *Memoirs of the Entomological Society of Canada* **164**: 1–144.

Byers, G.W. 1989. Homologies in wing venation of primitive Diptera and Mecoptera. *Proceedings of the Entomological Society of Washington* **91**: 497–501.

Cumming, J.M. & Wood, D.M. 2009. 2. Adult morphology and terminology. *In*: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A., eds, *Manual of Central American Diptera. Volume 1*. Ottawa: NRC Research Press, pp. 9–50.

Cumming, J.M., Sinclair, B.J. & Wood, D.M. 1995. Homology and phylogenetic implications of male genitalia in Diptera – Eremoneura. *Entomologica scandinavica* **26**: 121–151.

Disney, R.H.L. 2004. Genera resembling *Beckerina* Malloch (Diptera: Phoridae). *Zootaxa* **518**: 1–28.

Foote, R.H. & Steyskal, G.C. 1987. 66. Tephritidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 2*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **28**, pp. 817–831.

Freidberg, A. & Beschoski, V. 1996. A new species group within *Tethina* Haliday (Diptera: Tethinidae) with description of six new Mediterranean species. *Israel Journal of Entomology* **30**: 91–113.

Giroux, M., Pape, T. & Wheeler, T.A. 2010. Towards a phylogeny of the flesh flies (Diptera: Sarcophagidae): morphology and phylogenetic implications of the acrophallus in the subfamily Sarcophaginae. *Zoological Journal of the Linnean Society* **158**: 740–778.

Griffiths, G.C.D. 1972. *The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen*. Series entomologica 8. The Hague: Dr. W. Junk Publishers.

Griffiths, G.C.D. 1996. Review of the papers on the male genitalia of Diptera by D.M. Wood and associates. *Studia dipterologica* **3**: 107–123.

Hall, D.G. 1948. *The blowflies of North America*. Thomas Say Foundation. Volume 4. Entomological Society of America, Baltimore.

Hennig, W. 1973. Diptera (Zweiflügler). *In*: Helmcke, J.-G., Starck, D. & Wermuth, H., eds, *Handbuch der Zoologie*. Band 4, 2. Hälfte, 2. Teil, Nr. 31 (Lieferung 20). Berlin–New York: Walter de Gruyter, pp. 337.

Hennig, W. 1976. Das hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). *Stuttgarter Beiträge zur Naturkunde* **283**: 1–63.

James, M.T. & Turner, W.J. 1981. 33. Rhagionidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 483–488.

Jobling, B. 1976. On the fascicle of blood-sucking Diptera. In addition a description of the maxillary glands in *Phlebotomus papatasi*, together with the musculature of the labium and pulsatory organ of both the latter species and also of some other Diptera. *Journal of Natural History* **10**: 457–461.

Kotrba, M. 2000. 1.3. Morphology and terminology of the female postabdomen. *In*: Papp, L. & Darvas, B., eds, *Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance). Volume 1. General and applied dipterology*. Budapest: Science Herald, pp. 75–84.

Lonsdale, O. & Marshall, S.A. 2012. *Sobarocephala* (Diptera: Clusiidae: Sobarocesphalinae) – subgeneric classification and revision of the New World species. *Zootaxa* **3370**: 1–307.

Lonsdale, O., Marshall, S.A., Fu, J. & Wiegmann, B. 2010. Phylogenetic analysis of the druid flies (Diptera: Schizophora:

Clusiidae) based on morphological and molecular data. *Insect Systematics and Evolution* **41**: 231–274.

Matile, L. 1990. Recherches sur la systématique et l'évolution des Keroplatidae (Diptera, Mycetophiloidea). *Mémoires du Muséum national d'histoire naturelle, Série A, Zoologie* **148**: 1–682.

McAlpine, D.K. 2011. Observations on the antennal morphology in Diptera, with particular reference to the articular surfaces between segments 2 and 3 in the Cyclorrhapha. *Records of the Australian Museum* **63**: 113–166.

McAlpine, J.F. 1981. 2. Morphology and terminology – adults. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 9–63.

Merz, B. & Haenni, J.-P. 2000. 1.1. Morphology and terminology of adult Diptera (other than terminalia). *In*: Papp, L. & Darvas, B., eds, *Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance). Volume 1. General and applied dipterology*. Budapest: Science Herald, pp. 21–51.

Michelsen, V. 1996. Neodiptera: new insights into the adult morphology and higher level phylogeny of Diptera (Insecta). *Zoological Journal of the Linnean Society* **117**: 71–102.

Nichols, S.W. 1989. *The Torre-Bueno glossary of entomology*. New York: New York Entomological Society.

Nowakowski, J.T. 1973. Monographie der europäischen Arten der Gattung *Cerodontha* Rond. (Diptera, Agromyzidae). *Annales zoologici, Warszawa* **31**: 1–327.

Peterson, B.V. 1981. 27. Simuliidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 355–391.

Quate, L.W. & Vockeroth, J.R. 1981. 17. Psychodidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 293–300.

Ribeiro, G.C. 2006. Homology of the gonostylus parts in crane flies, with emphasis on the families Tipulidae and Limoniidae (Diptera, Tipulomorpha). *Zootaxa* **1110**: 47–57.

Roback, S.S. 1954. The evolution and taxonomy of the Sarcophaginae (Diptera: Sarcophagidae). *Illinois Biological Monograph* **23**: 1–181.

Röder, G. 1984. *Morphologische Untersuchungen an Praetarsen von Diptera und Mecoptera (Insecta).* PhD dissertation, Naturwissenschaftlichen Fakultäten der Friedrich-Alexander-Universität, Erlangen-Nürnberg. [Unpublished].

Röder, G. 1986. Zur Morphologie des Praetarsus der Diptera und Mecoptera. *Zoologische Jahrbücher Anatomie* **114**: 465–502.

Roháček, J. & Barber, K.N. 2005. Revision of the New World species of *Stiphrosoma* Czerny (Diptera: Anthomyzidae). *Beiträge zur Entomologie* **55**: 1–107.

Sabrosky, C.W. 1987. 80. Carnidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 2*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **28**, pp. 909–912.

Saigusa, T. 2006. *Homology of wing venation of Diptera*. Fukuoka. [Privately published].

Shcherbakov, D.E., Lukashevich, E.D. & Blagoderov, V.A. 1995. Triassic Diptera and initial radiation of the order. *An International Journal of Dipterological Research* **6**: 75–115.

Shewell, G.E. 1987. 106. Calliphoridae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 2*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **28**, pp. 1133–1145.

Sinclair, B.J. 2000. 1.2. Morphology and terminology of Diptera male terminalia. *In*: Papp, L. & Darvas, B., eds, *Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance). Volume 1. General and applied dipterology*. Budapest: Science Herald, pp. 53–74.

Sinclair, B.J. & Cumming, J.M. 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa* **1180**: 1–172.

Sinclair, B.J., Borkent, A. & Wood, D.M. 2007. The male genital tract and aedeagal components of the Diptera with a discussion of their phylogenetic significance. *Zoological Journal of the Linnean Society* **150**: 711–742.

Sinclair, B.J., Cumming, J.M. & Brooks, S.E. 2013. Male terminalia of Diptera (Insecta): a review of evolutionary trends, homology and phylogenetic implications. *Insect Systematics and Evolution* **44**: 373–415.

Sinclair, B.J., Cumming, J.M. & Wood, D.M. 1994 (1993). Homology and phylogenetic implications of male genitalia in Diptera – Lower Brachycera. *Entomologica scandinavica* **24**: 407–432.

Starý, J. 2008. The wing stalk in Diptera, with some notes on the higher-level phylogeny of the order. *European Journal of Entomology* **105**: 27–33.

Steyskal, G.C. 1984. A synoptic revision of the genus *Aciurina* Curran, 1932 (Diptera, Tephritidae). *Proceedings of the Entomological Society of Washington* **86**: 582–598.

Steyskal, G.C. & Knutson, L.V. 1981. 47. Empididae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 607–624.

Stoffolano, J.G., Jr., Woodley, N.E., Borkent, A. & Yin, L.R.S. 1988. Ultrastructual studies of the abdominal plaques of some Diptera. *Annals of the Entomological Society of America* **81**: 503–510.

Strickland, E.H. 1953. The ptilinal armature of flies (Diptera, Schizophora). *Canadian Journal of Zoology* **31**: 263–299.

Stuckenberg, B.R. 1999. Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. *Studia dipterologica* **6**: 33–48.

Stuckenberg, B.R. 2001. Pruning the tree: a critical review of classifications of the Homeodactyla (Diptera, Brachycera), with new perspectives and an alternate classification. *Studia dipterologica* **8**: 3–41.

Stuckenberg, B.R. 2004. Labial morphology in Blephariceridae (Diptera: Nematocera): a new interpretation with phylogenetic implications and a note on colocephaly. *African Invertebrates* **45**: 223–236.

Webb, D.W. 1981. 32. Athericidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 479–482.

White, I.M., Headrick, D.H., Norrbom, A.L. & Carroll, L.E. 1999. 33. Glossary. *In*: Aluja, M. & Norrbom, A.L., eds, *Fruit flies (Tephritidae): phylogeny and evolution of behavior*. Boca Raton: CRC Press, pp. 881–924.

Winterton, S.L., Merritt, D.J., O'Toole, A., Yeates, D.K. & Irwin, M.E. 1999. Morphology and histology of the spermathecal sac, a novel structure in the female reproductive system of Therevidae (Diptera: Asiloidea). *International Journal of Insect Morphology and Embryology* **28**: 273–279.

Wood, D.M. 1991. Homology and phylogenetic implications of male genitalia in Diptera. The groundplan. *In*: Weismann, L., Országh, I. & Pont, A.C., eds, *Proceedings of the Second International Congress of Dipterology*. The Hague: SPB Academic Publishing, pp. 255–284.

Wood, D.M. & Borkent, A. 1989. 114. Phylogeny and classification of the Nematocera. *In*: McAlpine, J.F., ed., *Manual of Nearctic Diptera. Volume 3*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **32**, pp. 1333–1370.

Wood, G.C. 1981. 42. Asilidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M., coordinators, *Manual of Nearctic Diptera. Volume 1*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **27**, pp. 549–573.

Woodley, N.E. 1989. 115. Phylogeny and classification of the "Orthorrhaphous" Brachycera. *In*: McAlpine, J.F., ed., *Manual of Nearctic Diptera. Volume 3*. Ottawa: Research Branch, Agriculture Canada, Monograph No. **32**, pp. 1371–1395.

Wootton, R.J. & Ennos, A.R. 1989. The implications of function on the origin and homologies of the dipterous wing. *Systematic Entomology* **14**: 507–520.

Yeates, D.K. 1994. The cladistics and classification of the Bombyliidae (Diptera: Asiloidea). *Bulletin of the American Museum of Natural History* **219**: 1–191.

Zatwarnicki, T. 1996. A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* **7**: 103–175.