Manual of Nearctic Diptera

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Coordinated by

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INTRODUCTION

Scope. This chapter deals primarily with the skeletal morphology of adult flies, particularly as applied in identification and classification. A similar chapter on the immature stages, prepared by H. J. Teskey, follows. A major difficulty for the student of Diptera is the plethora of terminologies used by different workers. These variations have arisen because specialists have independently developed terminologies suitable for their own purposes with little concern for homologies. The terms and definitions adopted in this manual are based mainly on the works of Crampton (1942), Colless and McAlpine (1970), Mackerras (1970), Matsuda (1965, 1970, 1976), van Emden and Hennig (1970), Tuxen (1970), and Hennig (1973). The paper by Hennig (1973) is the most up-to-date and most comprehensive review of the anatomy of all stages of Diptera yet produced, and this work in particular should be consulted for many details and references that do not appear here. Some of the terms adopted are conventional and topographical rather than strictly morphological, but an attempt is made to apply terms consistently throughout the order. For example, the terms katepisternum and paramere, both long employed in the Nematocera and some orthorrhaphous Brachycera, are adopted in the Muscomorpha (cyclorrhaphous Brachycera) in place of sternopleuron and postgonite, respectively. Such changes may cause some confusion for awhile, but the advantages of adopting a standard, universally acceptable terminology outweigh the short-term inconvenience.

Most of the morphological terms applied to adults throughout the manual are listed and defined in this chapter. However, additional ones with restricted application are sometimes found in the various family sections. Preferred terms appear in boldface at first appearance, sometimes followed in parentheses by the corresponding singular (*sing.*) or plural (*pl.*) form in boldface and by common synonyms in lightface; this synonymy is not intended to be complete. There is no glossary, but all terms used in the manual are defined in the text and entered in the index. In the index, the page number for the principal entry appears in boldface. For terms not included in the index, the reader can consult comprehensive glossaries, such as those by Torre-Bueno (1937) and Tuxen (1970), and the taxonomic glossary for mosquitoes by Knight (1970), Knight and Laffoon (1970a, 1970b, 1970c, 1971), and Laffoon and Knight (1971).

Orientation and relationship of parts. A fly is basically a bilaterally symmetric, horizontally oriented, for-wardly progressing animal. Its body can be divided into three primary anatomical planes oriented at right angles to each other (Fig. 1): *sagittal* (vertical longitudinal) *planes*, the median one of which passes through the central axis of the body; *horizontal planes*, also parallel to the long axis; and *transverse planes*, at right angles to the long axis and to the other two planes. The head end is *anterior* or *cephalic*, and the hind end is *posterior* or *caudal*; the upper surface is *dorsal*, and the lower one is *ventral*. A line traversing the surface of the body in the median sagittal plane is the *median line* (meson) and an area symmetrically disposed about it is the *median area*. An intermediate line or zone is termed *sublateral*, and the outer zone, including the side of the insect, is *lateral*. Structures lying farther from the median sagittal plane than do other structures are referred to as *lateral*, and those nearer this plane as *medial*. Similarly, parts of appendages and other attached structures that lie farther from the body are referred to as *distal* or *apical*, and those nearer to the body as *proximal* or *basal*. Many of these terms can be combined to give convenient descriptive words such as dorsolateral and anteroventral. Terms such as mesal for medial, and mesad, laterad, and distad for medially, laterally, and distally, are often found in entomological works, but as stated by Mackerras (1970) there is no good reason for using them.

All terms are used in relation to the morphologically horizontal position of the insect with its legs and wings fully extended laterally, regardless of its particular attitude. Consequently, care must be taken in defining surfaces and bristles, especially those of the legs (Fig. 1).

General organization. As in all insects, the body of an adult fly is divided into three familiar regions, *head*, *thorax*, and *abdomen*, each with its specially modified *appendages* (Figs. 2, 3). The segmentation of the insect head is controversial; a review of various theories is presented by Matsuda (1965). The head is usually considered to consist of three *preoral segments*, namely an *acron*, an *antennal segment*, and an *intercalary segment*; and three *gnathal* (postoral) *segments*, namely a *mandibular*, a *maxillary*, and a *labial segment*. The thorax consists of three primary segments, and the abdomen of 11. Sclerotization occurs in dorsal and ventral plates of each segment and extends from just anterior to each *intersegmental groove* for a varying distance toward the posterior end of the segment (Figs. 5, 6). The entire dorsum of a segment is referred to as the *tergum*, and the entire venter, as the *sternum*. The terms *tergite* and *sternite* were originally proposed for the sclerotized subdivisions (sclerites) of each surface, but they are now
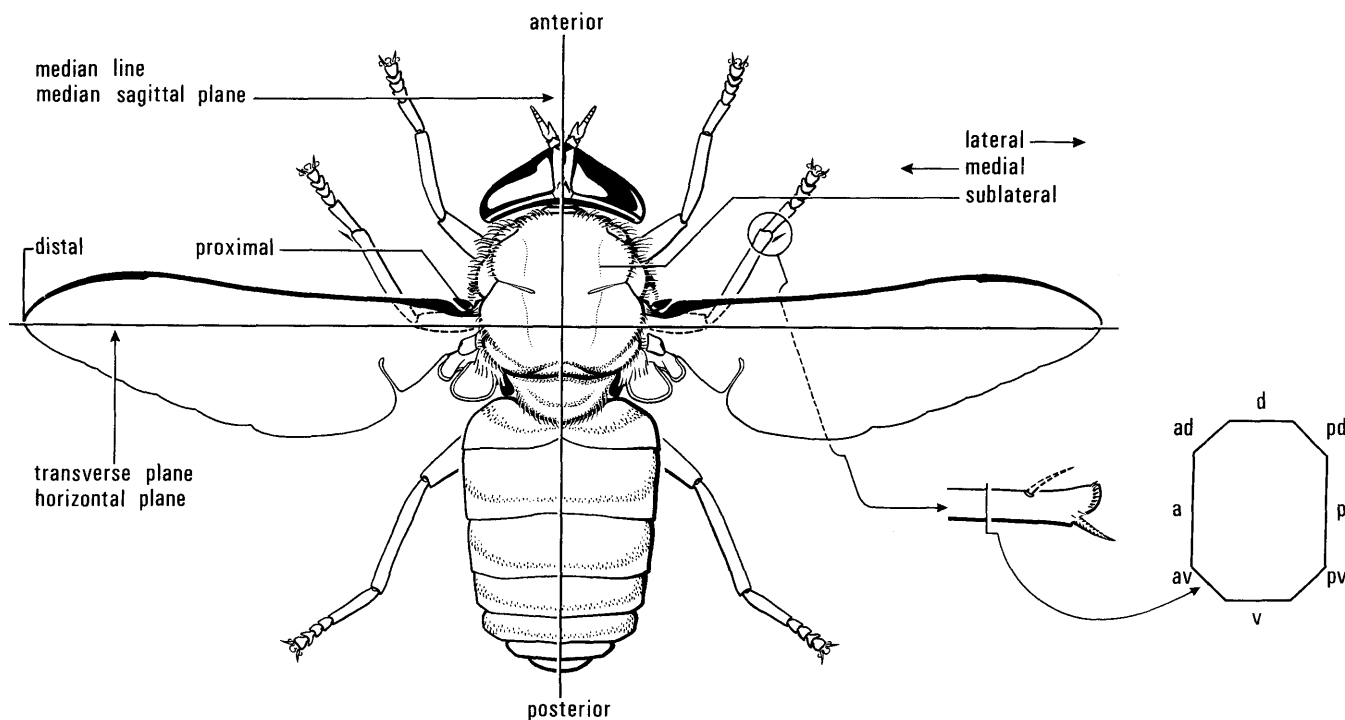
Fig. 2.1. A generalized fly, *Tabanus americanus* Forster, to show orientation and anatomical planes. *Inset:* Vertical section through distal portion of right mid tibia to show external surfaces.

Abbreviations: a, anterior; ad, anterodorsal; av, anteroventral; d, dorsal; p, posterior; pd, posterodorsal; pv, posteroventral; v, ventral.

commonly used almost synonymously with tergum and sternum. The unsclerotized part of the segmental *cuticle* between two adjacent tergal or sternal plates is the *intersegmental* or *conjunctival membrane* (Figs. 4, 5); it usually folds inwardly, and portions of it sometimes become sclerotized. In this way intersegmental sclerites arise and a secondary, functional segmentation may be imposed on the primary metameric segmentation (Figs. 5, 6). The preceding inflected part of each segment, called the *antecosta*, is indicated externally by the *antecostal suture*, and the sclerotized secondary strip anterior to this suture is the *acrotergite* dorsally and the *acrosternite* ventrally. Sclerotized infoldings called *apodemes* also develop and project into the body to add strength and to provide attachments for muscles. The apodemes arising from the antecostae of the mesonotum, metanotum, and first abdominal tergum are called *phragmata* (*sing. phragma*) (Fig. 7).

In the abdomen the side or *pleuron* (*pl. pleura*) of the body remains membranous. But in the thorax where greater rigidity is required, strengthening sclerites develop in the *pleural membrane*; these, together with the tergal and sternal plates, form a kind of box with precisely limited capacity for distortion. In the head, where little or no flexibility is needed, all the sclerites become fused into a single, strong *head capsule*.

Most appendages such as *antennae, palpi,* and *legs* are paired structures consisting of segmented tubes with flexible joints called *articulations* between the segments;

the *wings* and *halteres* are specialized outgrowths of the thorax. The *tracheae* of the respiratory system open at segmental *spiracles* on each side. Various parts of the *integument* may be more or less covered with *vestiture* of different kinds. *Macrotrichia* (*sing. macrotrichium*) or *setae* (*sing. seta*), which include *bristles, hairs,* and *setulae,* are connected with nerves and are surrounded at the base by a membranous ring or socket called an *alveolus* (*pl. alveoli*). *Microtrichia* are superficial extensions of the cuticle, such as the very fine hairs on wing membranes and the *pruinescence* (pollinosity) that dulls the surface of many sclerites. The disposition of bristles and hairs is called *chaetotaxy* (Figs. 65, 66) and it is extremely important in the taxonomy of flies. Likewise, the extent, intensity, and patterns of *pruinose* (pollinose) areas are often of taxonomic value. Markings of any sort that are broader than a line are usually referred to as *bands* if they are transverse, and *stripes* if they are longitudinal.

HEAD

Externally, the main parts of the head capsule (Figs. 8–11) are the *compound eyes*, the *genae* (*sing. gena*; bucca, cheek, jowl), and the *subgenae* laterally; the *vertex* (epicranium) dorsally; the *frons* (postfrons, front), *face* (prefrons), and *clypeus* (anteclypeus, prelabrum) anteriorly; and the *postcranium* (occiput), including the *occiput* above and the *postgenae* below, posteriorly. The *antennae* (*sing. antenna*) and *mouthparts* are
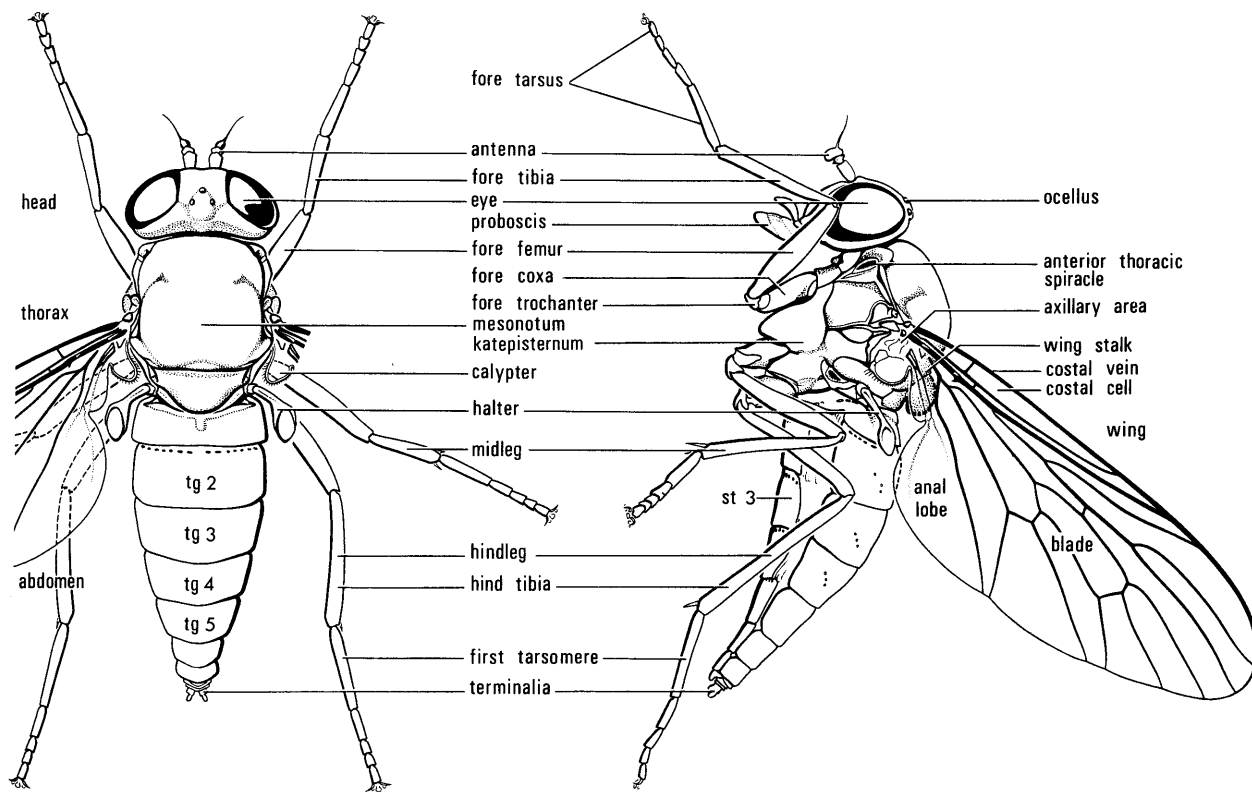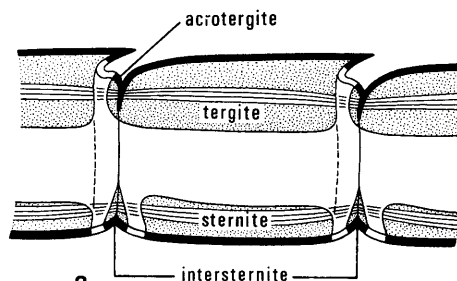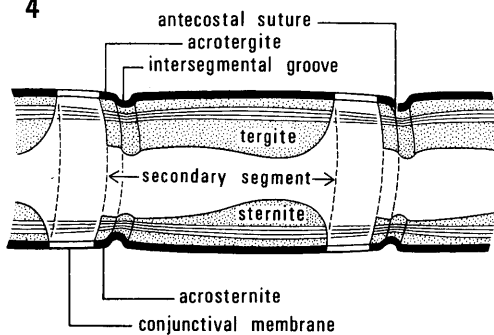
2 Symphoromyia montana ♀

3 Symphoromyia montana ♀
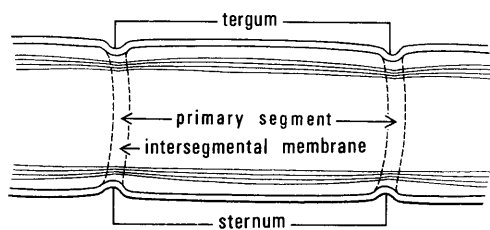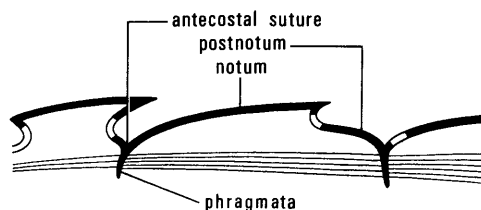
Figs. 2.2–7. Main divisions and parts of Diptera: (2) dorsal and (3) lateral view of *Symphoromyia montana* Aldrich, to show main anatomical divisions and parts; (4–7) diagrams of primary and secondary segmentation, based on Snodgrass (1935) and Matsuda (1970), showing (4) primary, (5) simple secondary, and (6) more advanced secondary segmentation and (7) dorsal sclerites of thorax in section.

Abbreviations: st, sternite; tg, tergite.

appendages. The parts of the head are defined principally by reference to the *occipital foramen* (through which pass the nerve cords, esophagus, aorta, and salivary ducts), the *ocelli* (*sing. ocellus*), the insertions of the antennae, the margins of the eyes, the *subcranial cavity* (oral cavity), and the *anterior tentorial pits*. The inner skeleton is formed by the *tentorium* (Fig. 51). Basically the tentorium consists of paired *anterior, dorsal*, and *posterior tentorial arms*. The anterior tentorial arms arise from the anterior tentorial pits and the posterior arms arise from the *posterior tentorial pits*. The dorsal tentorial arm is believed to be an outgrowth of the anterior arm (Matsuda 1965), which it joins near the junction of the anterior and posterior arms (Bonhag 1951). All three arms are frequently reduced and more or less consolidated in Diptera. In more primitive insects a median plate called the *corpotentorium* is sometimes formed between the two sides of the tentorium, but this plate is poorly developed or absent in Diptera. Likewise, in many insect groups the apices of the two posterior arms are fused medially, forming a *tentorial bridge* (Snodgrass 1935). This bridge also appears to be incomplete or absent in most Diptera. The anterior tentorial pits are sometimes poorly developed or absent, particularly in the Muscomorpha (cyclorrhaphous Brachycera); they are very large in some Nematocera, e.g. Culicidae, Chaoboridae (Fig. 24.4), and Chironomidae, and they are also easily seen in some Tabanomorpha, for example in the Tabanidae (Figs. 31.2–4). The posterior tentorial pits, at the ventral ends of the postoccipital suture, are usually less evident (Fig. 11).

Eye.   The eyes usually occupy most of the side of the head, but they may be greatly reduced or absent, especially in cavernicolous and some parasitic forms. When the eyes are so large that they meet or almost meet on the median line the condition is referred to as *holoptic* (Fig. 10), and when they are widely separate, as *dichoptic* (Fig. 8). The tendency toward a holoptic condition is usually restricted to the male, where it is associated with

swarming and aerial mating (McAlpine and Munroe 1968). Both the male and the female are holoptic in some members of some families, e.g. Blephariceridae, Thaumaleidae, Acroceridae, Bombyliidae, Empididae, and Pipunculidae, and they are nearly so in Synneuridae and in some Anthomyiidae. In some Nematocera, e.g. most Sciaridae (Fig. 15.4) and some Cecidomyiidae (Fig. 16.1), the eyes are narrowly connected by an *eye bridge*. Externally each eye consists of many *facets*, which are the corneas of individual *ommatidia* (*sing. ommatidium*). The upper facets may be larger than the lower ones and sometimes, e.g. Aulacigastridae, the anterior ones are larger than the posterior ones. Occasionally, as in some Blephariceridae (Fig. 8.1), Axymyiidae (Figs. 11.1–2), and in the cecidomyiid genus *Trisopsis* (Fig. 16.4), the eyes are divided into dorsal and ventral parts. Eye color varies considerably among species; a pattern of bands or patches of contrasting colors are often evident in life, as shown in the Tabanidae (Figs. 31.1–4). The spaces between the facets are often provided with fine hairs, which are frequently longer and denser in the male than in the female, especially in the Muscomorpha. Usually there are three ocelli in a triangular arrangement on a more or less distinct *ocellar triangle* (ocellar plate, vertical triangle) or *ocellar tubercle*; the anterior (median) ocellus, or the two posterior ocelli, or all three ocelli are sometimes absent. Some Chironomidae and Simuliidae, especially those with reduced compound eyes, have a small dark bulla near the posterior margin of the eye, e.g. *Oreadomyia albertae* Kevan & Cutten-Ali-Khan (Fig. 29.113) and *Twinnia* sp. (Fig. 27.2). This bulla is assumed to be a remnant of the larval eye; in the Simuliidae it is called a *stemmatic bulla*.

Vertex.   The median portion of the upper extremity of the head, bounded by the eyes laterally, the occiput posteriorly, and the frons anteriorly, is called the vertex (Figs. 9, 65). It is a relatively indefinite area, containing the ocellar triangle medially and, at least in the Mus-


Figs. 2.8–11. Head of *Hylemya alcathoe* (Walker): (8) anterior, (9) left lateral, and (11) posterior view of female; (10) anterior view of male. Note dichoptic condition of female (8) and holoptic condition of male (10).

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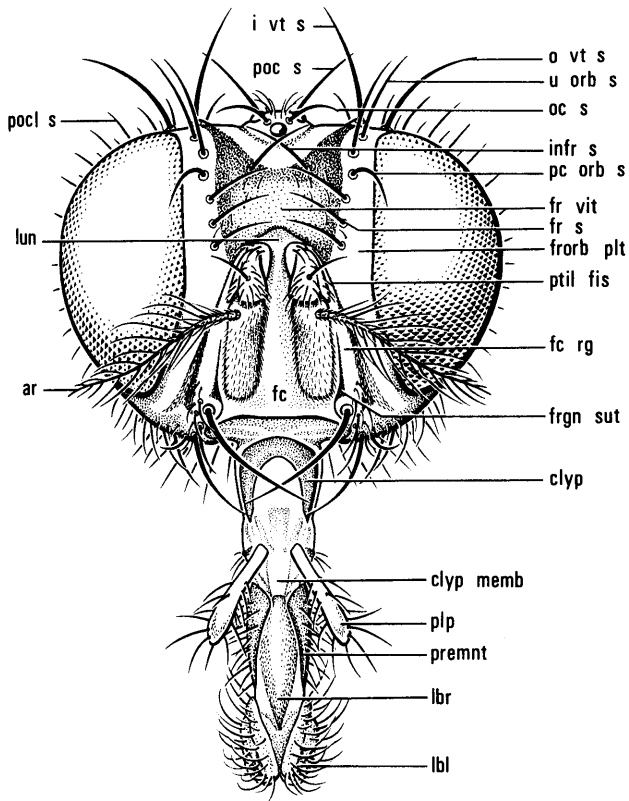
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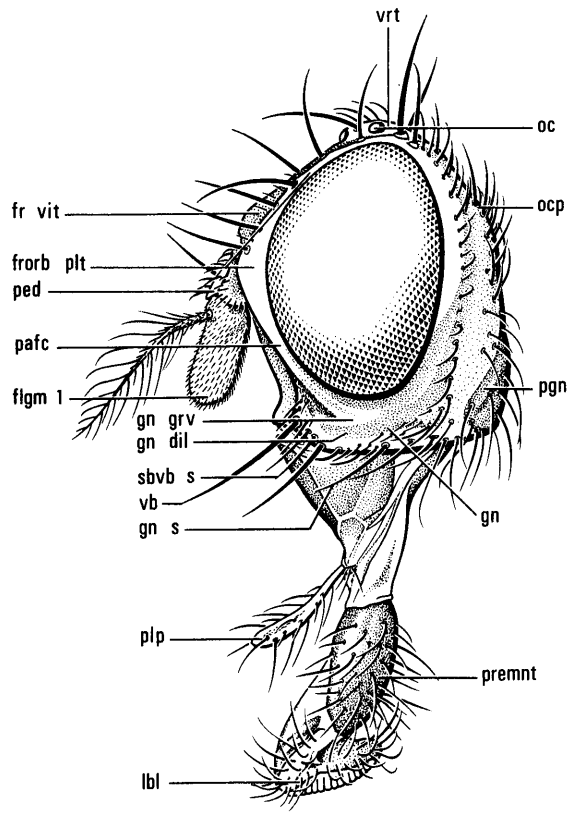
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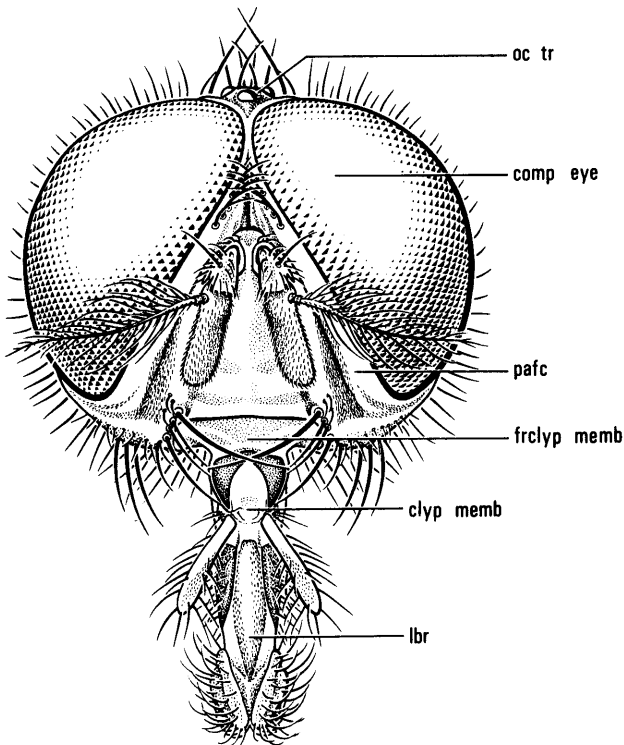
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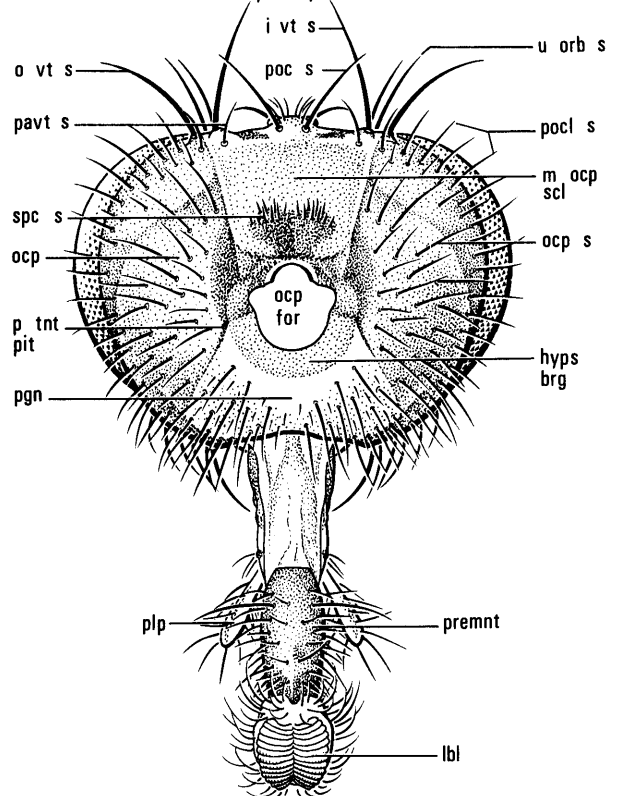
11 Hylemya alcathoe ♀

comorpha, the paired *orbital plates* (vertical plates) (*see* "Frons") laterally. In the Nematocera the term vertex is sometimes applied to most of the area here designated as the frons (*see* "Frons"). In many families, especially in the Muscomorpha (Figs. 8–11, 65, 66), *inner* and *outer vertical*, *paravertical*, and *postocellar bristles* are present; typically, *ocellar bristles* arise on the ocellar triangle near the anterior ocellus, but they are sometimes displaced. These bristles as well as those on the occiput in the higher Diptera were treated in detail by Steyskal (1976).

Frons.   In a generalized insect the frons extends from the vertex to the *frontoclypeal* (epistomal) *suture*, between the two anterior tentorial pits. These landmarks are not always clear, and some dipterists (de Meijere 1916, Hendel 1928, Crampton 1942, Hennig 1973) have adopted convenient topographical definitions of the frontal areas. The area dorsal to the insertions of the antennae (morphologically the postfrons) is usually called the frons, and the frontal area above the clypeus and below the antennae (morphologically the prefrons) is usually referred to as the face (*see* "Face").

In the Nematocera and orthorrhaphous Brachycera the frons is a simple, rather uniformly sclerotized plate, usually without specialized sclerites and bristles. In some Tabanomorpha, e.g. Tabanidae (Figs. 31.9–11), it has shining areas or *calli* (*sing. callus*), which are distinguished according to their positions as, for example, the *median callus*, the *basal callus*, and the *subcallus*. In the Muscomorpha the frons is of particular phylogenetic and systematic importance. In the Aschiza (Fig. 4.95) it is still uniformly sclerotized as in most lower Diptera, but in the Schizophora (Figs. 8, 10, 65) it has undergone characteristic modifications associated with the formation of a *ptilinum* (Hennig 1973). The ptilinum, which has been secondarily lost in some Sciomyzidae, is a peculiar, invaginated, sac-like organ armed with small scales (Strickland 1953), and it lies immediately above the bases of the antennae. It is everted with pulsating motions during emergence of the adult and assists the adult to escape from its puparium and the surrounding substrate. The arcuate slit through which the ptilinum is everted is called the *ptilinal fissure* (Fig. 8); its lateral extremities nearly coincide with the upper limits of the frontogenal sutures (*see* "Face"). After emergence the ptilinum is retracted within the head capsule and is hidden from view, but its position is marked by the ptilinal fissure. A crescentic median plate lying between the ptilinal fissure and the bases of the antennae is called the *lunule* (Fig. 8). A transverse groove, suggestive of an incipient ptilinal fissure and outlining a lunule-like area, is evident in some Aschiza, e.g. some Syrphidae and Platypezidae, as well as in some lower Brachycera, e.g. some Xylophagidae (Figs. 34.7, 34.10), Stratiomyidae, Rhagionidae (Fig. 33.1), Athericidae (Figs. 32.2–3), and Tabanidae (Figs. 31.7–11, subcallus); although no ptilinum is present in these groups, the external area in question may bear

some relation to the lunule and ptilinal fissure in the Schizophora (Crampton 1942, p. 18). In the Schizophora the frons (exclusive of the ocellar triangle, treated under "Vertex") is differentiated into a relatively elastic, median *frontal vitta* (interfrons, mesofrons) and paired, lateral *fronto-orbital plates* (orbits, parafrontal plates) (Fig. 8). Primitively each fronto-orbital plate extends from the vertex to the lower extremity of the frons, e.g. Neriidae and Clusiidae (Fig. 4.114); but with progressive lateral extension of the membranous frontal vitta in some groups, e.g. Heleomyzidae, the lower portion of each fronto-orbital plate is virtually obliterated (Fig. 4.98). However, a broad *frontal plate* sometimes arises secondarily from the resclerotized lower lateral margin of the frons (Hennig 1973). Thus each fronto-orbital plate may be differentiated into an upper orbital plate continuous with the vertex and a lower frontal plate continuous with the *parafacials* (*see* "Face") (Fig. 4.99). In acalyptrate families the frontal plate is frequently very narrow or undifferentiated, e.g. Heleomyzidae (Figs. 4.98, 4.112), but where it is secondarily enlarged, e.g. Tephritidae, it is at least partially separated from the orbital plate (Fig. 4.99). In the Calyptratae both the orbital plate and the frontal plate are usually strongly developed, but they are fused and practically indistinguishable from each other (Figs. 8, 65).

The frontal vitta frequently bears *interfrontal setae* or *hairs* or both (Fig. 8); it may also have heavily sclerotized, sometimes bristled *interfrontal plates*, as in the Sphaeroceridae and the Milichiidae (Figs. 4.117, 4.143, 4.149). Bristles on the fronto-orbital plates can be referred to simply as *fronto-orbital setae* or *setulae*. For purposes of distinction, however, those on the orbital plate are called *orbital setae* or *setulae* (superior orbital setae or setulae), and those on the frontal plate are called *frontal setae* or *setulae* (inferior orbital setae or setulae). Orbital setae may be differentiated further as *upper* and *lower orbital setae*; they are usually reclinate, proclinate, or lateroclinate (Figs. 8, 65, 66). Similarly frontal setae may be differentiated as *upper* and *lower frontal setae*; they, too, may be reclinate, proclinate, lateroclinate, or inclinate (Figs. 8, 65, 66), but usually at least some of the stronger frontal setae are more or less inclinate. In acalyptrate families the frontal setae arise laterally to the orbital setae (Fig. 4.99), but in the Calyptratae the frontal setae usually arise medially to the orbital setae (Figs. 8, 65). In holoptic males (Fig. 10) and a few holoptic females throughout the order the frons is virtually obliterated; frequently in these cases the orbital setae are also lost.

Face.   The anteromedial portion of the head, bounded dorsally by the insertions of the antennae, ventrally by the frontoclypeal suture, and laterally by the eyes, is the face. In most Nematocera (Figs. 17.2–3, 24.4) and many orthorrhaphous Brachycera (Figs. 32.2–3), this sclerite is relatively small, and often what at first sight appears to be the face is in fact the clypeus. In blood-

sucking groups in which the clypeus is enlarged, e.g. Culicidae (Fig. 25.46), Ceratopogonidae (Figs. 28.46–47), Simuliidae (Figs. 27.3–6), and Tabanidae (Figs. 31.2–4), the face is practically obliterated. However, in a few Nematocera, e.g. Anisopodidae (Fig. 48) and Blephariceridae, the face is fairly large and exposed but not nearly so large as in most Asilomorpha (Figs. 40.2, 40.5) and Muscomorpha (Fig. 8). Its larger size in higher Diptera appears to be correlated with the development of a movable proboscis.

In most Diptera each side of the face is marked by a suture that runs dorsally from the anterior tentorial pit toward the base of the antenna. These grooves are the *frontogenal sutures* (Matsuda 1965) (Fig. 8), and the median *facial plate* lies between them. In addition, in the Schizophora the two arms of the ptilinal fissure run ventrally outside the frontogenal sutures and form the inner margins of the parafacials (Fig. 8). Each parafacial abuts the fronto-orbital plate dorsally and the gena ventrally. Lying between the inner margin of each parafacial and the corresponding frontogenal suture is a strip, often convex and usually narrow, called the *facial ridge* (vibrissal ridge). Each facial ridge fades out dorsally, but ventrally it terminates in a more or less angular prominence, the *vibrissal angle*, which frequently bears one or more strong bristles, the *vibrissae (sing. vibrissa*; oral vibrissae) (Figs. 8, 9, 66). Both the facial ridges and the parafacials may be bare or setose; in the Tachinidae, especially, setae which are frequently present on the facial ridge are called *supravibrissal setae* (Fig. 66). The median facial plate is usually bare, but it is haired in some groups. In the Asilidae and related families it sometimes bears a cluster of hairs and bristles called the *mystax* (Figs. 42.36–42). Frequently, especially in the Schizophora, the facial plate has a pair of longitudinal *antennal grooves* (foveae) separated by a median ridge, the *facial carina.* The facial carina may be continuous with the lunule, e.g. Lonchaeidae (Fig. 4.109). Sometimes, as in many Piophilidae, the facial plate is concave and membranous along the midline (Fig. 4.110). In other cases, e.g. Ephydridae, it is entirely sclerotized and prominently convex (Fig. 4.155); in some Syrphidae (Fig. 4.126) and a few acalyptrates (Fig. 4.112) it is tuberculate. The *lower facial margin* is sometimes called the epistoma, but this term should be avoided because it is ambiguous (Crampton 1942, pp. 16–17).

Clypeus. The clypeus lies between the face and the labrum, and it supports the cibarial dilator muscles. It is limited dorsally by the frontoclypeal suture and anteriorly by the *clypeolabral articulation.* In the Muscomorpha, the clypeus is reduced to a narrow, usually U-shaped sclerite that is separated from the lower margin of the face by a broad, flexible *frontoclypeal membrane* (Figs. 8, 10). In most Nematocera and many orthorrhaphous Brachycera the clypeus is a relatively large, shield-shaped sclerite occupying a facial rather than a subcranial position (Figs. 17.2–3, 24.4, 32.2–3).

In many representatives, especially those with well-developed piercing and sucking mouthparts, the clypeus is greatly enlarged at the expense of the face. In a few groups such as the Blephariceridae and some *Xylophagidae* (Fig. 34.7) (but not the Mycetophilidae, contrary to Crampton 1942), the clypeus is divided into a proximal *postclypeus* and a distal **anteclypeus.** Here the anteclypeus is more or less deflected under the face as in many higher Diptera, perhaps indicating that the peculiar U-shaped clypeus of the Muscomorpha is in fact derived from the anteclypeus only (Crampton 1942). Throughout the Muscomorpha the clypeus is firmly connected internally by means of lateral apodemes to the skeleton of the **cibarial pump** (Fig. 58). The entire stirrup-shaped structure, including the external U-shaped clypeus, is called the *fulcrum.*

The region between the lower margin of the eye and the subcranial cavity consists of the gena above (Fig. 9) and a narrow, usually hairless strip, the subgena, below. The **subgenal suture,** which begins at the anterior tentorial pit and runs posteroventrally, separates these two sclerites. Sometimes the two sclerites are collectively called the cheek. Anterodorsally the gena unites with the lower extremity of the fronto-orbital plate in lower Diptera (Figs. 15.2–3, 34.7) and with the facial ridge and the parafacial in the Muscomorpha (Figs. 8, 9). Both the gena and the subgena are more or less fused posteriorly where they join with the postgena (Fig. 9). The gena is usually haired and sometimes also bears outstanding **genal bristles,** which should not be confused with vibrissae (*see* "Face"). The setulae along the anteroventral margin of the gena are referred to as the **subvibrissal setae** or **setulae** (oral setae or setulae, peristomal hairs) (Figs. 9, 66). In the schizophorous Muscomorpha there is a weakened, often depressed and groove-like area near the ventral limits of the ptilinal suture and the juncture of the gena and the parafacial (Figs. 9, 66). This area is called the **genal groove** (cheek groove, facial impression, facial warp, mediana, transverse impression, vibrissarium). It is usually bare and is particularly conspicuous in the Calyptratae, where it distinctly separates the parafacial above from the gena below. In many muscoid flies the hairy, strongly sclerotized portion of the gena lying below the genal groove and extending forward toward the vibrissal angle is called the **genal dilation** (occipital dilation, metacephalon) (Figs. 9, 66). The subgena is usually very narrow and bare; its lower extremity forms the lateral margin of the subcranial cavity. In the Tipulomorpha the clypeus, genae, subgenae, and related structures are fused and elongated to form a snout-like **rostrum** (Fig. 64). The position of the palpi, which are always attached immediately below the distal edge of the head capsule, serves to indicate where elongation has taken place.

In groups with a more or less retractable proboscis, the lower surface of the head has a well-developed subcranial cavity for reception of the basal part of the proboscis. In the Nematocera and certain orthorrhaphous Brachycera this cavity is little more than a

depression, and in forms with typical piercing and sucking mouthparts, e.g. Culicidae, Ceratopogonidae, Simuliidae, and Tabanidae, it is absent. Likewise, it is relatively poorly developed in orthorrhaphous forms with rigidly fixed, projecting mouthparts, e.g. many Asilidae. On the other hand it is well developed in the Empididae and the Dolichopodidae. It is best developed, however, in the Muscomorpha, where it appears to be correlated with the development of the very mobile, jointed proboscis so characteristic of higher Diptera.

Postcranium. The entire posterior surface of the head capsule (Fig. 11) is the postcranium. It is usually rounded in outline and may be strongly convex as in most Nematocera, flattened as in most Muscomorpha, or concave as in the Bombyliidae and the Pipunculidae. The principal landmarks are the occipital foramen and the posterior tentorial pits. According to Snodgrass (1935, p. 112) the narrow rim of the occipital foramen is the *postocciput*; it is separated from the remainder of the postcranium by the *postoccipital suture*. The upper half of the postcranium, the occiput, merges ventrally with the postgenae, which occupy the portion of the postcranium below the occipital foramen. The occiput of many orthorrhaphous Brachycera and all Muscomorpha contains a distinct *median occipital sclerite* (epicephalon, cerebrale), the upper margin of which passes over the vertex into the ocellar triangle (Fig. 11). This sclerite is indistinct or absent in the Nematocera (Hendel 1928). According to Crampton (1942) the ventral closing of the head capsule is formed by the median approximation and fusion of the postgenae. The fused median area is called the *hypostomal bridge* (pseudogula). It is closed in most Diptera but apparently is open in at least some species of Tanyderidae and Anisopodidae (Crampton 1942, Figs. 2H and 2K). Exclusive of the bristles on the vertex (*see* "Vertex") the principal bristles on the occiput are the *postocular* and *occipital bristles* and the *supracervical setulae* (Fig. 11).
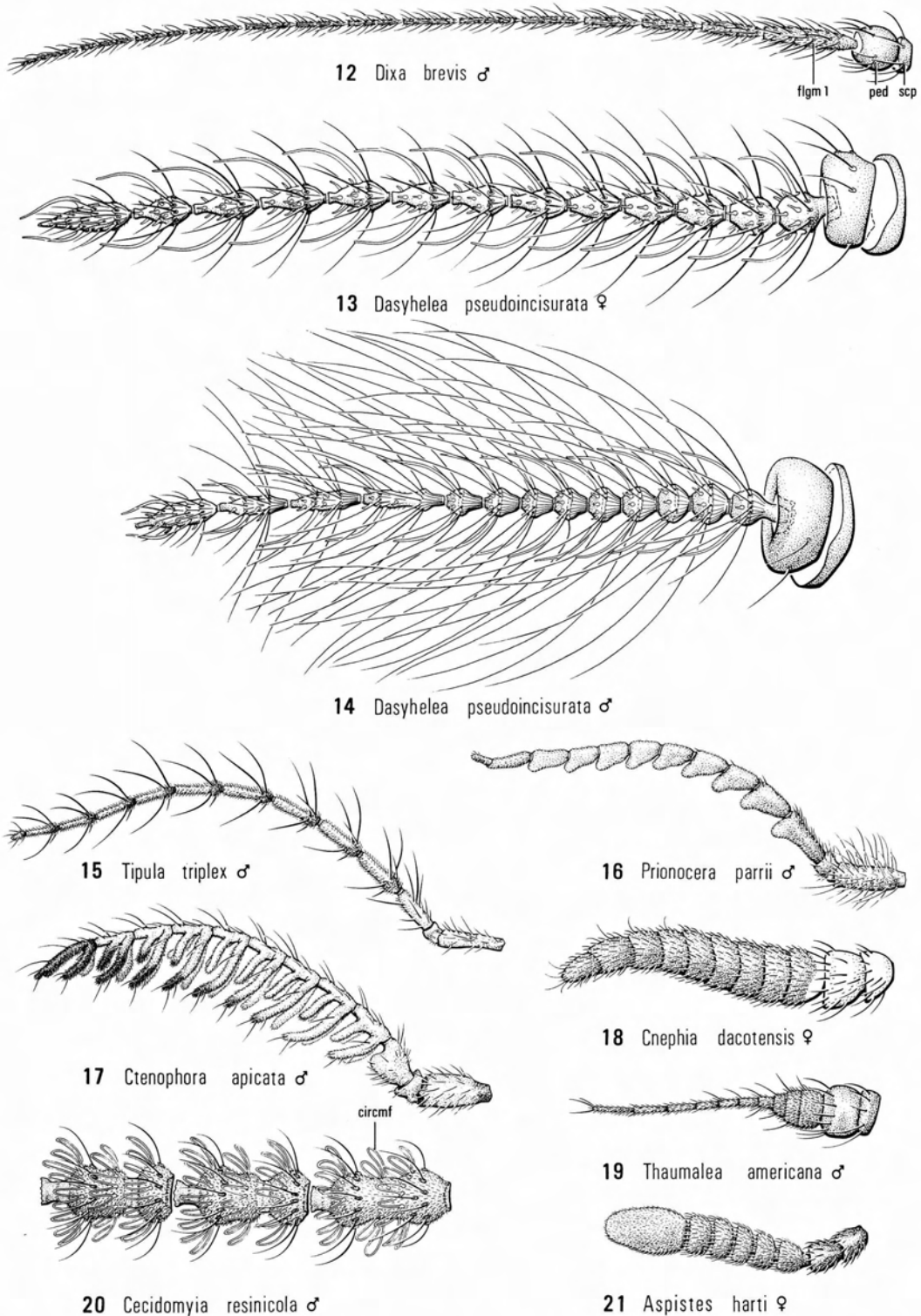
Antenna. The antennae are a pair of mobile, segmented, sensory appendages arising from membranous *antennal sockets* between the frons and the face. They vary extensively in structure (Figs. 12–45) and sometimes exhibit strong sexual dimorphism (Figs. 13, 14). They furnish excellent taxonomic characters and are much used in the classification of the Diptera. The basic number of antennal parts or segments is three. The basal segment is called the *scape*; the second segment, which encloses *Johnson's organ*, a mass of receptor cells for detecting movements of the flagellum, is called the *pedicel*; and the remaining part, which contains varying numbers of *flagellomeres*, is called the *flagellum* (Fig. 12). According to Hennig (1973) the basic number of flagellomeres is fourteen in the Nematocera (Figs. 12–21), eight in the primitive Brachycera (Figs. 22–30), three in the Asilomorpha (Figs. 31–36), and four in the Muscomorpha (Figs. 37–45). The scape is usually short and sometimes, as in the Culicidae and the Hippoboscidae, rudimentary. The pedicel may be enlarged as in

all Culicomorpha (Figs. 12–14) (except the Simuliidae) and in some Tabanidae, or it may be elongated as in many Conopidae (Fig. 38) and Sciomyzidae (Fig. 39); in the Calyptratae and some other Muscomorpha, it is marked dorsally by a longitudinal *antennal seam* (Figs. 43–45).

The flagellum is the most variable section. The thread-like form found in many Nematocera, e.g. Dixidae (Fig. 12), is called filiform; when the flagellomeres bear whorls of hairs as in the Culicomorpha (Figs. 13, 14), the antennae are called verticillate or plumose; if each flagellomere has one or more extensions as in certain Tipulidae (Figs. 16, 17), it is described as serrate or pectinate; if the flagellomeres are broad and flat, as in the mycetophilid genus *Keroplatus*, the antennae are said to be foliaceous. The nodose type occurring in many Nematocera, e.g. Cecidomyiidae, is called moniliform. Usually some or all of the flagellomeres bear sensory hairs, bristles, pegs, or related structures, or some combination of these. In many cecidomyiids they are provided with continuous thread-like sensoria called *circumfila* (*sing. circumfilum*) (Fig. 20).

In higher Diptera the first flagellomere (postpedicel) is usually enlarged and the distal segments are reduced to a *stylus* or an *arista* (Figs. 23–45). A stylus is usually rigid and either terminal or subterminal, whereas an arista is usually more slender and bristle-like, and may arise dorsally as well as apically. However, there is no sharp distinction between the two. An arista-bearing antenna is called aristate, and a stylus-bearing one is called stylate. The arista is dorsal if it arises on the top of the first flagellomere, and terminal if it arises at the apex; it may be bare, plumose, or pectinate according to the number and arrangement of the hairs it bears. The primary number of *aristomeres* in the Muscomorpha is three; in the Syrphoidea, however, it is usually reduced to two. Wherever an arista occurs in the lower Brachycera, e.g. some Stratiomyidae, Rhagionidae, Empididae, and Dolichopodidae, it is usually two-segmented. In stylate forms the segmentation is sometimes not apparent. The arista is occasionally greatly reduced or absent, as in the acalyptrate family Cryptochetidae and in the phorid genus *Abaristophora*.

Mouthparts. The mouthparts (Figs. 46–63) form a tubular sucking organ, the *proboscis*. In general there are two main types, the piercing and sucking type found in bloodsucking and predacious groups such as biting flies (Figs. 46, 47), Asilidae (Figs. 53, 54), and Empididae; and the lapping and sucking, nonbiting type found in the Anisopodidae (Figs. 48, 49), Tipulidae, Chironomidae, and Stratiomyidae and in most higher Diptera (Figs. 50–63). However, both these types vary considerably. Typically, the proboscis consists of three unpaired and two paired elements (Figs. 46, 47). The three unpaired elements are the *labrum* (labrum–epipharynx), forming the dorsal wall of the proboscis; the *labium*, forming the ventral wall of the proboscis; and

12 Dixa brevis ♂

flgm 1   ped scp

13 Dasyhelea pseudoincisurata ♀

14 Dasyhelea pseudoincisurata ♂

15 Tipula triplex ♂

16 Prionocera parrii ♂

17 Ctenophora apicata ♂

18 Cnephia dacotensis ♀

circmf

19 Thaumalea americana ♂

20 Cecidomyia resinicola ♂
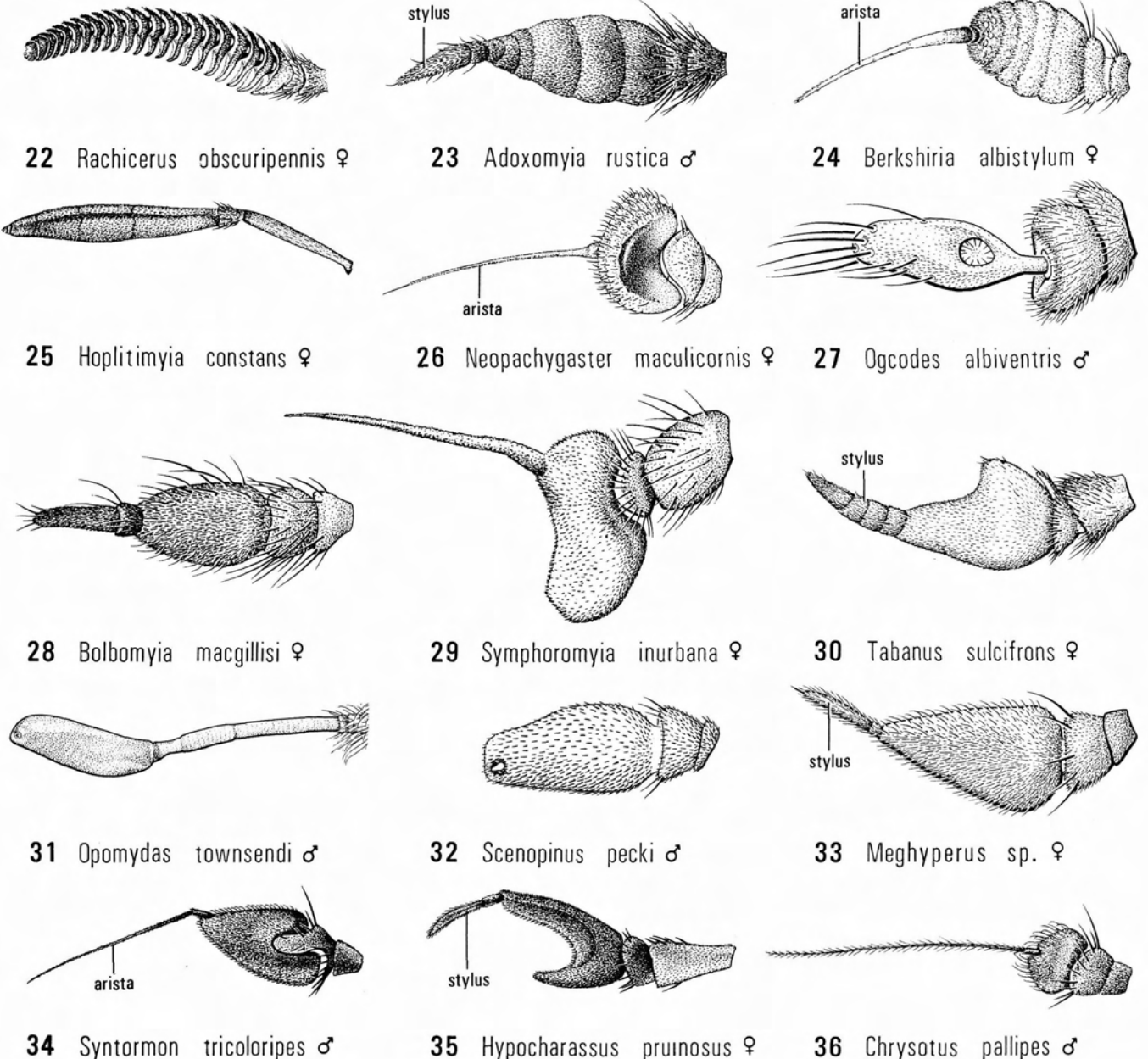
21 Aspistes harti ♀

Figs. 2.12–21. Left antennae of Nematocera, left lateral view: (12) *Dixa brevis* Garrett; (13) female and (14) male of *Dasyhelea pseudoincisurata* Waugh & Wirth; (15) *Tipula triplex* Walker; (16) *Prionocera parrii* (Kirby); (17) *Ctenophora apicata* Osten Sacken; (18) *Cnephia dacotensis* (Dyar & Shannon); (19) *Thaumalea americana* Bezzi; (20) *Cecidomyia resinicola* (Osten Sacken); (21) *Aspistes harti* Malloch.

Abbreviations: circmf, circumfilum; flgm, flagellomere; ped, pedicel; scp, scape.

the **hypopharynx**, projecting between the other two elements. The two paired elements, also arising between the labrum and the labium, are the **mandibles** anterolaterally and the **maxillae** (*sing.* **maxilla**) posterolaterally.

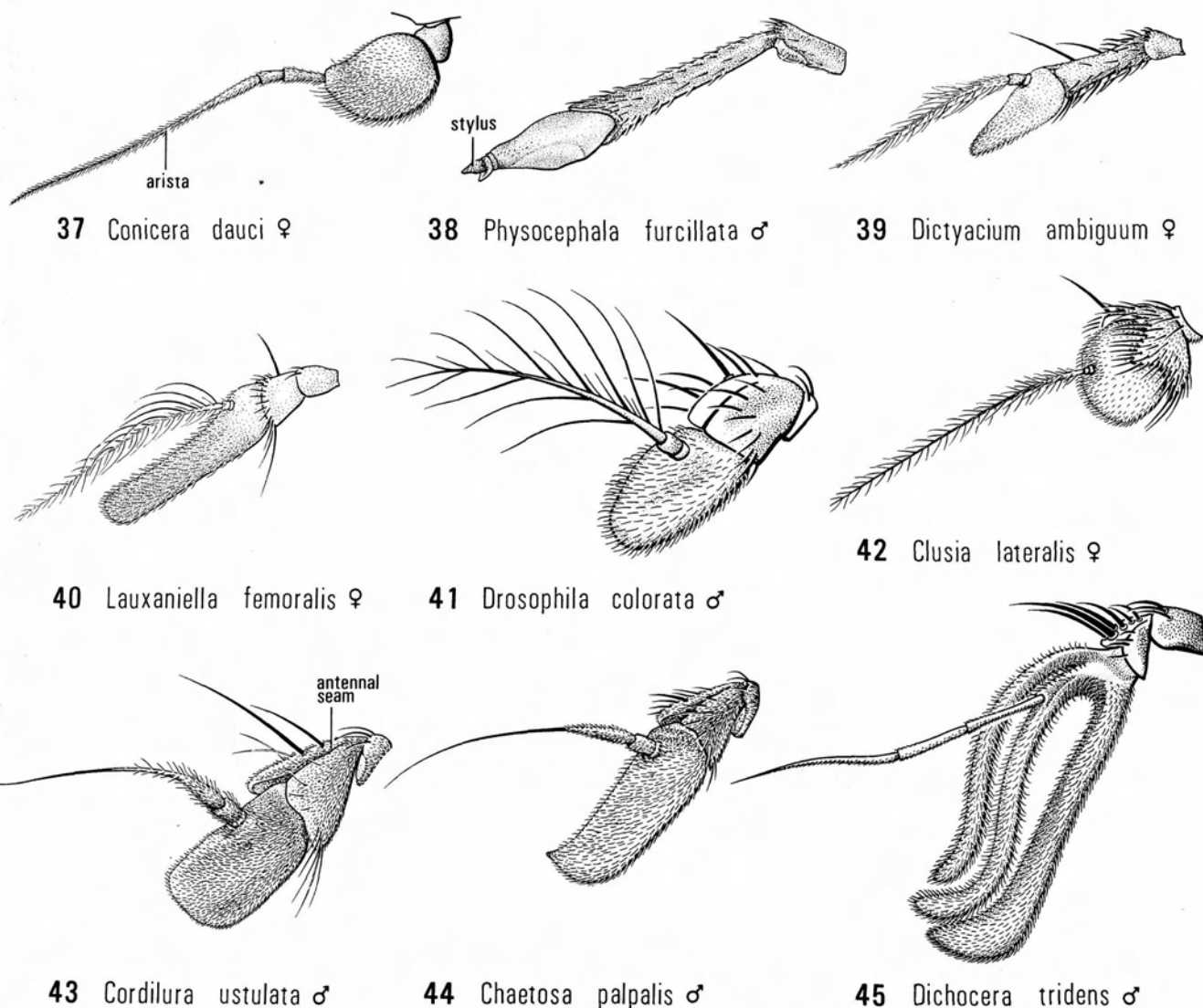The labrum is derived from a single preoral lobe (Snodgrass 1944), and although its ventral surface is frequently called the **epipharynx**, this structure is an integral part of the labrum. Situated on each side of the base of the epipharynx is a small sclerite called the **torma** (*pl.* **tormae**). It belongs to the epipharynx and connects with the clypeus at the lateral ends of the clypeolabral suture (Peterson 1916). Tormae are best developed in Nematocera and orthorrhaphous Brachycera that have mouthparts adapted for piercing, as in the Simuliidae (Fig. 27.8) and the Ceratopogonidae (Fig.

22 Rachicerus obscuripennis ♀   **23** Adoxomyia rustica ♂   **24** Berkshiria albistylum ♀

25 Hoplitimyia constans ♀   **26** Neopachygaster maculicornis ♀   **27** Ogcodes albiventris ♂

28 Bolbomyia macgillisi ♀   **29** Symphoromyia inurbana ♀   **30** Tabanus sulcifrons ♀

31 Opomydas townsendi ♂   **32** Scenopinus pecki ♂   **33** Meghyperus sp. ♀

34 Syntormon tricoloripes ♂   **35** Hypocharassus pruinosus ♀   **36** Chrysotus pallipes ♂

Figs. 2.22–36. Left antennae (except Fig. 34) of orthorrhaphous Brachycera, left lateral view: (22) *Rachicerus obscuripennis* Loew; (23) *Adoxomyia rustica* (Osten Sacken); (24) *Berkshiria albistylum* Johnson; (25) *Hoplitimyia constans* (Loew); (26) *Neopachygaster maculicornis* (Hine); (27) *Ogcodes albiventris* Johnson; (28) *Bolbomyia macgillisi* Chillcott; (29) *Symphoromyia inurbana* Aldrich; (30) *Tabanus sulcifrons* Macquart; (31) *Opomydas townsendi* (Williston); (32) *Scenopinus pecki* Kelsey; (33) *Meghyperus* sp.; (34) *Syntormon tricoloripes* Curran, right antenna, left side; (35) *Hypocharassus pruinosus* (Wheeler); (36) *Chrysotus pallipes* Loew.

28.46); they are usually not evident in higher Diptera. Peterson (1916) wrongfully interpreted the reduced clypeus in the Muscomorpha as tormae. Externally the labrum is hinged to the clypeus by the **clypeolabral suture** or **membrane**; internally its epipharyngeal surface forms the top of the **food canal**. The labrum is sometimes rather soft and membranous, as in *Rhabdophaga* (Cecidomyiidae), *Mycetobia* (Anisopodidae), *Chironomus*, and *Scenopinus*; small and flap-like, as in *Trichocera* and most Mycetophilidae; strongly sclerotized and blade-like, as in many bloodsucking and predacious flies; elongate with its sides curled ventromedially to form a closed food canal, as in the Culicidae (Fig. 47); moderately developed, as in most Muscomorpha (Figs. 55–60); or heavily sclerotized with strong, tooth-like projections laterally, as in the Dolichopodidae (Figs. 50–52). The hypopharynx forms the bottom of the food canal in most Diptera; it is usually stylet shaped and contains the **salivary canal**. In the Asilidae (Figs. 53, 54) it forms the piercing implement, like a hypodermic syringe, for injecting paralyzing saliva into prey. Internally at the bases of the labrum and the hypopharynx, especially in the Muscomorpha, are sometimes found two sclerites, a stirrup-shaped fulcrum proximally (its external, U-shaped dorsal plate forms the clypeus), and a crescentic **hyoid sclerite** distoventrally (Figs. 55, 59). Both are associated with the **cibarial pump** (food pump) at the base of the food canal. The apices of both the labrum and hypopharynx sometimes have tooth-like serrations in bloodsucking flies.

37 Conicera dauci ♀   **38** Physocephala furcillata ♂   **39** Dictyacium ambiguum ♀

40 Lauxaniella femoralis ♀   **41** Drosophila colorata ♂   **42** Clusia lateralis ♀

43 Cordilura ustulata ♂   **44** Chaetosa palpalis ♂   **45** Dichocera tridens ♂

Figs. 2.37–45. Left antennae of Muscomorpha, left lateral view: (37) *Conicera dauci* (Meigen); (38) *Physocephala furcillata* (Williston); (39) *Dictyacium ambiguum* (Loew); (40) *Lauxaniella femoralis* (Loew); (41) *Drosophila colorata* Walker; (42) *Clusia lateralis* (Walker); (43) *Cordilura ustulata* Zetterstedt; (44) *Chaetosa palpalis* (Coquillett); (45) *Dichocera tridens* (Walton).

Functional mandibles are found in the female only. They are usually flattened, blade-like structures, but in the Culicidae (Figs. 46, 47) they are slender and stylet-like. Frequently they are serrate along the median margins. Functional mandibles are present in the Tanyderidae, most Blephariceridae, and some Psychodidae; in most families of Culicomorpha, e.g. Dixidae, Culicidae, Ceratopogonidae, Simuliidae, and some Chaoboridae and Chironomidae; and in some Tabanoidea, e.g. Athericidae, Rhagionidae, and Tabanidae. Vestigial mandibles usually occur in the male of species in which the female has mandibles, but they are never functional. In the Tabanoidea, however, they are absent in the male and present in the female, only. No case is known where they are present in the male but absent in the female. When present in either sex they fit between the labrum and the hypopharynx (Fig. 47).

The maxillae are also stylet-like, but they retain more evidence of their derivation from primitive leg-like appendages and are therefore more complex than mandibles. Each maxilla is composed of a basal *cardo* and a distal *stipes*. The stipes bears the principal maxillary blade (endite). It has been interpreted by some authors (Crampton 1942, Snodgrass 1944) as the galea, but by others (Imms 1944, Wenk 1962, Hennig 1973) as the *lacinia*; the latter interpretation is adopted here. The stipes also bears a maxillary palpus, usually referred to as the palpus; it has five segments in many Nematocera, two in most orthorrhaphous Brachycera, and one in most Muscomorpha. The third segment bears a characteristic *sensory area*, which is invaginated as a *sensory pit* or *vesicle* in many Nematocera (Fig. 48). The entire palpus shows sexual dimorphism in several instances throughout the order and it is absent in certain representatives of many groups.

The labium, derived from a pair of united second maxillae (Snodgrass 1935), is the largest of the mouthparts. It usually forms a trough in which the other mouthparts lie. Basically it consists of a proximal *postmentum* (mentum of Crampton 1942) and a distal *prementum* (theca, part of haustellum of some authors). The postmentum is frequently greatly reduced or absent, but it is sometimes present as a distinct plate as in the anisopodid genus *Sylvicola*, and it is very long in the Chilean genus *Tanyderus*. The prementum is one of the most important of the labial sclerites. At its distal end it bears the *labella* (*sing. labellum*) derived from a pair of united two-segmented labial palpi; the two-segmented

condition is plesiomorphic and is most evident in primitive Nematocera, e.g. Blephariceridae and Tanyderidae. The labella usually consist of two membranous, cushion-like lobes. In the Brachycera, and perhaps rarely in the Nematocera (Hennig 1973), the inner surfaces of these lobes are furnished with varying numbers of small, sclerotized, trachea-like grooves called *pseudotracheae* (*sing. pseudotrachea*) (Figs. 58, 61–63), which radiate from the terminus of the food canal. These microcanals, best known in the Calliphoridae (Graham-Smith 1930), serve to distribute saliva and to take up dissolved food. In association with the pseudotracheae, many muscoid flies have developed small *prestomal teeth*, which are used as rasping structures for rupturing surfaces and breaking up food particles. In bloodsucking forms such as *Stomoxys* (Figs. 55–57) and *Glossina*, the labella are greatly reduced, but the prestomal teeth (Fig. 57) are relatively large and are the main implements used for piercing. In some forms, e.g. the tipulid genus *Geranomyia*, certain Blephariceridae, and the empidid species *Empis clausa* Coquillett, the labella are very long and slender. In other cases, e.g. the mycetophilid genus *Mycetophila*, they are extremely broad.

This discussion shows that although the mouthparts of all Diptera are primarily adapted for sucking up liquid or liquefied food, the components of the proboscis vary considerably among groups both in structure and in function. Even among the so-called biting flies with typical piercing and sucking mouthparts, there are marked differences in the ways the parts are inserted and are utilized during feeding. In bloodsucking Nematocera and tabanoids the actual incision is made by the stylet-like mandibles. In mosquitoes all six stylets, namely the labrum, the two mandibles and maxillae, and the hypopharynx, are inserted into the wound during feeding. In black flies, however, and probably also in some insectivorous ceratopogonids, the labrum is folded against the external surface of the host so that only five stylets are inserted into the wound. In predatory Dolichopodidae the sides of the labrum are armed with blade- and tooth-like processes, called the *epipharyngeal armature* (Fig. 51), that are presumably used for cutting and tearing tissues; in these species, also, the labrum is probably inserted into the wound during feeding.

In all the above forms the labium and the labella are not inserted. However, in higher Diptera such as *Stomoxys* and *Glossina*, the prestomal teeth of the labella


Figs. 2.46–52. Mouthparts of Culicidae, Anisopodidae, and Dolichopodidae: (46) *Aedes canadensis* (Theobald), anterior view, with parts displayed to show forms and relationships; (47) *Culex pipiens* Linnaeus, cross section through proboscis (after Hennig 1973); (48) *Sylvicola fenestralis* (Scopoli), anterior view; (49) *S. fenestralis*, cross section through proboscis; (50) *Condylostylus sipho* (Say), cross section through proboscis; (51) *C. sipho*, anterolateral view of proboscis showing relationship with cibarium and tentorium, with (52) enlargement of right epipharyngeal armature.

Abbreviations: ant soc, antennal socket; a tnt pit, anterior tentorial pit; cib, cibarium; clyp, clypeus; epiphar arm, epipharyngeal armature; fc, face; fd can, food canal; hyphar, hypopharynx; lab, labium; lbl, labellum; lbr, labrum; md, mandible; mx, maxilla; plp, palpus; sen pit, sensory pit; tnt, tentorium.
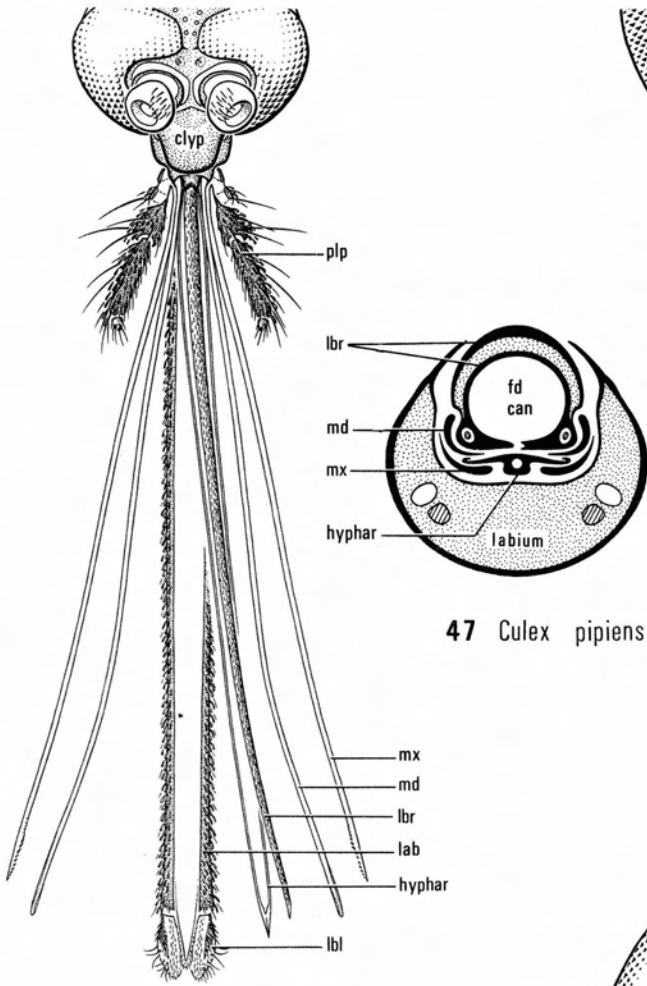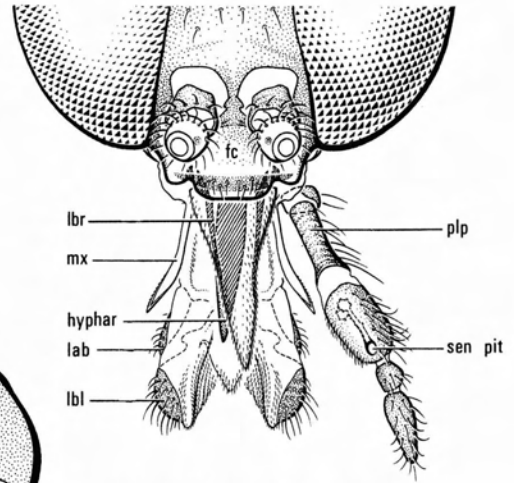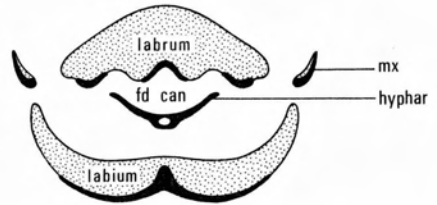
46 Aedes canadensis ♀
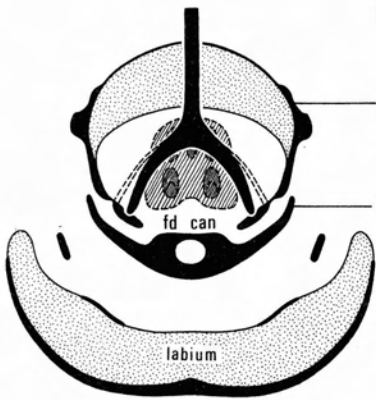
47 Culex pipiens ♀

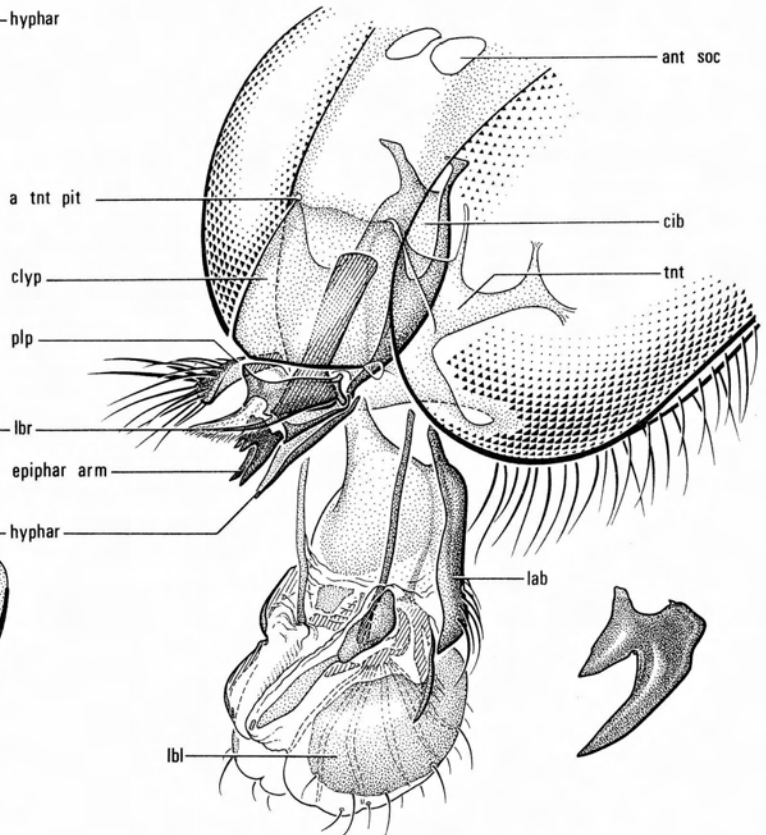**48** Sylvicola fenestralis ♀

49 Sylvicola fenestralis ♀

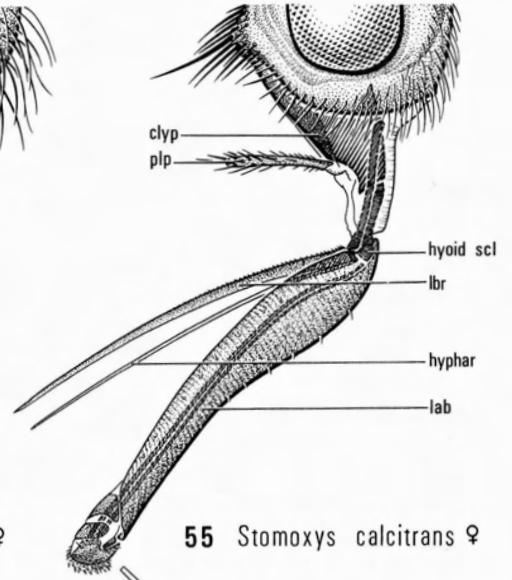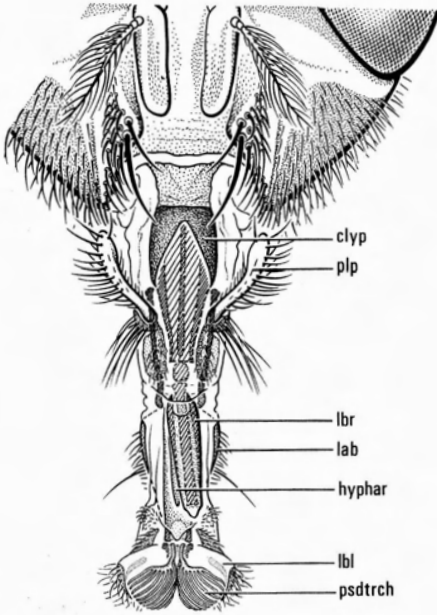**50** Condylostylus sipho ♀

51 Condylostylus sipho ♀ **52**
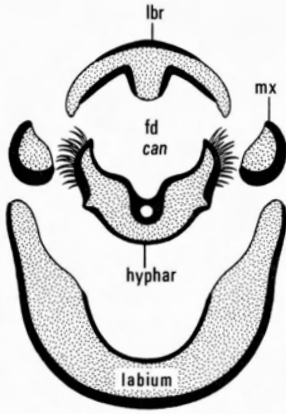
53 Laphria thoracica
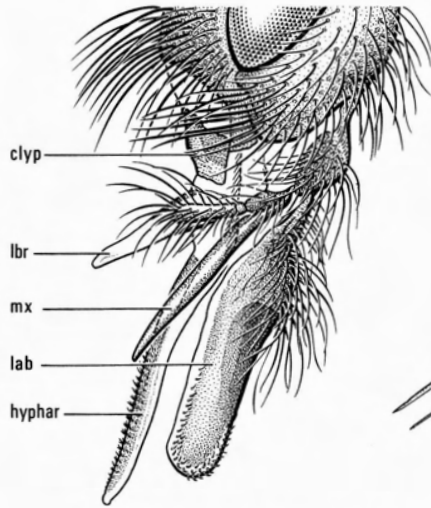
54 Laphria thoracica ♀

55 Stomoxys calcitrans ♀

56 Stomoxys calcitrans

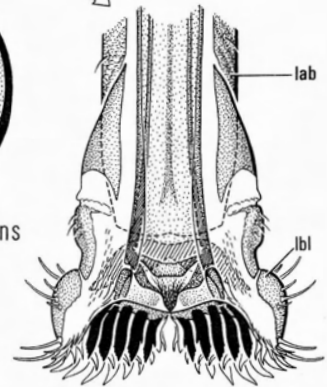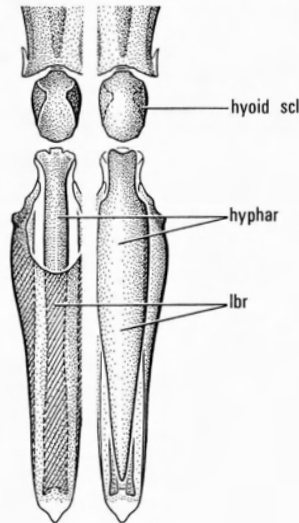**57** Stomoxys calcitrans ♀

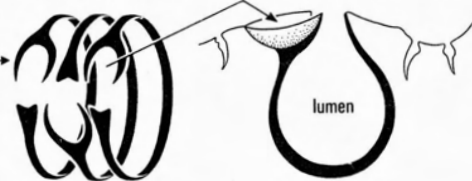**58** Calliphora vomitoria ♀

59 Calliphora vomitoria ♀
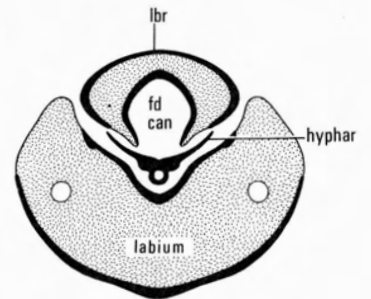
60 Calliphora vomitoria
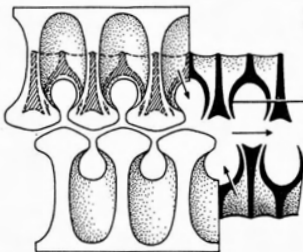
61 Calliphora sp.

62 Calliphora sp.

63 Calliphora sp.

have become the effective cutting tools; in these flies both the labrum and the labium, including the reduced labella, are inserted into the host during feeding.

In Diptera that are neither predacious nor bloodsucking, which include most of the order, food is imbibed by applying the soft labella to liquid substances such as nectar or to dry food sources such as pollen grains and dried honeydew that have first been suitably liquefied with saliva.

THORAX

The segments of the thorax (Figs. 64–66) are the *prothorax, mesothorax,* and *metathorax.* An outstanding feature of the Diptera is that the mesothorax is greatly enlarged to accommodate the muscles for the single pair of wings, whereas both the prothorax and metathorax are very reduced. The prefixes pro-, meso-, and meta- are usually attached to the different sclerites of the corresponding thoracic segments, e.g. prosternum, mesonotum, and metepimeron, but because of the predominance of the mesothorax, the prefix meso- is frequently omitted when referring to the sclerites of that segment (*see* "Mesothorax"). These prefixes are not to be confused with ante-, pre-, and post-, which are used to define particular parts of each sclerite, e.g. ante-pronotum, prescutellum, and postpronotum.

Basically each thoracic segment of an insect has a dorsal tergal plate, the *notum;* a lateral plate, the *pleuron;* and a ventral plate, the *sternum.* Generally, the notum can be more or less divided into the *prescutum, scutum,* and *scutellum;* in the Diptera, however, this division of the notum is usually made only for the mesonotum. The lateral pleural sclerites are considered to have been derived from subcoxal elements of ancestral legs, which became incorporated into the body wall. They consist of an anterior *episternum* and a posterior *epimeron* separated by a *pleural suture* which runs between the leg base and the wing base and serves to strengthen the pleuron. The episternum may be divided into an upper *anepisternum* and a lower *katepisternum;* the epimeron may similarly be separated into the *anepimeron* and the *katepimeron.* These general terms can all be modified by the suffixes pro-, meso-, and meta- to designate the particular segment of the thorax with which they are associated. However, as indicated above, when referring to the sclerites of the mesothorax, all

these terms are usually used unmodified except for the term mesonotum. The principal thoracic landmarks in the Diptera are the attachments of the head, abdomen, legs, wings, and halteres, and the *anterior* (mesothoracic) and *posterior* (metathoracic) *thoracic spiracles.* In the Diptera, as in all insects, true prothoracic spiracles are absent, but the mesothoracic spiracles frequently migrate forward and hence are often incorrectly called the prothoracic spiracles (*see* "Mesothorax").

Prothorax. The head is joined to the thorax by a membranous area of the prothorax called the *cervix* (neck), which bears one to three pairs of *cervical sclerites.* The *pronotum* is usually clearly divided into anterior and posterior parts; the *antepronotum* (anterior pronotum) is best developed in the Nematocera, especially the Tipulidae (Fig. 64), in which the lateral portions are enlarged to form a pair of prominent *antepronotal lobes.* The *postpronotum* (posterior pronotum), better developed in higher Diptera (Figs. 65, 66), is usually intimately associated with the mesonotum, and its posterolateral margins form the *postpronotal lobes* (humeri, humeral calli). The number, size, and position of the *postpronotal* (humeral) *bristles* provide useful taxonomic characters in many groups throughout the order, especially in higher Diptera. Laterally the *propleuron* may be rather indistinctly divided into an anterior *proepisternum* and a small *proepimeron;* together, the two parts usually form an arch over the base of the anterior coxa, especially in higher Diptera (Fig. 66). The *propleural suture* that separates them is usually at least partly obliterated; it is most apparent along the ventral margin, running from just above the anterior coxa toward the anterior spiracle. The proepimeron blends into the fused junction of the mesopleural katepisternum and anepisternum. The presence or absence of *proepisternal* (propleural) *bristles* and hairs is important in the taxonomy of many families, especially in higher Diptera; the same is true for *proepimeral* (stigmatal) *bristles.* The principal sternal sclerite is the *prosternum,* which may be divided externally into an anterior *presternum* and a posterior *basisternum.* The prosternum is usually separated from adjacent sclerites by a membrane, but it is sometimes joined with the proepisternum by a sclerotized *precoxal bridge* (Fig. 4.162). The morphology of the prothorax, especially the prosternum, in acalyptrate flies was treated in detail by Speight (1969).

Figs. 2.53–63. Mouthparts of Asilidae, Muscidae, and Calliphoridae: (53) *Laphria thoracica* Fabricius, cross section through proboscis; (54) *L. thoracica,* lateral view; (55) *Stomoxys calcitrans* (Linnaeus), lateral view; (56) *S. calcitrans,* cross section through proboscis; (57) *S. calcitrans,* enlargement of labella, front view, showing prestomal teeth; (58) *Calliphora vomitoria* (Linnaeus), anterior view; (59) *C. vomitoria,* enlargement of labrum, hypopharynx, and hyoid sclerite, dorsal and ventral views; (60) *C. vomitoria,* cross section through proboscis; (61) enlargement of pseudotracheae of *Calliphora* sp. (adapted from Graham-Smith 1930), showing openings to main lumen and pseudotracheal rings as seen externally, (62) alternating relationships of the bifid and flattened extremities of three consecutive pseudotracheal rings as seen from the external surface, and (63) interbifid space at bifid extremity and flattened portion at opposite extremity of a pseudotracheal ring as seen from the side view.
    Abbreviations: clyp, clypeus; fd can, food canal; hyoid scl, hyoid sclerite; hyphar, hypopharynx; lab, labium; lbl, labellum; lbr, labrum; mx, maxilla; plp, palpus; psdtrch, pseudotrachea.

Mesothorax.   The *mesonotum* (Figs. 64–66) includes the entire dorsum of the mesothorax. Its three basic components are the *prescutum*, the *scutum* (mesoscutum, mesonotum), and the *scutellum*; it also includes a fourth part posteriorly, the *postnotum* (metanotum, postscutellum), which is probably derived from an intersegmental acrotergite. Unfortunately, many dipterists have misapplied the term mesonotum to the scutum only.

The true prescutum, as opposed to an anterior portion of the scutum that Curran and others incorrectly called the prescutum, is greatly reduced in the Diptera. A portion of the *prescutal suture* (prescutoscutal suture, pseudosuture), separating the prescutum from the

scutum, is evident in some Nematocera, e.g. Tipulidae, Blephariceridae, Axymyiidae, and Psychodidae; its position coincides closely with the *prescutal pits* (humeral pits, humeral scars, tuberculate pits, pseudosutural foveae) present in some Tipulidae (Fig. 64), Ceratopogonidae, and Chironomidae. In the mature pupa these pits lie beneath the bases of the pupal horns. In many Nematocera and orthorrhaphous Brachycera the posterolateral margin of the prescutal area is traversed by a longitudinal suture, probably the base of the *lateral parapsidal suture* (notaulices), which marks off a narrow lateral sclerite called the *paratergite*; this sclerite is believed to be a vestige of the prescutum (Colless and McAlpine 1970, Hennig 1973).
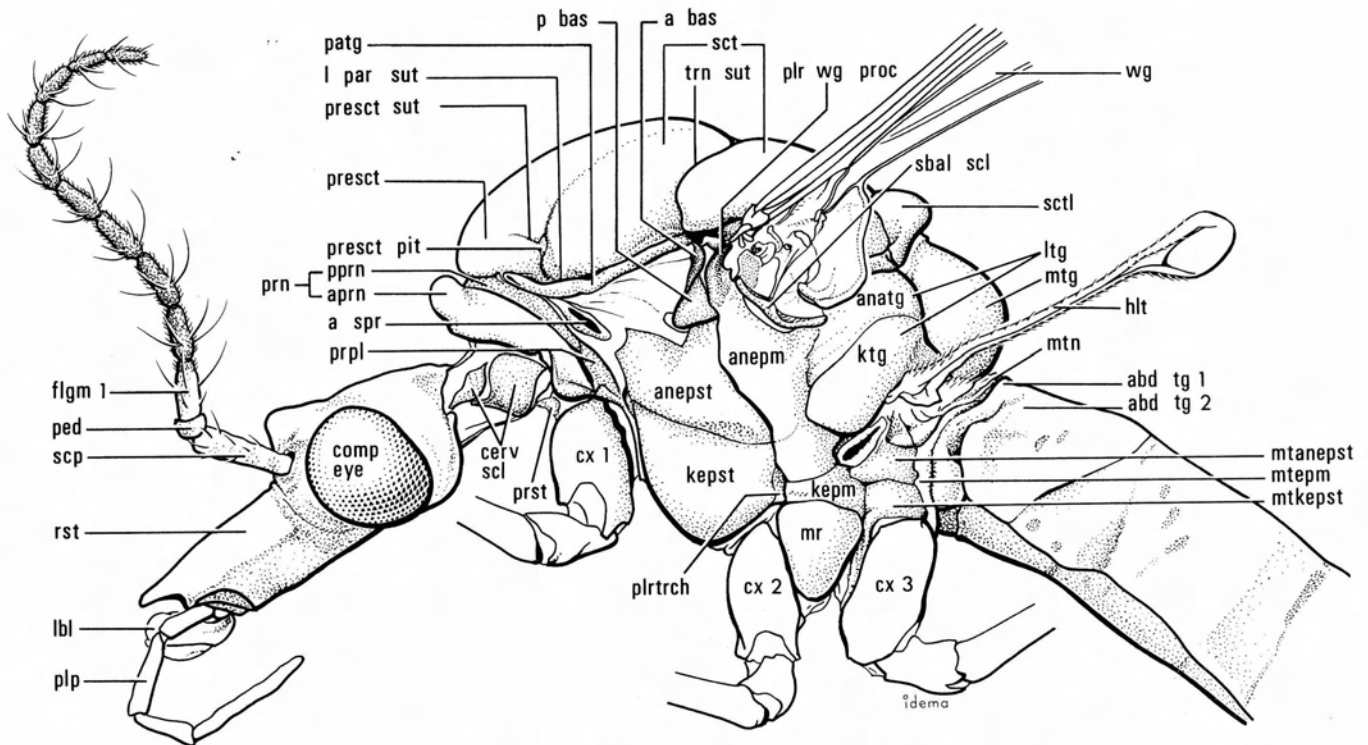
Fig. 2.64. Morphology and terminology of head and thorax of *Tipula trivittata* Say, lateral view.

a bas, anterior basalare
abd tg, abdominal tergite
anatg, anatergite
anepm, anepimeron
anepst, anepisternum
aprn, antepronotum
a spr, anterior spiracle
cerv scl, cervical sclerite
comp eye, compound eye
cx, coxa
flgm, flagellomere
hlt, halter
kepm, katepimeron
kepst, katepisternum
ktg, katatergite

lbl, labellum
l par sut, lateral parapsidal suture
ltg, laterotergite
mr, meron
mtanepst, metanepisternum
mtepm, metepimeron
mtg, mediotergite
mtkepst, metakatepisternum
mtn, metanotum
patg, paratergite
p bas, posterior basalare
ped, pedicel
plp, palpus
plrtrch, pleurotrochantin
plr wg proc, pleural wing process

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

The true scutum occupies most of the thoracic dorsum in the Diptera, and its gross development is an outstanding apomorphic character of the order. Because of its greatly expanded condition and concomitant distortion, the homologies of its features are not easily recognized. A predominant feature of the scutum in most Diptera is the *transverse suture*, sometimes incorrectly called the transcutal or scutal suture. It is derived from a pair of lateral sutures that divide the scutum into an anterior *presutural area* (prescutum of Curran and others) and a posterior *postsutural area* (scutum of some authors). Each half of this suture arises laterally in front of the *anterior notal wing process* and continues toward the midline of the scutum. In the Tipulidae and some related families, e.g. Ptychopteridae, these sutures meet on the midline, forming a characteristic V-shaped groove, but in most other groups they are weaker and do not meet in the middle. In most Calyptratae, however, and in some acalyptrate families, e.g. Somatiidae, they also meet in the middle. They tend to be more directly transverse in higher Diptera than in most Nematocera. In certain forms, e.g. all Bibionomorpha and most Culicomorpha, they are scarcely evident. The origin and homology of the transverse suture is somewhat controversial. The terms transcutal suture or scutal suture are certainly incorrect. The true transcutal suture is a continuation of the *tergal fissure*, which is located between the *median* and *posterior notal wing processes*, whereas the transverse suture arises in front of the anterior notal wing processes. Matsuda (1970) interpreted the transverse suture of the Diptera as the lateral parapsidal sutures, which arise from the lateral extremities of the prescutal suture in plecopteroid and neuropteroid orders. This interpretation accords well with that of Hendel (1928) and with the observable facts in many Diptera. As pointed out by Hendel (1928), the suture that separates the paratergite from the lateral margin of the scutum in many Nematocera is continuous with the transverse suture; together these sutures in the Diptera appear to be homologous with true lateral parapsidal sutures in lower orders. Any or all of the following additional sutures can be distinguished on the scutum of various Diptera. The paired, more or less longitudinally aligned *parapsidal sutures* arise from the prescutal sutures and continue caudally in a sublateral (dorsocentral) position in many Nematocera; they are particularly strong in certain Psychodidae. A distinct *median scutal* (acrostichal) *suture* is often very distinct in the Chironomidae and the Chaoboridae; it is also present in many Psychodidae and in some Bibionomorpha. The *scutoscutellar suture*, separating the scutum and the scutellum, is the hindmost transcutal suture. Two other short, paired, more or less transverse sutures are sometimes present between the transverse suture and the scutoscutellar suture, namely a true *scutal* (transcutal) *suture* anteriorly near the tergal fissure, and a *posterolateral scutal suture* posteriorly. The following designations are applied to other features of the scutum. In the higher Diptera (Figs. 65, 66) the anterolateral region of the scutum, between the postpronotal lobe and the wing base, is a clearly delimited, sunken area called the *notopleuron*; this area corresponds closely to the sclerite called the paratergite in many Nematocera and may be partially homologous. The swollen area lying just behind the lateral extremities of the transverse suture and anteromedial to the anterior notal wing process is called the *prealar callus*. Similarly the swollen area between the scutellum and the posterior base of the wing, marked off anteriorly by the posterolateral scutal suture and posteriorly by the scutoscutellar suture, is called the *postalar callus*. A ridge running from the anterolateral angle of the scutellum to the wing base is called the *postalar ridge*, and the ventrolateral surface below the postalar ridge is called the *postalar wall* (postalar declivity). The lateral margin of the scutum immediately above the attachment of the wing is the *supra-alar area*. Sometimes, as in the Blephariceridae, Deuterophlebiidae, Simuliidae, and Thaumaleidae, this area is modified to form a distinct concavity, the *supra-alar depression*, over the wing base. The upper margin of this depression is called the *supra-alar ridge*.

The scutellum is a clearly defined, rounded or triangular lobe bounding the posterior margin of the scutum. In the Diptera it is almost always evaginated and its apex frequently projects roof-like over the postnotum, more so in higher Diptera than in the Nematocera. It is grossly developed in the Celyphidae and is unusually elongate in certain Stratiomyidae and Piophilidae. Frequently it is immediately preceded by a small, transverse, lenticular bulge, the *prescutellum*. A ridge running from the base of the lower calypter to the anterolateral angle of the scutellum is called the *suprasquamal ridge*. A largely membranous area between the suprasquamal ridge and the lower margin of the postalar wall is called the *tympanal fossa*. It is usually strengthened by a rib-like sclerite called the *tympanal ridge*. In many Muscomorpha, at least, the tympanal ridge is forked anteriorly and forms a single Y; in some families such as the Calliphoridae and the Oestridae it is doubly forked and forms a double Y. In these groups the two lowermost arms enclose a membranous *tympanic pit* that opens toward the base of the wing. The tympanal fossa, the tympanal ridge, and the tympanal pit are best seen in a posterodorsal view with the wing in a downward position.

The postnotum has been incorrectly called the metanotum and the postscutellum by some authors; it includes all the parts behind and below the scutellum. The postnotum is sometimes large and exposed, especially in the Nematocera (Fig. 64), or relatively small and withdrawn, as in the Tabanidae. It consists of a *mediotergite* and two *laterotergites* (pleurotergites, metapleura), one on each side. The mediotergite sometimes has a median suture or groove, as in most Chironomidae (Figs. 29.26–29) and Chaoboridae (Fig. 24.5). The anterior (dorsal) portion of the mediotergite is usually concave, but in some forms, especially the Tachinidae (Fig. 66), this area is differentiated as a convex, transverse, lenticular bulge, the *subscutellum* (postscutellum,

infrascutellum). Each laterotergite extends down to the posterior thoracic spiracle and is sometimes divided into a dorsal *anatergite* and a ventral *katatergite* (Fig. 64).

The chaetotaxy of the thoracic sclerites, shown in Figs. 65 and 66, is extremely important in taxonomy.

The *mesopleuron* includes the entire pleuron of the mesothorax and is divided by the pleural suture into an anterior *episternum* and a posterior *epimeron*. The pleural suture is relatively straight in most Nematocera, but it follows an increasingly zigzag course in higher Diptera. The episternum is divided transversely by the *anapleural suture* into an upper part, the *anepisternum* (mesopleuron of many dipterists), and a lower part, the *katepisternum* (sternopleuron, preepisternum). Similarly the epimeron is transversely divided into the *anepimeron*

(pteropleuron) and the *katepimeron* (barrette), separated by the *transepimeral suture* (anepimeral suture of Crampton). The anepisternum is divided by a membranous area, the *anepisternal cleft* (episternal fissure, basalar cleft), which extends downward in front of the pleural suture to the anapleural suture. In the Simuliidae the anepisternal cleft is unusually large and is referred to as the *anepisternal membrane* (pleural membrane). The parts of the anepisternum lying on each side of this cleft are sometimes given different names, as in the Chironomidae (see Hansen and Cook 1976). Posterodorsally, in the mouth of the anepisternal cleft and near the lower base of the wing, is a relatively small, usually subdivided sclerite called the *basalare* (Fig. 64). It is derived from the anepisternum and provides a base for the insertion of wing muscles (Snodgrass 1935). The
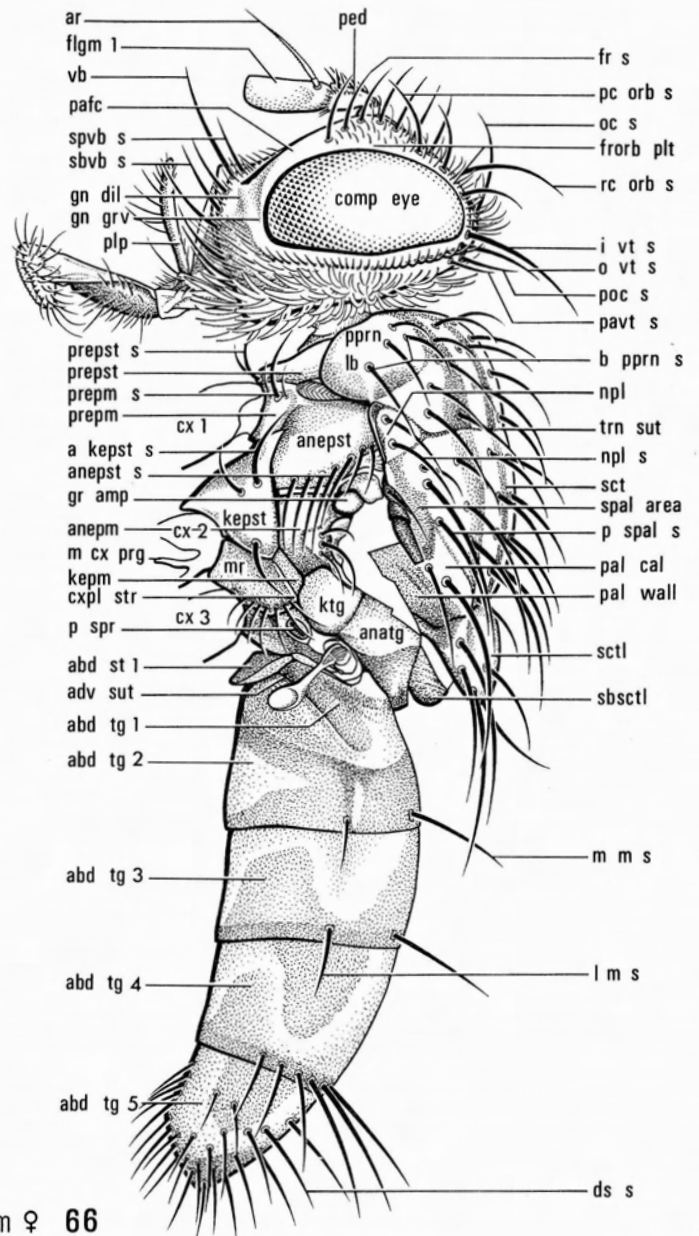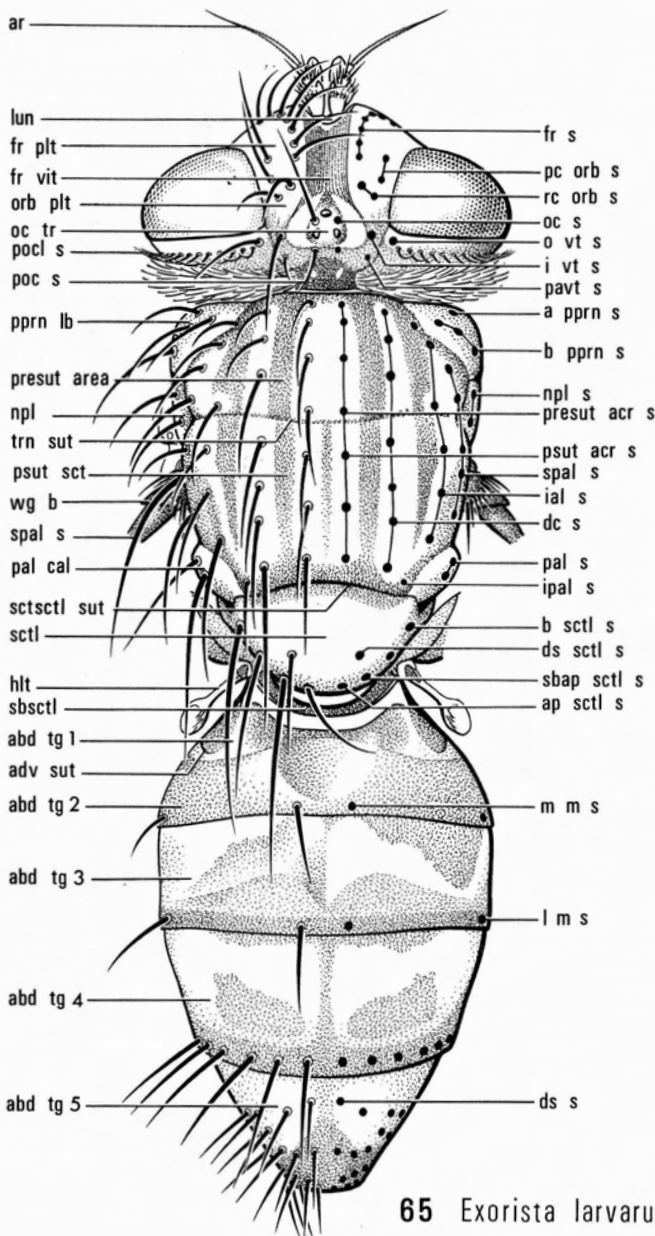
65 Exorista larvarum ♀ **66**

anterior part of the basalare, called the **anterior basalare**, is usually joined dorsally to the scutum just behind the lateral extremity of the transverse suture by a narrow strip which, in the Tipulidae, is called the **prealar bridge**. The posterior part, called the **posterior basalare**, is usually attached posteroventrally to the anterodorsal margin of the epimeron. The posterior basalare is sometimes setose, as in certain Asilidae.

The anterior spiracle lies toward the anterodorsal angle of the anepisternum, near the junction of the pronotum and the mesonotum.

The mesothoracic katepisternum is a constant, easily recognized feature throughout the order, but its interpretation and naming is rather contradictory and confusing (Hennig 1973). It is always greatly extended ventrally at the expense of the **mesosternum**, the ventral sclerite of the mesothorax. The mesosternum is reduced in the Diptera to a narrow, usually wholly internal phragma, and early workers incorrectly assumed that it was combined with the katepisternum. Hence, the katepisternum is frequently, but inappropriately, called the sternopleuron (sternopleurite of Crampton 1925), especially in systematic works. Crampton (1909) proposed the name katepisternum for the part of the episternum lying below the anapleural suture. He interpreted this large sclerite in the Diptera as the "fusion product of the katepisternum [erroneously called katepimeron in text, but correctly called katepisternum in figures and resumé], part of the trochantin, and a portion of the antecoxal laterale." In his figures of *Tipula* and *Musca* he labeled it as the "katepisternal complex (ES$_{KX}$)." According to Matsuda (1970) the sclerite in question is derived from anapleural, not katapleural, elements, and this interpretation adds to the confusion concerning its proper name. The name katepisternum has usually been applied in Crampton's (1909) sense in the Nematocera and it has often been applied in the same sense in the orthorrhaphous Brachycera and the Muscomorpha (Crampton 1942, Bonhag 1949, Downes 1955). However, some authors (Rees and Ferris 1939, Matsuda 1970, Saether 1971, Hansen and Cook 1976) misapplied the term katepisternum in the Diptera to a small sclerite of katapleural origin, the **pleurotrochantin** (Fig. 64) of Crampton (1925, 1942), which is known only in *Tipula* (Rees and Ferris 1939), *Plecia* of the Bibionidae (Crampton 1925), and the Culicomorpha (Crampton 1925). These same authors (except Crampton) used the term preepisternum for the major portion of the katepisternum. The name preepisternum was first used by Hopkins (1909) for an anterior part of the episternum of *Dendroctonus* (Coleoptera). Subsequent usage of the term by Snodgrass (1909, 1910, 1959), Comstock (1920), Imms (1925), Rees and Ferris (1939), and Matsuda (1970) is inconsistent and contradictory. For the Diptera, at least, it is preferable to retain the names katepisternum and pleurotrochantin for the sclerites in question. The katepisternum (Figs. 64–65) is usually a simple, convex, somewhat triangular sclerite, with or without **katepisternal bristles** or **setulae** or both. In some Simuliidae it is divided into an upper and a lower

Figs. 2.65–66. Morphology, chaetotaxy, and terminology of body of *Exorista larvarum* (Linnaeus), in (65) dorsal and (66) lateral views.

abd st, abdominal sternite
abd tg, abdominal tergite
acr s, acrostichal seta
adv sut, adventitious suture
a kepst s, anterior katepisternal seta
anatg, anatergite
anepm, anepimeron
anepst, anepisternum
anepst s, anepisternal seta
a pprn s, anterior postpronotal 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
flgm, flagellomere
frorb plt, fronto-orbital plate
fr s, frontal seta
fr vit, frontal vitta
gn dil, genal dilation
gn grv, genal groove
gr amp, greater ampulla

hlt, halter
ial s, intra-alar seta
ipal s, intrapostalar seta
i vt s, inner vertical seta
kepm, katepimeron
kepst, katepisternum
ktg, katatergite
l m s, lateral marginal seta
lun, lunule
m cx prg, mid coxal prong
m m s, median marginal seta
mr, meron
npl, notopleuron
npl s, notopleural seta
oc s, ocellar seta
oc tr, ocellar triangle
orb plt, orbital plate
o vt s, outer vertical seta
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
pocl s, postocular setae

poc s, postocellar seta
pprn, postpronotum
pprn lb, postpronotal lobe
prepm, proepimeron
prepm s, proepimeral seta
prepst, proepisternum
prepst s, proepisternal seta
presut acr s, presutural acrostichal seta
presut area, presutural area of scutum
p spal s, posterior supra-alar seta
p spr, posterior spiracle
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

part by a horizontal groove called the *katepisternal sulcus* (mesepisternal groove) (Figs. 27.10, 27.12–13).

The mediodorsal margin of the anepimeron extends dorsally and articulates with the wing; this extension is called the *pleural wing process* (subalifer). In Calyptratae its basal portion bears a bulbous swelling; this structure, first discovered and named in the Calliphoridae (Lowne 1890–1895), is called the *greater ampulla* (*pl.* ampullae; infra-alar bulla, subalar knob) (Fig. 66). It is greatly inflated in many Syrphidae but is undeveloped in the Nematocera and in all acalyptrate families except the Periscelididae and the Ropalomeridae, as well as some Psilidae, Sciomyzidae, and Tephritidae. Behind the pleural wing process in most Diptera a well-developed *subalar sclerite* (subalar ridge, vallar ridge) lies in the subalar membrane between the insertion of the wing and the dorsal margin of the anepimeron. In the Syrphidae the posteroventral margin of this sclerite is produced to form the *plumule,* and the anterodorsal portion is frequently inflated to form one or more peculiarly shaped dilations. The so-called *vallar bristles*, present in some Sciomyzidae, arise on the subalar sclerite. In certain Calyptratae, e.g. Calliphoridae and Sarcophagidae, the swollen anterior part is called the *lesser ampulla.* The occurrence of both the greater and the lesser ampullae may be correlated with the ability to make bee-like buzzing sounds. The transepimeral suture extends from near the hindmost point of the bend in the lower portion of the pleural suture toward the posterior (metathoracic) spiracle. The katepimeron is a narrow, more or less horizontal sclerite immediately below the transepimeral suture (Figs. 64, 66). It lies along the dorsal rim of the *meron* (meropleuron, hypopleuron) and is sometimes separated from it, as in some Sarcophagidae, Calliphoridae, Muscidae, and Tachinidae, by a suture-like depression called the *coxopleural streak* (Fig. 66). When the lower margin of the katepimeron is indistinguishably fused with the meron, the two sclerites together are called the *meropleurite.* The meron is particularly strongly developed in some primitive families such as the Tanyderidae, Ptychopteridae, Blephariceridae, and Axymyiidae; in the Mycetophilidae, Sciaridae, and Cecidomyiidae, however, it is greatly reduced. The chaetotaxy of it and the adjoining katepimeron affords useful taxonomic characters in many families, especially in the Calyptratae.

The mesosternum is mostly invaginated in the Diptera, but it is relatively large and exposed in the Deuterophlebiidae, the Nymphomyiidae, some Blephariceridae, and some Anisopodidae. It is also wide and exposed in the tipulid genera *Gnophomyia* and *Chionea* (Matsuda 1970).

Metathorax. The metathorax is reduced and its dorsum, the *metanotum*, is usually scarcely visible externally (Fig. 64). The metanotum connects the mesothoracic postnotum to the first abdominal tergite and is a narrow, transverse band extending from the base of

one halter to the other. It is relatively large and exposed only in a few forms, e.g. Psychodidae and the xylophagid genus *Coenomyia*; usually, it is concealed beneath the base of the first abdominal tergite.

Laterally the *metapleural suture* extends from the coxa to the halter and separates the *metapleuron* into the *metepisternum* anteriorly and the *metepimeron* posteriorly (Fig. 64). A clear division of the metepisternum into a dorsal *metanepisternum* and a ventral *metakatepisternum* occurs, for example, in the tipulid genus *Dolichopeza*, but this division is usually indistinct. An intersegmental suture separating the metepisternum from the mesothoracic meron can usually be distinguished; it runs ventrally from the posterior spiracle, thence anteromedially between the mesothoracic and metathoracic coxae. The metepimeron is frequently closely associated with the anterolateral extremities of the first abdominal tergite. Sometimes, especially in groups with petiolate abdomens, the two metepimera become fused ventromedially behind the bases of the hind coxae to form a *postcoxal bridge.*

The *metasternum*, like the mesosternum, is usually almost entirely invaginated. However, a small external metasternum is present in the Deuterophlebiidae and the Nymphomyiidae. The area lying between and in front of the metathoracic coxae in higher Diptera (basisternum of Crampton 1942), sometimes referred to as the 'metasternum' as in Syrphidae, is probably at least partially derived from the pleuron.

Wing. In the Diptera only the front or mesothoracic pair of wings is developed as functional flight organs; the metathoracic pair is reduced to small club-like structures, the *halteres* (*sing. halter*). This feature is an outstanding apomorphic character of the order. Other special features of dipterous wings are discussed under venation below.

For convenience the wing is treated under three headings: the *axillary area* containing the *axillary plates* between the lateral margins of the notum and the bases of the wing veins, the basal *stalk* containing the bases of the wing veins and associated plates and membranes, and the *blade* or main area of the wing (Fig. 3).

The axillary area is illustrated in Fig. 68. The anterior margin of the wing is called the *costal margin*. The most proximal plate, at the extreme base of the costal margin, is the *tegula* (costal plate, epaulet); the adjacent, more distal plate, articulating with the base of the *costa* (*C*), is called the *basicosta* (humeral plate, subepaulet). In addition to these two plates there are at least three axillary plates. The *first axillary plate* articulates with the anterior notal wing process and the *subcostal sclerite*. The *second axillary plate* articulates proximally with the first axillary plate, anteriorly with the base of the *radius* (*R*), posteriorly with the *third axillary plate*, and ventrally with the pleural wing process. The third axillary plate articulates with the posterior notal wing process, the bases of the *cubitus* (*Cu*) and the *anal vein*

(*A*), and the second axillary plate. Sometimes a *fourth axillary plate*, lying more or less proximal to the third axillary plate, has been distinguished (Bonhag 1949); it is really the apical part of the posterior notal wing process that has become more or less detached (Snodgrass 1935). Lying in the median area of the wing base more or less distal to the second and third axillary plates is a pair of hinged plates called the *proximal* and *distal median plates* (m and m' of Snodgrass 1935). The proximal median plate (m of Snodgrass 1935, m' of Bonhag 1949) is really part of the third axillary plate (Snodgrass 1952) derived from the basal parts of M and Cu (Matsuda 1970). It is separated from the distal median plate by a *basal fold*. The distal median plate is a secondary sclerite that must have segregated simultaneously with the formation of the basal fold (Matsuda 1970). The posterobasal portion of the axillary membrane, joining the hind margin of the wing to the thorax, forms two basal lobes called the *calypteres* (*sing. calypter*; squamae, squamulae). The proximal lobe, called the *lower calypter* (basicalypter, squamula thoracica), begins as a narrow, membranous ligament arising from the furrow between the scutellum and the postnotum and ends where the more distal lobe, the *upper calypter* (disticalypter, squamula alaris), folds sharply over it. The upper calypter is believed to be homologous with the jugal region or neala of higher insects, e.g. Neoptera, including the jugal lobe of the Mecoptera (Hennig 1973). It is usually larger than the lower calypter, but in some groups, e.g. Tabanidae, Acroceridae, and many Calyptratae, the lower calypter is larger than the upper one. The fringe of hairs along the posterior margin of each calypter is called the *calyptral fringe*, and the fold between the two lobes is the *calyptral fold*.
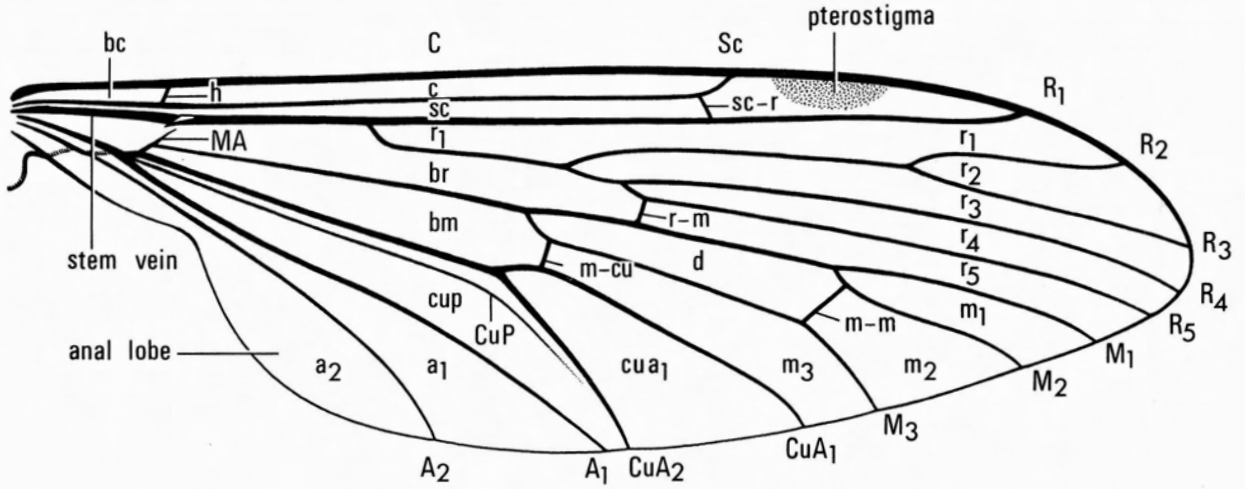
The wing stalk is also illustrated in Fig. 68. It contains the bases of all the main wing veins as well as their basal plates and basal brace veins. The subcostal sclerite, linking the *subcosta* (*Sc*) with the first axillary plate, is wedged between the basicosta and the anteroproximal margin of the basal section of R. The basal section of R is called the *stem vein* (incorrectly called remigium by some dipterists); it is usually marked off apically by a transverse, suture-like constriction close to the level of the *humeral crossvein* (*crossvein h*); the broad proximal part of the stem vein corresponds to the median plate of Hamilton (1971, 1972a, 1972b, 1972c). The posterior margin of the wing stalk usually has a broad lobe called the *alula* (axillary lobe). Proximally this lobe is continuous with the upper calypter and distally it is usually separated from the rest of the wing by an indentation called the *alular incision*. The alula represents a newly acquired feature of the Diptera (Hennig 1973); it is usually absent or poorly developed in the Nematocera, except in Anisopodidae, but is usually relatively large in the Brachycera.

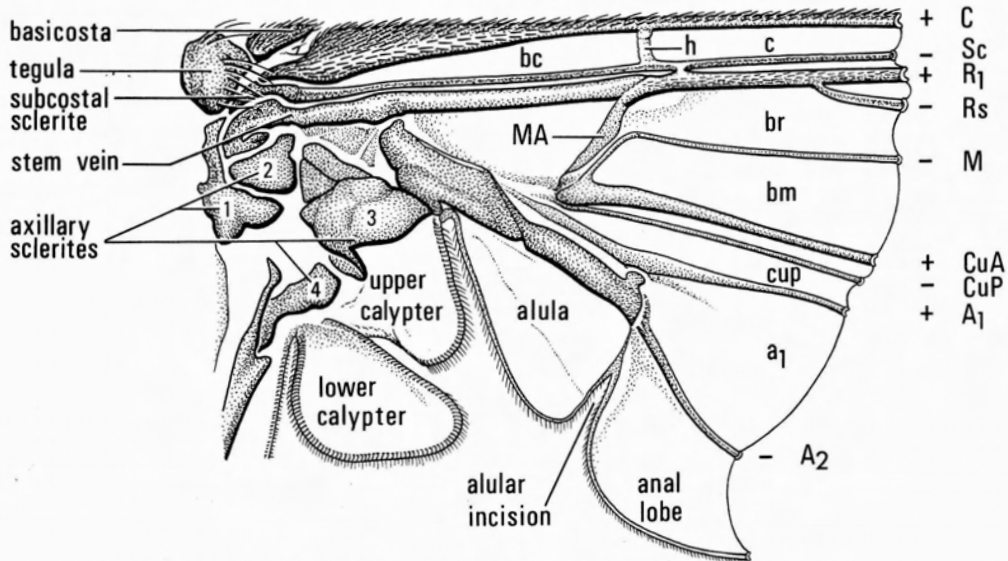The wing blade is illustrated in Figs. 67 and 69. Frequently, especially in the Nematocera and in orthorrhaphous Brachycera, a sharply defined, somewhat thickened, opaque or pigmented area called the *pterostigma* is evident in the membrane near the point where R_1 joins C; according to Arnold (1964), it marks the position of a costal blood sinus. In the Diptera the *anal lobe* is a rather flexible, more or less triangular area, containing at most two branches of the anal vein, both of which may be atrophied.

The venation of the wing varies greatly throughout the order (Figs. 4.1–76) and is of fundamental taxonomic value. The veins are essentially remnants of the body hemocoel (Martynov 1930, Arnold 1964). They develop from cuticularized blood lacunae, which are usually occupied by tracheae during morphogenesis (Carpenter 1966). The system adopted here for interpreting and naming the veins and cells is fundamentally the Redtenbacher (1886) system, usually referred to as the Comstock–Needham (1898–1899) system, as improved by workers such as Comstock (1918), Comstock and Needham (1922), Lameere (1923), Martynov (1930), Carpenter (1966), Hennig (1973), Séguy (1973), and Kukalova-Peck (1978); Carpenter's review of this controversial subject is exceptionally clear and concise. This system is founded on the recognition in insect wings of six primary veins that Redtenbacher called the *costa* (*C*), *subcosta* (*Sc*), *radius* (*R*), *media* (*M*), *cubitus* (*Cu*), and *anal vein* (*A*). In the most generalized condition each of these veins consists of two main branches: a convex (+) anterior branch (A) and a concave (−) posterior (sectoral) branch (P) (Kukalova-Peck 1978) (Fig. 68). Primitively both branches of each vein arose from a common basal blood sinus (Kukalova-Peck 1978), and both branches of each vein were further branched. In many modern insects, especially those with membranous wings, the subsequent branches frequently retain some degrees of their original convex or concave properties. Correlation of this fundamental pattern of venation and *fluting* (alternating ridges and valleys) in the wings of both fossil and living members of the Pterygota is the principal basis for homologizing the wing veins in all orders.

Although this interpretation is accepted for the origins of the veins, traditionally established names for some veins do not entirely conform with the system. In practical taxonomy the names usually applied to the C, Sc, R, and M veins in all orders do not reflect their anterior (A) or posterior (P) (sectoral) origins. For the sake of simplicity new, perhaps more appropriate, names (*see* Wootton 1979) are not introduced here for the Diptera. Both C and Sc are represented by single veins called simply C and Sc. In the case of R, the anterior branch (RA in the strict sense) is called R_1, and the remaining four posterior branches making up the posterior branch (RP in the strict sense) or *radial sector* (*Rs*) are called R_2, R_3, R_4, and R_5, rather than RP$_1$, RP$_2$, RP$_3$, and RP$_4$ or Rs$_1$, Rs$_2$, Rs$_3$, and Rs$_4$. In the case of M the anterior branch (*MA*) is extremely reduced and never reaches the wing margin. The components of the posterior branch (*MP*) are called M_1, M_2, and M_3.

bc
C
Sc
pterostigma
h
c
sc
sc-r
R_1
MA
r_1
R_2
stem vein
br
r_1
r_2
r_3
r_4
r_5
R_3
bm
r-m
d
R_4
R_5
cup
m-cu
m_1
anal lobe
CuP
m-m
M_1
a_2
a_1
cua_1
m_3
m_2
M_2
A_2
A_1
CuA_2
CuA_1
M_3

67 Ground–plan of Diptera wing

basicosta
bc
h
c
+ C
tegula
– Sc
subcostal sclerite
+ R_1
MA
br
– Rs
stem vein
2
bm
– M
1
3
axillary sclerites
cup
+ CuA
4
upper calypter
alula
– CuP
+ A_1
lower calypter
a_1
alular incision
anal lobe
– A_2

68 Tabanus americanus ♀

basicosta
costagial break
humeral break
subcostal break
Sc
tegula
R_1
C
c
sc
bc
h
r_1
R_{2+3}
br
r_{2+3}
bm
r-m
R_{4+5}
upper
bm-cu
r_{4+5}
M
CuP
cup
CuA_2
dm
alula
stem vein
lower
dm-cu
cua_1
calypteres
alular incision
anal lobe
A_2
A_1+CuA_2
CuA_1

69 Paralucilia wheeleri ♀

However, in the case of Cu the A and P designations have often been used for naming the branches, for purposes of clarity. Accordingly, the forked anterior branch of Cu (*CuA*) consists of *CuA₁* and *CuA₂*; the posterior branch of Cu is *CuP*. In the case of A the anterior branch is called *A₁* and the posterior branch is *A₂* (Figs. 67, 69).

The nearest approach to the primordial venation of pterygote insects is found in fossil Paleoptera. Special features of the Neoptera, to which the Diptera belong, are as follows: the ability to flex the wings over the back, the fusion of MA with R (Martynov 1930), sometimes the fusion of M_4 with CuA, and the partial to complete loss of the primary fluting of many of the veins in the central portion of the wing (Kukalova-Peck 1978). Generally also C, Sc, and R are subparallel along the anterior margin of the wing, whereas the others are directed more or less fanwise in the posterior part of the wing. The Tanyderidae (Fig. 4.1) and the Psychodidae (Fig. 4.2) show what is believed to be the most primitive venational pattern of the Diptera. The following features of the supposed primordial venation of the order (Fig. 67) are the most distinctive.

- C completely surrounds the wing but is strongest along the anterior margin.
- Sc has one free longitudinal vein. Some authors (Alexander 1927, 1929; Friend 1942; Hennig 1954; Colless and McAlpine 1970) assume that Sc is primitively two-branched (Sc₁ and Sc₂) near its apex. In this assumption the transverse vein between Sc and R₁ is interpreted as a branch (Sc₂) that fuses with R₁; it is believed to reappear as a separate vein only in the Australian tanyderid *Nothoderus australiensis* Alexander. Other workers (Curran 1934, Hamilton 1972*a*) treat the transverse vein between Sc and R₁ as the subcostal-radial crossvein (sc-r), a common feature of neuropteroid wings. In the latter interpretation the

so-called free Sc₂ of *Nothoderus* might be considered a *secondary veinlet* in the vicinity of the pterostigma, also a common feature in neuropteroid groups. The matter is of little or no taxonomic importance, and because there is no unequivocal evidence that Sc₂ ever occurs in the Diptera it seems preferable to omit any reference to it.

- The base of R has a transverse suture-like constriction marking off the stem vein.
- Rs has four free veins (R_2 to R_5).
- The base of M is atrophied, giving the appearance that M arises from Cu.
- MA occurs as a short, transverse vein (arculus, brace vein, phragma; see Hennig 1968) between MP and R.
- MP has only three free branches, M_1 to M_3 (Comstock 1918, Friend 1942, Hennig 1973). M_4 never occurs as a separate, free vein in the Diptera, and for practical taxonomic purposes it seems preferable to adopt Comstock's (1918) recommendation to omit any reference to it in the designation of veins throughout the order. Comstock (1918) believed that it coalesced with either M_3 or CuA_1. Tillyard (1926) interpreted CuA_1 as a free M_4. However, the distinctive nature of the *cubital fork* throughout the Diptera and the strong convexity of both its branches (as opposed to a primitively concave condition in all branches of MP) indicate that the vein in question is primarily derived from CuA rather than from M_4.
- CuA has two free branches (CuA_1 and CuA_2), these forming a distinctive cubital fork.
- CuP is weak and untracheated; it lies close behind CuA and never reaches the wing margin.
- A consists of a strong convex anterior branch (A_1) and a weak concave posterior branch (A_2).
- The following *crossveins* are present: *humeral* (*h*), *subcostal-radial* (*sc-r*) (Sc₂ of some authors),

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Figs. 2.67–69. Dorsal views of right wing to show structure and venation: (67) wing stalk and blade of hypothetical primitive Diptera; (68) axillary area and wing stalk of *Tabanus americanus* Forster; (69) complete wing of *Paralucilia wheeleri* (Hough).

veins	cells	crossveins
A₁, A₂; branches of anal veins	a₁, a₂; anal	bm-cu, basal medial-cubital*
C, costa	bc, basal costal	dm-cu, discal medial-cubital
Cu, cubitus	bm, basal medial	h, humeral
CuA, anterior branch of cubitus	br, basal radial	m-cu, medial-cubital*
CuA₁, CuA₂; anterior branches of cubitus	c, costal	m-m, medial
CuP, posterior branch of cubitus	cua₁, anterior cubital	r-m, radial-medial
M, media	(cubital fork)	sc-r, subcostal-radial
M₁, M₂, M₃; posterior (sectoral) branches	cu*p*, posterior cubital	
of media	d, discal (1m₂)	* Crossvein bm-cu is the
MA, anterior branch of media	dm, discal medial	same as crossvein m-cu,
R, radius	m₁, m₂, m₃; medial	but the designation
R₁, anterior branch of radius	r₁, r₂, r₃, r₄, r₅; radial	'b'm-cu is used to distin-
R₂, R₃, R₄, R₅; posterior (sectoral) branches	sc, subcostal	guish crossveins bm-cu
of radius		from m-cu when both
Rs, radial sector		occur.
Sc, subcosta		

radial-medial (*r-m*) (anterior crossvein, ta), *medial-cubital* (*m-cu* or *bm-cu*) (tb, possibly the base of M_4), and *medial* (*m-m*) (M_2-M_3). The *sectoral crossvein* (*crossvein r-s*) between R_1 and R_2 is considered to be absent by Alexander (1927, 1929), but this opinion is not universal.

- The following closed *cells* are present: *basal costal* (*bc*), *costal* (*c*), *subcostal* (*sc*), *basal radial* (*br*) (1st basal), *basal medial* (*bm*) (2nd basal), and *discal* (*d*) ($1M_2$) [see discal medial cell (cell dm), p. 33].

The following peculiarities and transformation series are among the most important venational specializations that occur within the Diptera (see Figs. 4.1–76).

C fades out and becomes absent beyond the insertions of R and M in the Deuterophlebiidae, in some Blephariceridae, in all Chironomoidea, in all Bibionomorpha except Cecidomyiidae, in all Stratiomyoidea, in most Empididae, in all Dolichopodidae, and in all Muscomorpha except the Lonchopteridae and some Platypezidae (*Opetia*). One to three weakenings or *costal breaks* frequently occur in the Diptera, especially in the Schizophora (Fig. 69). Usually these breaks are located proximal to the insertion of Sc. They are believed to be special points for flexing the wings during flight (Hennig 1971, p. 30; 1973, p. 192), and they are also associated with folds in the wing during pupation (Hennig 1973, p. 192). The most frequent break occurs just proximal to where Sc joins C or to the point where it would join C if Sc were complete. A similar break, occurring almost as frequently, is located slightly distal to crossvein h. The third break, considerably less frequent than the others, is found slightly proximal to crossvein h and marks off a short, thickened, relatively heavily bristled section at the base of C, the *costagium* (Séguy 1973). None of these breaks have been previously named, and it is here proposed to call them the *costagial*, *humeral*, and *subcostal breaks*. Costal breaks are rare in the Nematocera and lower Brachycera. One to several are found in some Psychodidae (Fig. 4.2), and one, corresponding to the humeral break, is fairly common in the Ceratopogonidae (Figs. 4.15–16). A somewhat similar interruption occurs in the Cecidomyiidae at the point near the apex of the wing where C is suddenly attenuated (Fig. 4.22). This characteristic may indicate that the thickening of C on the posterior margin of the wing in this family is a secondary condition. All three main breaks usually occur in the Calyptratae (Fig. 69). All or none may occur in other Schizophora (Figs. 4.53–76) providing many useful characters for separating the various taxa.

Both the apex of Sc and crossvein sc-r are weak or absent in many groups. Sometimes the end of Sc is atrophied but crossvein sc-r remains, as in many Tipulidae. Sometimes the ends of both Sc and crossvein sc-r disappear, as in many Empididae (Figs. 4.42–44) and in all Drosophilidae. Occasionally Sc joins R_1, possibly through the agency of a reduced crossvein sc-r, as in

some Tipulidae and Empididae, in some Dolichopodidae (Fig. 4.46), in some Platypezoidea (Fig. 4.49) except Platypezidae, and in some acalyptrates. Although crossvein sc-r is seldom recognized in the Muscomorpha, it is clearly present and complete in some Syrphidae (Fig. 4.51) and Conopidae (Fig. 4.53). In most other Muscomorpha there is a peculiar swelling on R_1 near the point where Sc bends forward (Fig. 69); this thickening is probably a remnant of crossvein sc-r.

The anterior convex branch of R (R_1) is practically always present as a free unbranched vein. Plesiomorphically Rs is dichotomously twice branched to form R_2 and R_3, and R_4 and R_5 (Fig. 67), but as stated above, four free branches are retained only in the Tanyderidae (Fig. 4.1) and the Psychodidae (Fig. 4.2). In all other Diptera one or more of these branches has been lost by fusion or atrophy (Figs. 4.3–76). Apparently reductions from the original four branches to three branches, two branches, one branch, or complete absence evolved in different ways in the various groups of Diptera (Hennig 1954). In the Tipulidae the apex of R_2 curves forward and is permanently attached to R_1 (capture of R_2 by R_1), usually in the manner of a crossvein (Alexander 1927, 1929). Alexander (1927, 1929) believes that R_2 is atrophied in the Culicomorpha, Bibionomorpha, and Brachycera, but many authors do not agree. In the Culicomorpha, for example, most workers see the first branch of the three-branched radial sector as a free R_2 and the last branch as a fusion product of R_4 and R_5 (R_{4+5}) (Figs. 4.11–14). Many workers (Hennig 1954, 1973; Colless and McAlpine 1970) ascribe the loss of R_2 in the Brachycera and all Nematocera except the Tipulidae to a fusion of R_2 with R_3 (R_{2+3}). Also, in many Nematocera, e.g. some Tipulidae, the Ptychopteridae, the Trichoceridae, and some Psychodidae, the base of R_4 is fused with the base of R_3, described as a capture of R_4 by R_3. In addition, a *supernumerary radial crossvein* sometimes occurs between R_4 and R_5 in the Tanyderidae and the Tipulidae (Alexander 1929). A similar venational pattern occurs in some orthorrhaphous Brachycera, e.g. certain Asilidae (Fig. 4.32), Nemestrinidae, and Bombyliidae (Fig. 4.36). Here, what appears to be the entire basal connection of R_4 is sometimes retained (Fig. 4.32), but frequently it is reduced to a *stump vein* (Fig. 4.36). From these patterns Alexander (1929), following Shannon and Bromley (1924), concluded that in all Brachycera where the free tip of R_4 is retained, e.g. Tabanomorpha, Asilomorpha, and Muscomorpha, R_4 is connected to R_5 through the agency of a supernumerary crossvein. This theory, like Alexander's theory relating to the loss of R_2, is not accepted by all workers as being as broadly applicable as Alexander concluded. Thus, some differences are to be expected in the names applied to some veins in the radial sector by different workers.

As indicated above, MA fuses with R shortly after its origin. The brace vein between MP and R is derived from MA, but a high convexity lying close behind the last branch of Rs in most species is probably a secondary aerodynamic feature. This convexity is unusually elon-

gated and pigmented in the Syrphidae, where it is called the *spurious vein* (Figs. 4.51–52). Although it is untracheated, it functions as an afferent blood vessel in this family (Arnold 1964). Somewhat similar *false veins* or fold-like thickenings (usually concave) in the wing membrane between the main veins occur sporadically throughout the order, but especially in families of the Nematocera where the main veins are weak or reduced. Such a false vein is often evident between the posterior branch of M and CuA_1 in the Ceratopogonidae (Figs. 4.15–16), Chironomidae (Fig. 4.13), Simuliidae (Fig. 4.18), Mycetophilidae (Fig. 4.19), Cecidomyiidae (Fig. 4.22), and Scatopsidae (Fig. 4.26). There is a tendency throughout the Diptera for M_2 and M_3 to coalesce with adjacent veins or to disappear. Frequently M_{1+2} bends forward and joins R_{4+5}, and in cases where the bend is relatively sharp, as in certain Syrphidae (Fig. 4.52) and in many Calyptratae (Fig. 69), the apical portion is sometimes referred to as the 'apical crossvein'.

Primitively in the Diptera the true discal cell is present and bounded proximally by the base of M_3, posteriorly by a long, free vein (probably M_3), and distally by a true crossvein m-m (Fig. 67). However, in some Nematocera, some orthorrhaphous Brachycera, and all Muscomorpha in which a 'discal cell' is present, M_3 disappears or combines with *crossvein m-m* to form the *discal medial-cubital crossvein* (*crossvein dm-cu*; posterior crossvein, tp) and joins CuA_1 near its base (Figs. 4.6–7, 4.34, 4.36–37, 4.41–42, etc.). In this way cell m_3 is eliminated and a new *discal medial cell* (*cell dm*) abuts directly on the cubital fork, as in all Muscomorpha (Fig. 69). Moreover, crossvein dm-cu, which closes cell dm distally, is something more than the original crossvein m-m. It now connects M and CuA_1 rather than M_2 and M_3. This transformation series is best seen by comparing the wings of certain Vermileonidae (Fig. 4.35), Apioceridae (Fig. 4.31), Bombyliidae (Figs. 4.36–37), Empididae (Figs. 4.41–42), and Platypezidae (Fig. 4.48).

In most orthorrhaphous Brachycera and Muscomorpha CuA_2 joins A_1, enclosing CuP and forming a closed *posterior cubital cell* (*cell cup*) (anal cell of most dipterists) (Fig. 69). The size and shape of this cell is governed by the position of CuA_2, which ends on A_1 instead of reaching the wing margin, and it provides many useful taxonomic characters. For example, cell cup is much longer in the Syrphoidea (Figs. 4.51–52) than in most Schizophora (Figs. 4.53–76); it is relatively squarely closed in most schizophorous Muscomorpha but has an angular point in the Tephritidae (Fig. 4.56) and many Otitidae (Fig. 4.55); it is usually short but present throughout the schizophorous Muscomorpha (Figs. 4.53–76), but it is sometimes very small or absent in many acalyptrate families (Figs. 4.58, 4.65, 4.67–68) because of the absence of CuA_2. CuP is weak and untracheated in all Diptera and is seldom used as a taxonomic character. It is usually more strongly developed in the Nematocera and lower Brachycera than in the Muscomorpha. In the Muscomorpha it is strongest in the Syrphidae.

Primitively A_1 is complete and reaches the wing margin as a free vein, but there is a strong tendency, especially in the Muscomorpha, for it to be abbreviated and even absent. When it is absent, as in the Chloropidae (Fig. 4.68) and the Ephydridae (Fig. 4.67), cell cup is also absent. A_2 ends before the wing margin in all Diptera except the Tipulidae (Fig. 4.6) and the Trichoceridae (Fig. 4.8). Its sharp curvature toward A_1 (Fig. 4.73) is an apomorphic feature of all Fanniinae (Muscidae). The anal lobe varies greatly in size and shape throughout the order (Figs. 4.1–76). It is larger and more angulate in flies that swarm and complete the initial stages of mating while in flight than in weaker fliers that mate while grounded (McAlpine and Munroe 1968). Sometimes characters of the anal lobe are expressed in terms of the *anal cell* (axillary cell), which usually includes all of the wing surface behind A_1, exclusive of the alular lobe. Additional venational peculiarities are described under the different families in which they occur.

Diptera wings show a wide array of colorations and designs (de Meijere 1916); these color patterns provide useful characters in many families throughout the order. Clear wings are often described as hyaline and darkened ones as infuscated or fumose. Predominantly fumose wings with clear or pale punctuations are termed irrorated (Fig. 4.56); the clear areas are called irrorations. Dark areas are usually referred to as spots or bands, and wings possessing them are spotted, mottled, or banded.

The wing surfaces sometimes bear both macrotrichia and microtrichia. Except in many Nematocera macrotrichia are usually restricted to the veins; occasionally, as in the Culicidae (Fig. 4.14), they form scales, and in the Psychodidae (Fig. 4.2) they are lanceolate. Microtrichia may be relatively long and easily seen or very short and fine. They vary in density from partially to completely absent to uniformly very dense; bare areas on the wings of some groups, e.g. Stratiomyidae, Syrphidae, and Hippoboscidae, provide useful taxonomic characters (Vockeroth 1957). The structure of the wing membrane itself has scarcely been investigated; in the Simuliidae both surfaces are covered with small, raised buttons from which wax filaments extend through the cuticle (Hannay and Bond 1971). Information concerning various chordotonal organs and sensilla found on the wings of flies is summarized by Fudalewicz-Niemczyk (1963).

Halter. The halteres (Figs. 70–72) are reduced and highly specialized metathoracic wings; they serve as balancing organs to maintain stability in flight (Faust 1952, Pringle 1948), and their original development in the Diptera was probably an adaptation for aerial swarming (McAlpine and Munroe 1968, p. 1167). Each halter has three main parts: the *base* (scabellum), the *stem* (pedicel), and the *knob* (capitulum). The base is provided with a variety of sense organs, including *chordotonal organs*, *Hicks' papillae*, and other *campaniform sensilla* (Hennig 1973); a peculiar appendage, the *pre-*
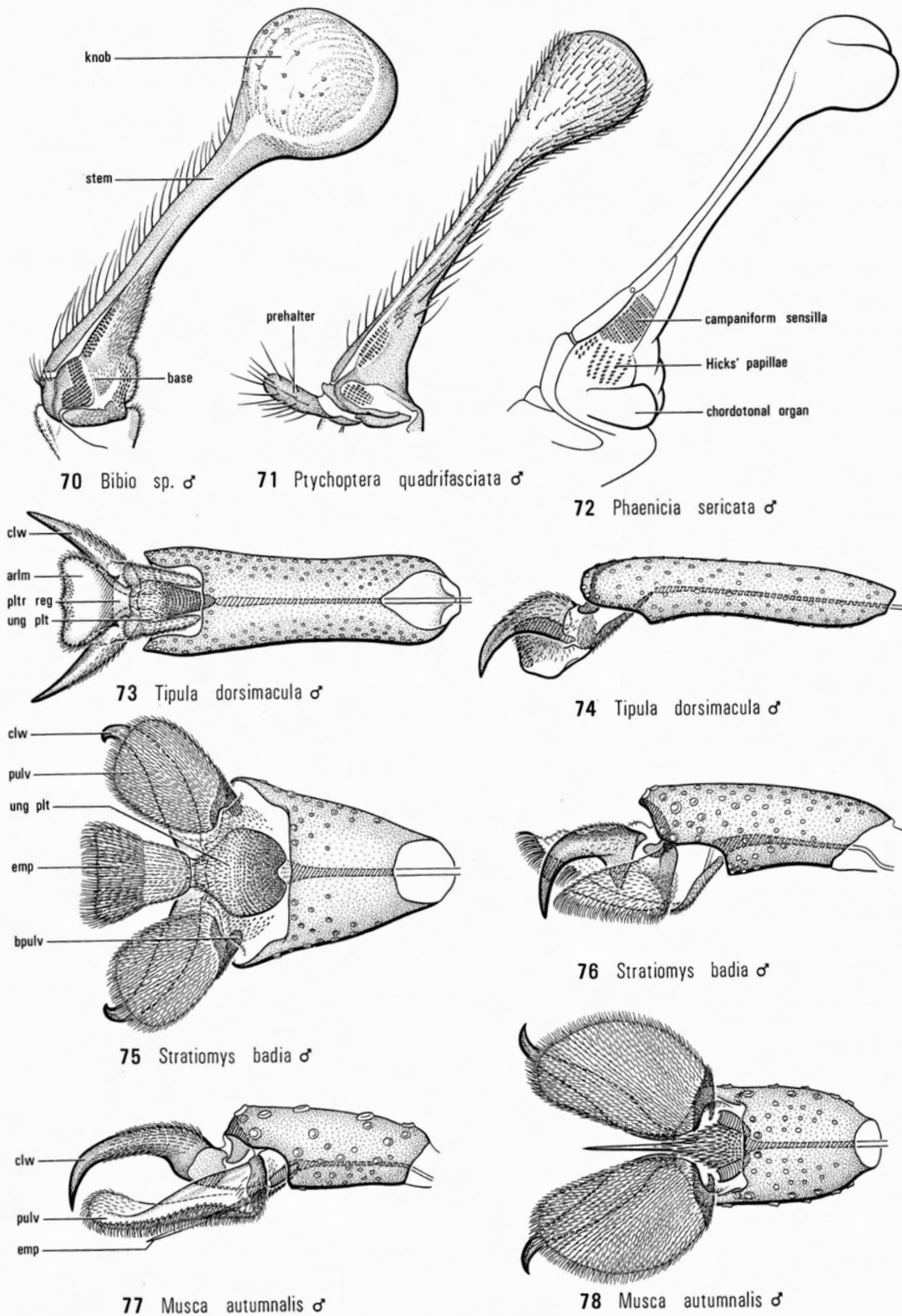
Figs. 2.70–78. Halteres and acropods: dorsal view of halter of (70) *Bibio* sp., (71) *Ptychoptera quadrifasciata* Say, and (72) *Phaenicia sericata* (Meigen) (redrawn from Pringle 1948); ventral and lateral views of acropod of (73, 74) *Tipula dorsimacula* Walker, (75, 76) *Stratiomys badia* Walker, and (77, 78) *Musca autumnalis* De Geer.

Abbreviations: arlm, arolium; bpulv, basipulvillus; clw, claw; emp, empodium; pltr reg, plantar region; pulv, pulvillus; ung plt, unguitractor plate.

halter, arises from the base in the Ptychopteridae (Fig. 71). The stem sometimes bears rows of setulae, corresponding to the setulae on C and other main veins of the fore wing, as in the Tipulidae, the Pachyneuridae, and the Tanypezidae. The knob is bulb-shaped, and according to Brauns (1939) it usually contains large-sized cells. In mature specimens it varies from whitish to brown or black. Black-knobbed halteres frequently serve as a useful character at the species level as in *Leptometopa halteralis* Coquillett (Milichiidae), at the generic level as in *Melanagromyza* (Agromyzidae), and at the family level as in Lonchaeidae.

Legs. Each leg consists of a *coxa* (*pl. coxae*), *trochanter*, *femur* (*pl. femora*), *tibia* (*pl. tibiae*), and *tarsus* (*pl. tarsi*) (Figs. 2, 3). The structure of these segments differs in the *foreleg*, *midleg*, and *hindleg* (pro-, meso-, and meta-thoracic legs), and all legs sometimes show striking modifications on all segments. The diversity of leg structure provides many taxonomic characters in most families throughout the order. The different leg surfaces are ascertained by imagining that all the legs are fully extended laterally, parallel to each other and at right angles to the main axis of the body. Thus each segment of each leg has an anterior, posterior, dorsal, and ventral surface (Fig. 1). Other surfaces are named on the same basis, e.g. anterodorsal and posteroventral.

All coxae articulate dorsally with a *coxifer* or pleural process at the ventral end of the pleural suture of each thoracic segment. Ventrally the fore coxa articulates with the side of the exposed prosternum. The mid and hind coxae adjoin their corresponding invaginated *furcasterna*. Usually all coxae are short and stout, but in some forms with raptoral legs, e.g. certain Empididae (Fig. 47.2), the fore coxa is as long as or longer than the femur and relatively slender. In the Mycetophilidae all coxae are rather long. The mid coxa is divided into an anterior region, the *eucoxa*, and a posterior region, the meron. The meron is more or less incorporated with the lower portion of the epimeron (*see* "Mesopleuron"). To restore the mobility of the mid coxa, its eucoxa is transversely divided into a *basicoxa* and a *disticoxa*. Examples of special coxal processes include the *mid coxal prong* of most Muscomorpha (Fig. 66) (absent in the Platypezidae, the Pipunculidae, the Conopidae, and most Pyrgotidae), the hooked spines on the mid coxa of *Fannia* (Muscidae) and *Amphipogon* (Piophilidae), and the male *coxal processes* in some Mycetophilidae. The fore and mid coxae, at least, of most species have one or more discrete clusters of sensory setulae near their outer bases.

The trochanter is usually small and immovably united with the femur, as in most insects. From a taxonomic standpoint it is relatively unimportant in the Diptera. In many Syrphidae and Sarcophagidae it bears a spur, a tubercle, or specialized setae.

The femora and tibiae are usually about the same length and are almost always the longest of the leg segments. Both are extremely long and slender in many Tipulomorpha, but the femora are usually stouter than the tibiae. The fore femur is particularly strongly developed in forms with raptorial forelegs, e.g. some Ceratopogonidae, certain Empididae (Figs. 47.2, 47.8), and a few Ephydridae. All femora may be armed with specialized spines, tubercles, or processes, especially on the ventral surfaces. In many groups the distal end of the anteroventral surface of the fore femur bears a comb-like row of spinules called a *ctenidium* (*pl. ctenidia*); frequently one bristle in this position is outstanding and it is sometimes referred to as a *ctenidial spine* (Fig. 4.140). Similar ctenidia may be found on the other femora. Sometimes, as in the Sepsidae and in *Hydrotaea* (Muscidae), special modifications of the fore femur and tibia occur in the male for holding the wings of the female during copulation. The hind femur and tibia of the male of *Sepedon* (Sciomyzidae) are bent in a peculiar fashion, and the femur is provided with stout processes, also for use during mating. A crest-like, sound-producing *scraper* occurs on the posterior surface of the hind femur as part of a stridulation mechanism (*see* "Abdomen") in certain Agromyzidae and Chamaemyiidae (von Tschirnhaus 1972). The hind femur of a few forms, e.g. Megamerinidae and *Meromyza* (Chloropidae), are unusually strongly developed.

The tibiae are usually provided with serially arranged setulae and bristles, and they may also possess spurs, spines, flanges, and various kinds of processes and ctenidia. Sometimes, as mentioned above, the armature varies between the sexes, and special clasping modifications are developed in the male for holding the female during copulation. The tibiae may bear apical combs of setulae, as in many Chironomidae (Figs. 29.59–66) and Anisopodidae (Figs. 19.8–10); in some families, e.g. Mycetophilidae, articulated *spurs* are present (Figs. 14.79–80); in others, e.g. Bibionidae (Figs. 13.4–5) and Scatopsidae, the fore tibia has strong digging spines utilized for depositing the eggs in the ground. In the Calyptratae, there is sometimes an outstanding posterodorsal bristle called the *calcar* situated on the hind tibia at or beyond the middle. Specialized areas occur on the tibiae in several families; examples include the *tibial organ* (sensory area) on the hind tibia of many Chloropidae (Anderson 1977) and a similar area called the *osmeterium* (*pl. osmeteria*) on the hind tibia of some Sepsidae. In the Sepsidae these specialized areas have been interpreted as producers of a sexual scent substance (Šulc 1928–1929). Hennig (1973) suggested that perhaps a similar tibial gland that Kazjakina (1966) found in *Dolichopus*, and a gland in the proximal section of the fore tibia of the ocydromioid section of the Empididae described by Tuomikoski (1966), have a similar function.

Virtually all Diptera have five *tarsomeres* (tarsal segments) on all legs (Figs. 2, 3). They are called *first*

(basitarsus, metatarsus, proximal tarsal segment), *second*, *third*, *fourth*, and *fifth* (distitarsus) *tarsomeres*. All the first tarsomeres are greatly shortened in the trichocerid genus *Paracladura* (Fig. 18.6). The number of tarsomeres, however, is reduced only in a few Cecidomyiidae and Phoridae. In the cecidomyiid subfamilies Cecidomyiinae and Porricondylinae the first tarsomere is very short and more or less fused with the second tarsomere (Fig. 16.81), but in the tribe Heteropezini (Porricondylinae) there may be as few as two distinguishable tarsomeres. In the myrmecophilous phorid genus *Myrmosicarius*, the four distal tarsomeres of the female are completely fused (Borgmeier 1929). All tarsomeres are generously provided with various setae, setulae, sensory hairs, and chemoreceptors. The first tarsomere, especially on the foreleg and hindleg, is frequently modified. In the male of certain Drosophilidae the first tarsomere of the foreleg bears *sex combs*; in the male of Coelopidae and Dryomyzidae it usually has a number of stout setae and a ventral claw-like process. In the male of the dolichopodid genus *Enlinia* the entire tarsus is sometimes greatly modified (Steyskal 1975). Peculiar structures also occur on the first tarsomeres of the midleg and hindleg in some members of these groups. The male of the dolichopodid genus *Campsicnemus* often has a greatly modified mid tarsus. The female of *Eurygnathomyia* (Pallopteridae) has two unusually stout bristles arising from the ventral surface of the first tarsomere of the foreleg only. The male of certain species of *Hylemya* (Anthomyiidae) possesses a series of long, closely placed setae on the dorsal surface of the first tarsomere of the midleg. The male of *Lonchaea striatifrons* Malloch (Lonchaeidae) has several stout setae ventrally near the base of the first tarsomere of the hindleg. The first tarsomere of the hindleg is swollen in the male of several families, especially some Bibionidae (Fig. 13.1), Empididae (Fig. 47.1), and Platypezidae (Fig. 4.124); in the Platypezidae the other segments of the hind tarsus are also sometimes greatly broadened and flattened. In the Sphaeroceridae the first tarsomere of the hindleg is unusually short and stout (Fig. 4.149). Each first tarsomere of *Bittacomorpha* (Ptychopteridae) contains a tracheal sac, possibly for assisting in its peculiar drifting flight (Brues 1900; Alexander, Ch. 22).

On the distal end of the fifth tarsomere is the *acropod* (posttarsus, also sometimes inappropriately called the pretarsus) (Figs. 73–78). It is a small terminal segment believed to be homologous with the dactylopodite of a crustacean limb (de Meijere 1901). Because it is so closely associated with the fifth tarsomere it is usually wrongly regarded as an integral component of that segment. Its evolutionary development in the Diptera provides some characters that are of fundamental importance in the general classification of the order. The principal sclerite of the acropod is the ventrally located *unguitractor plate*; distally it bears a pair of *claws* (ungues), and proximally it is attached to the distal margin of the fifth tarsomere. The distal end of

the acropod sometimes protrudes as a median, more or less membranous, sac-like *arolium*. The ventral surface of the arolium sometimes forms a *plantar region* that merges with the distal end of the unguitractor plate. An unpaired median process, the *empodium* (*pl. empodia*), arising from the ventral or plantar region of the arolium, is usually present; when present it is *pulvilliform* or *setiform* in structure. On each side of the acropod near the lateral margins of the unguitractor plate is a small sclerite called the *basipulvillus*; this pair of plates provide the bases for a pair of flap-like processes, the *pulvilli* (*sing. pulvillus*). Both the pulvilli and the empodium act as adhesive organs and sometimes possess hollow hairs called *retineriae* (*sing. retineria*), through which a viscous substance is secreted.

The presence or absence of pulvilli or an empodium or both, together with the form of the empodium, serve as important characters in the Diptera. So far as is known true pulvilli are absent in the Tipulomorpha (Figs. 73, 74) and the Psychodomorpha (Hennig 1973). They are present in some form in practically all other groups. A discrete empodium is also lacking in the Tipulomorpha; here the arolium forms a simple, rounded, sac-like median lobe. But some form of a distinct empodium can usually be distinguished in all other families. A pulvilliform empodium occurs in certain Ptychopteridae, in most Bibionomorpha (absent in many Mycetophilidae), in most Tabanomorpha (Figs. 75, 76), and in a few Asilomorpha [Acroceridae (Fig. 43.36), some Nemestrinidae, several clinoceratine Empididae, and the dolichopodid genus *Hydrophorus*]. A setiform empodium occurs in most Culicomorpha (Figs. 29.73–76) and Asilomorpha, and in practically all Muscomorpha (Figs. 77, 78).

Besides being organs of locomotion, the legs of Diptera serve many other purposes. The fore tarsus is usually provided with chemoreceptors for tasting; several contact chemoreceptors have also been found on the tibiae and femora (Hennig 1973). Almost certainly, all tarsi are used as tactile organs. The forelegs of many Chironomidae and the hindlegs of the Culicidae are used somewhat like antennae. As mentioned above, the forelegs of certain Ceratopogonidae, Empididae, and Ephydridae have become raptorial, and in the male of certain groups these and other legs are frequently modified for holding onto the female during copulation. Nearly all flies use their legs to clean and preen themselves, and comb and brush-like patches of setulae are sometimes present in various places for these purposes. In many groups the legs are peculiarly decorated for sexual or combative display. Frequently the color patterns of legs in the Diptera appear to mimic similar patterns found in the Hymenoptera. For example, the forelegs of some Micropezidae simulate ichneumonid antennae in having a transverse white band and in being vibrated in front of the head. Similarly, the forelegs of many Syrphidae simulate the antennae of aculeate Hymenoptera. Such patterns are assumed to be protective adaptations.

ABDOMEN

As in all insects, the abdomen of a fly (Figs. 79–141) is primitively composed of 11 segments. The terminal portion, consisting of the rudiments of segment 11, namely a pair of *cerci* (*sing. cercus*) and the *anus*, is called the *proctiger* (anal segment). There is no evidence of a 12th segment.

By inference, the primitive number of *abdominal spiracles* (stigmata) in the Diptera is eight, and eight pairs still occur in the female of some Tipulidae, Bibionidae, Chironomidae, Thaumaleidae, Stratiomyidae, Scenopinidae, Rhagionidae, Mydidae, Apioceridae, and Asilidae (Crampton 1942). But the occurrence of seven pairs is typical of the Diptera in general, and a maximum of this number in the male is an apomorphic character of the order (Hennig 1973). Loss of certain spiracles is relatively common throughout the order. Abdominal spiracles are said to be missing entirely in *Deuterophlebia*, *Nymphomyia*, and *Psychoda phalaenoides* (Linnaeus) (Tokunaga 1936), and the absence of spiracles 6 and 7 is fairly common, especially in the male of many Schizophora and in the female of almost all Muscidae. In male Schizophora, the number of abdominal spiracles (five or six pairs versus seven pairs) is sometimes a useful taxonomic character at family and subfamily levels (Griffiths 1972). In both sexes the spiracles are usually borne in the pleural membrane just below the lateral margins of the tergites (Figs. 79, 98, 111, 134); frequently some or all of them become enclosed within the lateral extremities of the tergites, as in the Calyptratae (Figs. 104, 137). Usually each spiracle is associated with its own segment, but some shifting may occur, especially of spiracles 6 and 7 in the male of the Muscomorpha and of spiracle 7 only in the female of the Scathophagidae and the Anthomyiidae (Fig. 104).

The genital opening is located anteroventrally to the anus in both sexes. The female genital opening is between sternites 8 and 9 (Hennig 1973) and serves to identify those two segments in that sex. The *aedeagus* (copulatory organ, intromittent organ, mesosome, penis, phallosome, phallus) is the male organ that bears the genital opening or openings; it arises immediately behind sternite 9 and serves to identify sternites 9 and 10 in the male.

The basal segments of the abdomen (preabdomen), consisting of segments 1–5 or 1–6, are frequently broader than the terminal portion of the abdomen, referred to as the *terminalia* (postabdomen, hypopygium) (Figs. 79, 109, 112). The distinction between the basal and terminal sections is much more evident in the Muscomorpha (Figs. 109, 134), especially, than in more primitive Diptera (Figs. 79, 112). The terminalia consist of the terminal complex of modified genital and anal segments, plus any adjacent segments that show modifications for copulation and oviposition.

Basically each abdominal segment consists of a dorsal tergite and a ventral sternite connected laterally by the pleural membrane. The density, size, and arrangement of hairs and bristles on any or all of both the tergites and sternites frequently provide useful taxonomic characters. Of special interest are one or more pairs of peculiar *sensory setulae* (alphasetae, sensilla trichodia) that are frequently present on the anterior margin of the sternites (Fig. 135); these setulae are very persistent and serve to mark the positions of sternites even when the sternites are displaced or atrophied, as they are in the rotated terminalia of the male Muscomorpha. Similar setulae are sometimes present on the tergites as well. Abdominal glands, such as dermal glands, scent-producing organs, ampullae, or tubes, occur in several groups (Hennig 1973, pp. 204–205). A *stridulatory file*, activated by a *resonator ridge* on the hind femur, is present on the lateral extremities of the fused *syntergite 1 + 2* and on the pleural membrane in both the male and the female of certain representatives of a few families, e.g. Agromyzidae and Chamaemyiidae (von Tschirnhaus 1972). An abdominal stridulation organ that interacts with the wings occurs in certain Tephritidae (Hennig 1973).

A general trend toward shortening of the abdomen is evident throughout the order. Although exceptions occur, the abdomen is usually longer and more slender, and with more of the terminal segments exposed, in the Nematocera and orthorrhaphous Brachycera than in the Muscomorpha. This shortening takes place by coalescence of the basal segments, reduction or coalescence of terminal segments, telescopic retraction of the terminal segments into proximal segments, or downward and forward folding (flexion) of the terminal segments, or some combination of these ways.

Tergite 1 is almost always shortened and closely associated with tergite 2 (Young 1921). In the Muscomorpha (Figs. 110, 134) it is reduced to a narrow band and is fused with tergite 2 to form syntergite 1 + 2. This syntergite is usually marked laterally by a transverse suture of varying degrees of completeness, called the *adventitious suture*. Sternite 1, also, is usually more or less reduced and is sometimes closely associated with sternite 2 (Figs. 112, 137). It is said to be absent in a few forms, e.g. *Anopheles* (Culicidae), *Mydas*, *Lonchoptera*, *Pipunculus*, and *Copromyza* (Sphaeroceridae) (Young 1921); probably it is frequently fused with sternite 2, as in the Tabanidae (Bonhag 1951). Fusion of various abdominal tergites sometimes occurs; for example tergites 2 and 3 are fused in the Ptychopteridae and several tergites are fused in certain Tachinidae and Cryptochetidae. Abdominal segments 3–5 are frequently much reduced in the Asteiidae.

Lateral extension of the abdominal tergites is characteristic of the Calyptratae; the lateral margins of tergites 2–5 therefore sometimes extend over the reduced, frequently narrow sternites. In many Tachinidae the sternites are so reduced that the tergites almost encircle the segments. The enclosure of the spiracles in the margins of the tergites, which is especially characteristic

in the Calyptratae (Fig. 137), may be related to this lateral expansion of the tergites.

In some Muscomorpha, especially in the Calyptratae, sternite 5 of the male is excised posteriorly and forms part of the male copulatory apparatus; frequently it is adorned with *sternal processes*, lobes, tubercles, setae, and other modifications (Fig. 137). In a few groups, e.g. Micropezidae and Sepsidae, somewhat similar processes sometimes occur on some of the preceding sternites as well.

In the Nematocera and orthorrhaphous Brachycera segments 6–8 of both sexes are usually more or less permanently exposed in much the same manner as the more proximal segments. Throughout the Muscomorpha there is an increased tendency for more of these segments to be telescoped into each other and withdrawn into segment 5 in the female, or folded into a ventral *genital pouch* in the membrane adjoining the posterior margin of sternite 5 in the male. In discussing both male and female terminalia the *pregenital segments* are sometimes distinguished from the *postgenital segments*; the pregenital segments of the terminalia refer to those segments proximal to the main genital opening, and the postgenital segments are those distal to it. In the Nematocera and lower Brachycera usually only the segments beyond segment 7 are modified for some aspect of reproduction. In males of the Muscomorpha (Figs. 132–138) both the tergal and sternal elements of the pregenital segments, namely segments 6, 7, and 8, are more or less reduced, asymmetric, and often fused into a composite sclerite or *syntergosternite* (Figs. 134, 137) (first genital sclerite, prehypopygial sclerite, protandrium) (*see* "Flexion and rotation," last paragraph).

Female terminalia. Representative female terminalia are illustrated in Figs. 79–110. In higher Brachycera the segments beyond segment 5 or 6 form a more or less tapered tube with various modifications for egg laying. Often in the Diptera all the elements of the terminalia, including the cerci, are called the *ovipositor* (oviposition tube, oviscapt, ovicauda), but the dipterous ovipositor as such is not homologous with the true orthopteroid-type ovipositor. The orthopteroid ovipositor is formed from two pairs of appendages, the anterior and posterior gonapophyses, that arise from sternites 8 and 9, respectively, whereas the dipterous ovipositor may also include elements of segments that are proximal to and distal to segments 8 and 9. Moreover, it has no gonapophyses, at least on sternite 9.

The *genital opening* (genital aperture, genital orifice, gonotrema, reproductive opening, vulva) between segments 8 and 9 leads to a pouch-like or tubiform *genital chamber* (vagina, atrium). In the Diptera, as in most insects, the paired oviducts unite to form a common oviduct that opens by means of the *primary gonopore* in the dorsal wall of the genital chamber. A saccate, dorsal invagination of the genital chamber called the *bursa* (bursa copulatrix, bursa inseminalis) occurs in some

families, e.g. Tipulidae (Byers 1961, Frommer 1963), Culicidae (Laffoon and Knight 1971), and Asilidae (Reichardt 1929), but it is not known how widely this structure is distributed in the order (Hennig 1973). In the Muscomorpha the anterior portion of the genital chamber is sometimes enlarged for retaining developing eggs and is called the *uterus* (ovisac), which is distinguished from the posterior part, the *vagina*. In the Hippoboscoidea, the larvae develop in the uterus until they are ready to pupate. In viviparous Sarcophagidae and Oestridae the uterus has an enlarged pouch for retaining developing larvae. In most Tachinidae the uterus is lengthened and often coiled for retaining developing eggs.

The internal structures of ectodermal origin associated with the female reproductive system include the *spermathecae*, the *accessory glands* (appendicular glands, colleterial glands, parovaria), and the *ventral receptacle*.

The spermathecae are more or less spherical or cylindrical, usually heavily sclerotized, strongly differentiated receptacles in which the spermatozoa are stored and from which the spermatozoa are released onto the eggs as they are passed from the oviduct. They are located at the ends of slender *spermathecal ducts* that lead to the *spermathecal openings*. The predominant number of spermathecae in all major sections of the Diptera is three (Sturtevant 1925–1926, Hennig 1958), and three is considered the basic number for the order (Downes 1968, Hennig 1973) as opposed to one in most other orders. However, their number is frequently reduced to two or one, and in a few groups, e.g. most Chamaemyiidae (Figs. 107, 108), there are four. The spermathecae may be relatively smooth and spherical, wrinkled and cylindrical, telescoped, or corkscrew-like in shape. Sometimes they are weakly sclerotized, and in the few instances where they have been reported absent the faintly differentiated membranous sacs have probably been overlooked.

Primitively there are three separate spermathecal openings, and they are located on a free, relatively unmodified sternite 9 (Downes 1968). This condition still exists in a few primitive families, e.g. Blephariceridae, Tanyderidae, and some Tipulidae, but in most Nematocera a common spermathecal duct opens on sternite 9 some distance behind the primary gonopore (Downes 1968). Usually the spermathecal opening is found internally, in the dorsal wall of the genital chamber. In the Nematocera and many orthorrhaphous Brachycera it is often associated with modified derivatives of sternite 9.

The accessory glands are unsclerotized organs that are usually associated with egg laying. One or two are usually present, depending on the species or group (Sturtevant 1925–1926). Generally, they produce an adhesive for attaching eggs to a substrate or for gluing the eggs together in a mass as they are laid. In some pupiparous groups, e.g. Glossinidae and Hippoboscidae,
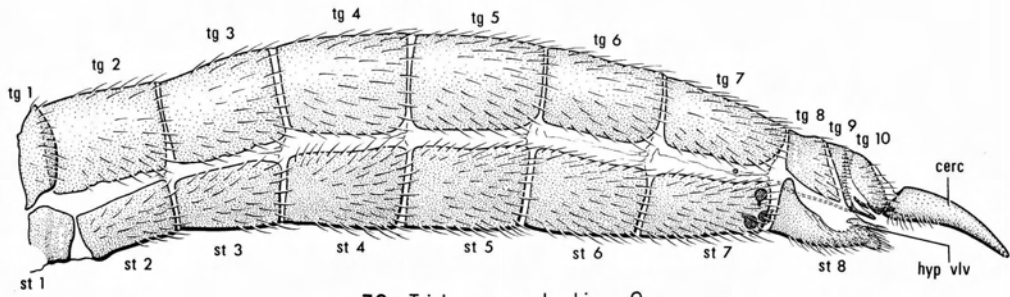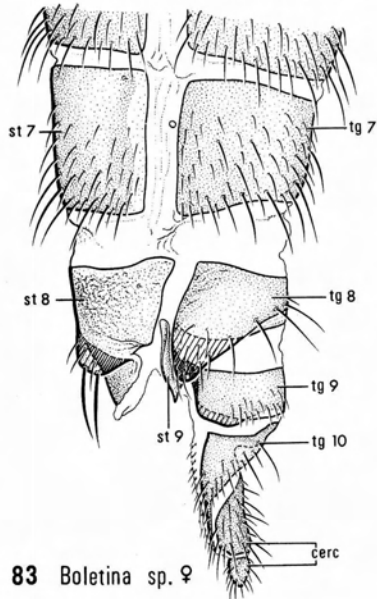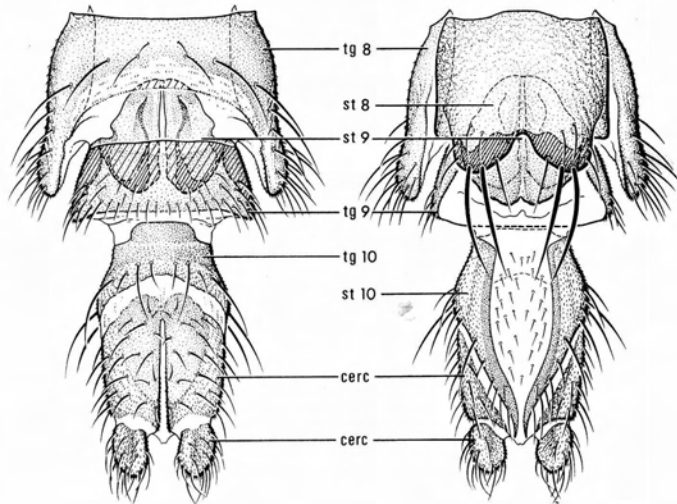
79 Trichocera columbiana ♀
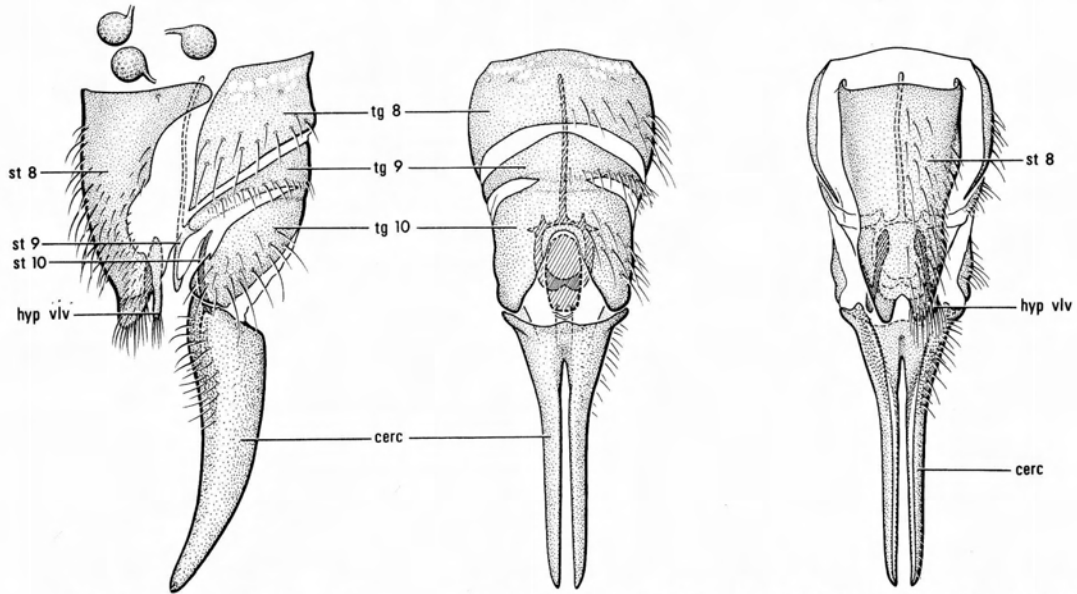
**80** Trichocera columbiana ♀   **81** Trichocera columbiana ♀   **82** Trichocera columbiana ♀

83 Boletina sp. ♀   **84** Boletina sp. ♀   **85** Boletina sp. ♀

Figs. 2.79–85. Female abdomens and terminalia: (79) left lateral view of entire abdomen of *Trichocera columbiana* Alexander; (80) left lateral, (81) dorsal, and (82) ventral views of terminalia of *T. columbiana*; (83) left lateral, (84) dorsal, and (85) ventral views of terminalia of *Boletina* sp. (Fig. 83 drawn to larger scale than Figs. 84 and 85).

Abbreviations: cerc, cercus; hyprct, hypoproct; hyp vlv, hypogynial valve; st, sternite; tg, tergite.
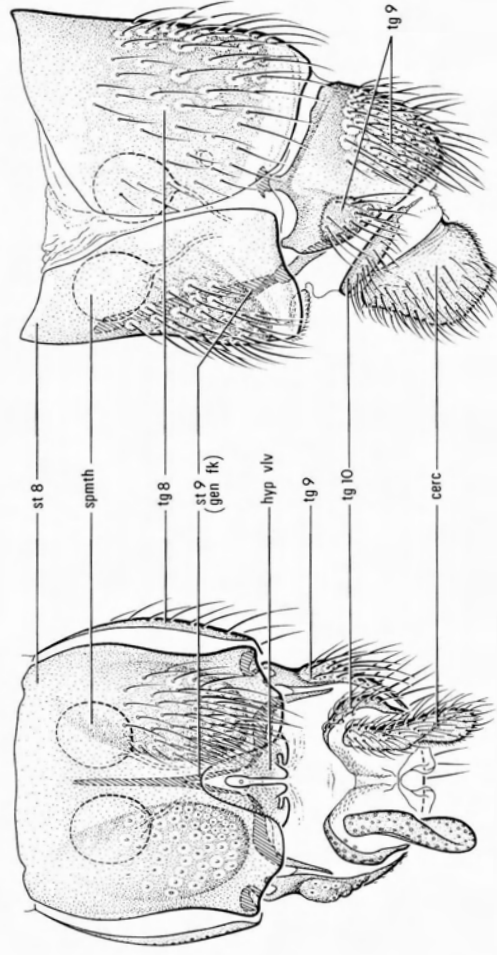
86 Chironomus plumosus ♀

87 Chironomus plumosus ♀
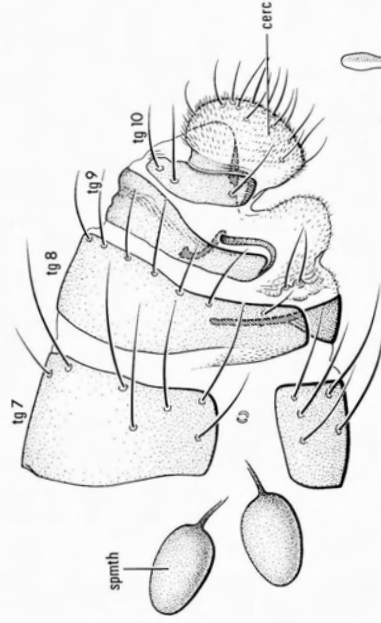
88 Leptoconops (Brachyconops) californiensis ♀
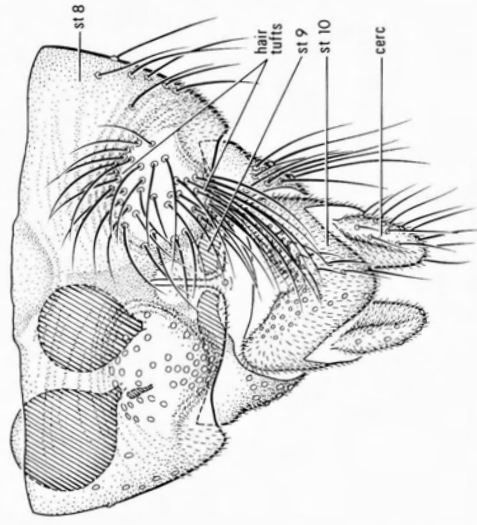
89 Probezzia concinna ♀
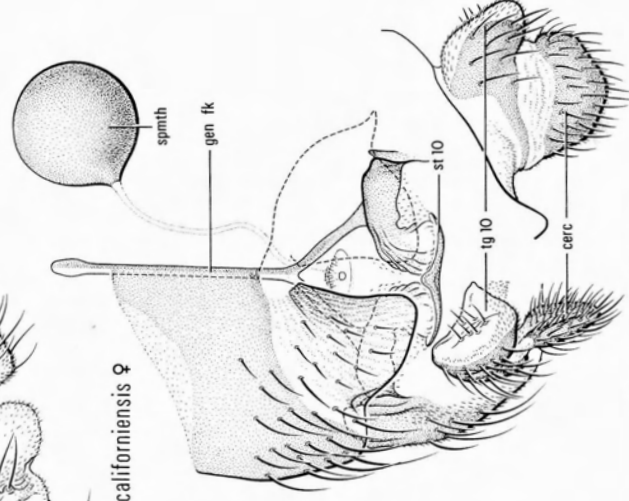
90 Prosimulium decemarticulatum ♀

Figs. 2.86–90. Female terminalia of Culicomorpha: (86) ventral and (87) left lateral views of *Chironomus plumosus* (Linnaeus); (88) *Leptoconops (Brachyconops) californiensis* Wirth & Atchley, left lateral view; (89) *Probezzia concinna* (Meigen), ventral view; (90) *Prosimulium decemarticulatum* (Twinn), ventral and left lateral (*inset*) views.

Abbreviations: cerc, cercus; gen fk, genital fork; hyprct, hypoproct; hyp vlv, hypogynial valve; spmth, spermatheca; st, sternite; tg, tergite.
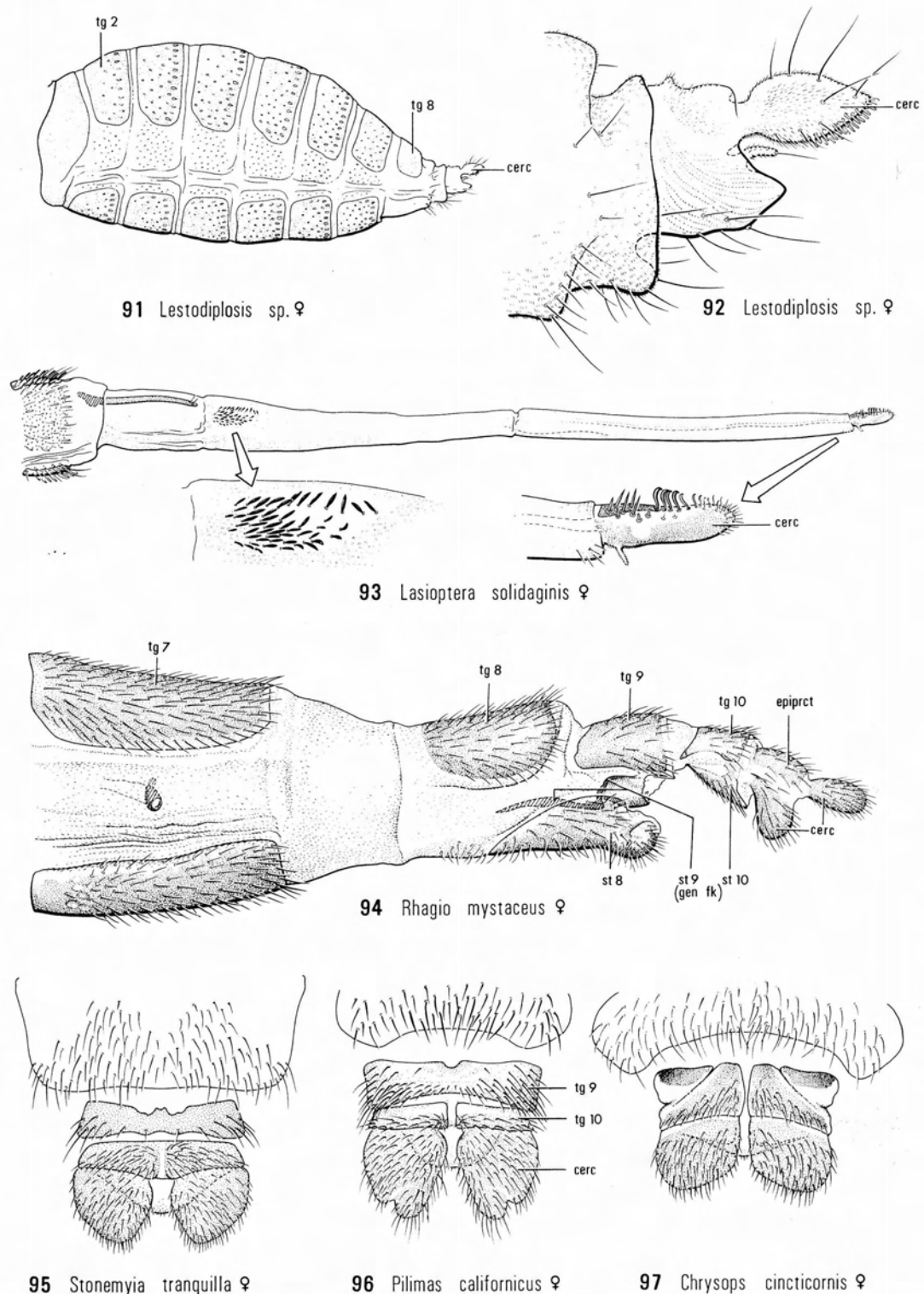
Figs. 2.91–97. Female abdomens and terminalia of Cecidomyiidae and Tabanomorpha: (91) entire abdomen and (92) terminalia in greater detail of *Lestodiplosis* sp., left lateral view; (93) specialized terminalia of *Lasioptera solidaginis* Osten Sacken, left lateral view; (94) abdomen of *Rhagio mystaceus* (Macquart), left lateral view; (95) terminalia of *Stonemyia tranquilla* (Osten Sacken); (96) terminalia of *Pilimas californicus* (Bigot) and (97) terminalia of *Chrysops cincticornis* Walker, dorsal view, showing various conditions of tergites 9 and 10.

Abbreviations: cerc, cercus; gen fk, genital fork; st, sternite; tg, tergite.

98 Rhaphiomidas acton ♀

99 Rhaphiomidas acton ♀

100 Rhaphiomidas acton ♀

101 Rhamphomyia filicauda ♀

102 Dolichopus brevipennis ♀ **103**
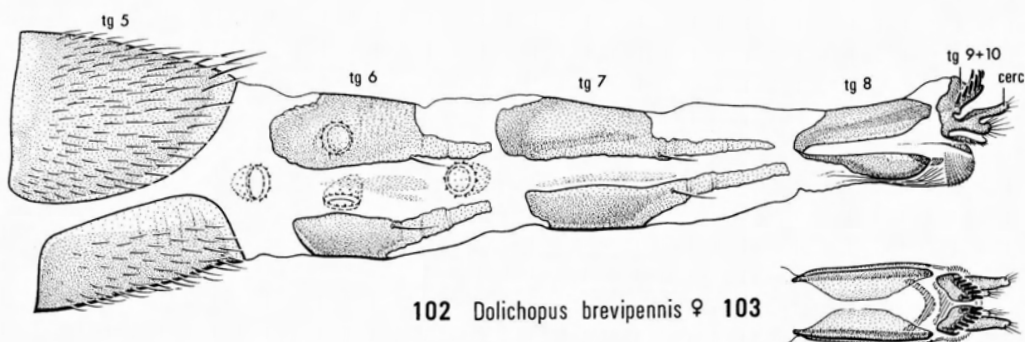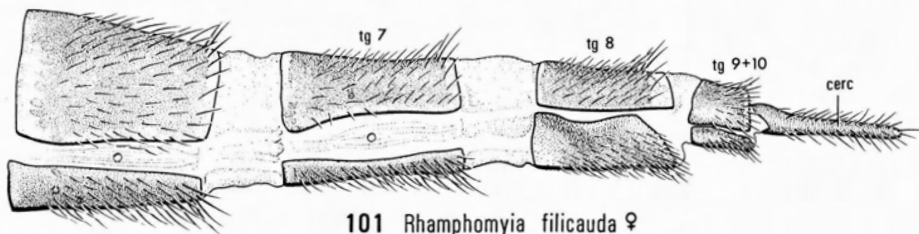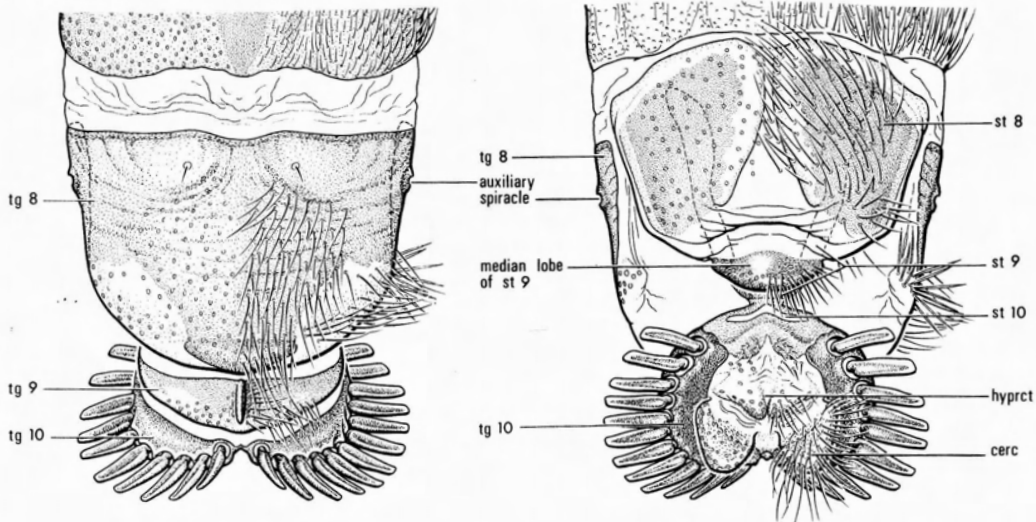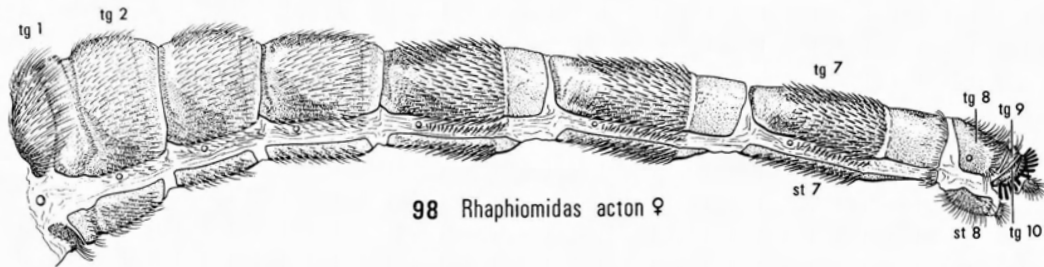
Figs. 2.98–103. Female abdomens and terminalia of Asilomorpha: (98) left lateral, (99) dorsal, and (100) ventral views of entire abdomen of *Rhaphiomidas acton* Coquillett (Apioceridae); (101) *Rhamphomyia filicauda* Henriksen & Lundbeck (Empididae), left lateral view; (102) left lateral and (103) ventral views of *Dolichopus brevipennis* Meigen.

Abbreviations: cerc, cercus; hyprct, hypoproct; st, sternite; tg, tergite.
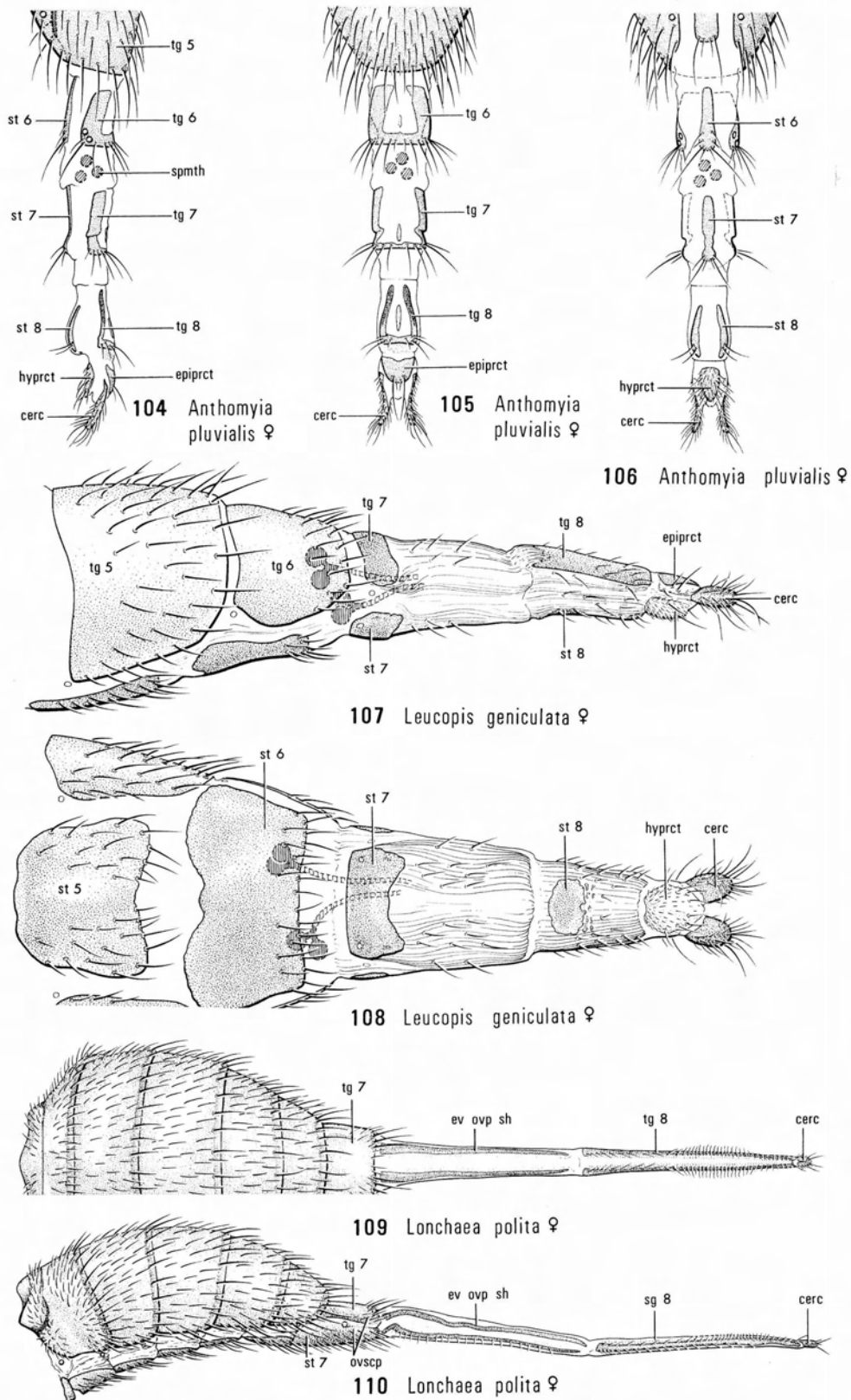
Figs. 2.104–110. Female terminalia of Schizophora: (104) left lateral, (105) dorsal, and (106) ventral views of *Anthomyia pluvialis* (Linnaeus); (107) left lateral and (108) ventral views of *Leucopis geniculata* Zetterstedt; (109) left lateral and (110) ventral views of *Lonchaea polita* Say.

Abbreviations: adv sut, adventitious suture; cerc, cercus; epiprct, epiproct; ev ovp sh, eversible ovipositor sheath; hyprct, hypoproct; ovscp, oviscape; sg, segment; spmth, spermatheca; st, sternite; tg, tergite.

they serve as 'milk glands' for the nourishment of the larvae. They may be pear-shaped, subspherical, long and cylindrical, or complex ramose structures. The ducts of the accessory glands open into the anterodorsal part of the genital chamber, usually close behind the spermathecal openings.

The ventral receptacle is known only in certain acalyptrate families (Sturtevant 1925–1926). It arises from the anteroventral portion of the genital chamber and functions as a sperm reservoir. It may be a simple membranous pocket, as in *Thaumatomyia* (Chloropidae); a long, fine, much coiled tube, as in *Stegana* (Drosophilidae); or a large, heavily sclerotized pouch, as in Ephydridae. Unlike other uterine pouches that may also occur, the ventral receptacle never has a muscular wall of its own.

In the Nematocera and orthorrhaphous Brachycera the pregenital segments of the female terminalia are usually relatively unmodified. The membranous intersegmental region between them is short and the sclerites themselves usually remain more or less permanently exposed. There is a trend, however, beginning with the orthorrhaphous Brachycera (especially in the Rhagionidae, Fig. 94) and progressing through the Muscomorpha in which the main segments of the terminalia become more slender and more widely spaced, with relatively long, membranous intersegmental regions to permit a greater degree of telescoping. Special names have not been applied to the parts of segment 6, but segment 7 is modified to form a bulbous *oviscape* in several family groups of the Muscomorpha, e.g. Nerioidea, Tephritoidea (Figs. 109, 110), and Agromyzidae. Frequently, especially in the Calyptratae, spiracle 7 becomes shifted forward to segment 6, which thus exhibits two pairs of spiracles (Fig. 104). In many cases throughout the order, but especially in the Muscomorpha, both the tergites and the sternites of segments 7 and 8 are mainly membranous and they are sometimes reduced to elongate, single or paired strips or rods (Fig. 106). In the piercing-type ovipositor of the Tephritoidea (Figs. 109, 110) both the tergite and sternite of segment 8 are divided into elongate rods to form the main shaft of the ovipositor tube. Sometimes segment 8 is referred to as the *gynium*; thus, in the Tipulidae at least, its tergite and sternite are called the *epigynium* and the *hypogynium* (subgenital plate), respectively. A pair of processes arising from the hypogynium, possibly homologous with the anterior gonapophyses of the orthopteroid ovipositor, are called *hypogynial valves* (hypovalvae, sternal valves, ovipositor lobes) (Figs. 79–82). A single, median plate in the same position in the Blephariceridae is called the *hypogynial plate* (oviscapt).

The tergites and sternites of segments 9 and 10 are present in the basic pattern of the Diptera (Hennig 1973). They are clearly evident in several primitive groups (Saether 1977), including the Tipulidae (Frommer 1963), the Sciaridae (Colless and McAlpine 1970),

orthorrhaphous Brachycera (Nagatomi and Iwata 1976), and the Tabanoidea (Stuckenberg 1973). They are said to be present in some Syrphidae (Lehrer 1971) and are also evident in some Phoridae, e.g. *Spinophora*. As noted above, sternite 9 is usually highly modified and is frequently greatly reduced or absent. In many Nematocera and orthorrhaphous Brachycera it occurs as a mainly internal *genital fork* (furca, vaginal apodeme) in the dorsal wall of the genital chamber; differences in its shape sometimes provide useful taxonomic characters, as in the Simuliidae (Fig. 90). The *preatrial* and *postatrial sclerites* of the Culicidae are probably also derived from sternite 9. Nagatomi and Iwata (1976) reported that sternite 9 is usually absent in orthorrhaphous Brachycera, but they evidently did not realize that the structure that they called the genital fork is a derivative of sternite 9 (Bonhag 1951, pp. 156–157). In most Muscomorpha, however, sternite 9 is indistinguishable or absent. Tergite 9 is usually present as a dorsal plate in the Nematocera and orthorrhaphous Brachycera, but beginning in the Asilomorpha and throughout the Muscomorpha it is usually indistinguishably fused with a composite sclerite sometimes incorrectly called the epiproct or it is absent (Herting 1957).

Tergite 10 is frequently present as a dorsal plate in the Nematocera (Figs. 79–90) and orthorrhaphous Brachycera (Figs. 94–103). Sometimes it is closely associated or fused with tergite 9. It is sometimes divided into two plates, which often become very small or disappear (Nagatomi and Iwata 1976). In many orthorrhaphous Brachycera, e.g. Mydidae, Asilidae, Apioceridae (Figs. 98–100), Therevidae, Scenopinidae, and Dolichopodidae (Figs. 102, 103) (for references, see Hennig 1973), tergite 10 (not tergite 9 as interpreted by Hennig and others) is divided into a pair of spine-bearing hemitergites, sometimes called acanthophorites, used for digging during oviposition; these structures have usually been wrongly assumed to be derived from tergite 9 (Adisoemarto and Wood 1975, Irwin 1976). Sternite 10 (intra-anal plates of the Tipulidae, ventral plates of the Tabanidae) may be fused with sternite 11 or virtually absent (Frommer 1963, Bonhag 1951).

The true proctiger, possibly including vestiges of segment 11, is the anus-bearing region behind segment 10. Some authors refer to elements of segment 11 in some primitive families (Frommer 1963, Tipulidae; Bonhag 1951, Tabanidae), but in general no separate tergite (true epiproct) or sternite (true hypoproct) of segment 11 is found in the female Diptera. Because of the absence of segment 11 and because segment 10, especially, is so closely integrated with the true proctiger, the term is often extended by dipterists to include all the structures behind segment 9.

The paired cerci are usually the most prominent elements of the proctiger. Each cercus is primitively two-segmented in the female of both the Nematocera and the Brachycera, but it is independently reduced to one segment in many groups in both suborders, e.g. most

Nematocera, Athericidae, Tabanidae, and Nemestrinidae, and perhaps all Asilomorpha and Muscomorpha (Hennig 1973, Nagatomi and Iwata 1976, Saether 1977). They are sometimes well developed and elongate as in the Tipulidae and Trichoceridae (Figs. 79–82), or reduced to tiny lobes (Figs. 99,108). In lower Diptera, as in most insects, they are activated by muscles from segment 10. In certain Cecidomyiidae (Fig. 93) and in the Tephritoidea (Figs. 109, 110) the cerci are fused and form the apex of the piercing-type ovipositor.

The anus opens on the midline between the cerci in a more or less apicoventral position.

Male terminalia.   The eight main elements of the male terminalia (Figs. 111–141) in the basic pattern of the Diptera are as follows:

- tergite 9, the *epandrium* (genital arch)
- sternite 9, the *hypandrium* (Gabelplatte, penis sheath of the Syrphidae, vinculum of the Calliphoridae)
- a pair of primitively two-segmented arms, the *gonopods* (claspers, forcipate claspers, anterior gonapophyses, pregonites, harpagones, parameres) arising posterolaterally on sternite 9 and consisting of a basal *gonocoxite* (basimere, basistyle, side-piece) and a distal *gonostylus* (distimere, dististyle, clasper)
- a pair of unsegmented paraphallic processes, the *parameres* (harpes, parandrites, paraphyses, penis valves, posterior gonapophyses), situated between the posterolateral base of the aedeagus and the dorsomedial base of the gonocoxite
- a median phallic organ, the aedeagus, arising behind sternite 9
- a reduced *tergite 10*, which is closely associated with tergite 9 and tends to form a pair of lateral lobes, the *surstyli* (*sing. surstylus*)
- a simple *sternite 10* (ventral epandrial plate)
- the vestigial tergite and sternite of segment 11, more or less consolidated to form a proctiger bearing the cerci and the anus.

These eight items comprise the basic elements of the male terminalia in most orders of insects (Snodgrass 1935, Sharov 1966, Tuxen 1970, Matsuda 1976), but they vary greatly in occurrence and form. In the Diptera, as in other orders, they provide an unparalleled array of taxonomic characters. For convenience tergite 9, the epandrium, is discussed in conjunction with tergite 10. The remaining elements are discussed in the order they are listed.

Sternite 9, the hypandrium, is usually considerably modified in the male Diptera. In many Nematocera it is joined laterally with tergite 9, the epandrium, and the two together are then frequently called the *basal ring* (genital ring) (Figs. 114, 119). There is also a strong tendency for the gonopods to become fused with sternite 9, in which case the sternite is often virtually obliterated and replaced by the more or less fused bases of the gonopods (Figs. 122, 11.4–5). In the Muscomorpha (Figs. 135, 141) the hypandrium is usually somewhat U-shaped, with the arms of the U more or less encompassing the base of the aedeagus. Single median and paired lateral hypandrial apodemes sometimes project internally. Throughout the order there is a tendency for a pair of lobes to occur medially at the posterior margin of the hypandrium, between the inner ventral bases of the gonocoxites and the anteroventral base of the aedeagus. These lobes are usually at least partially fused medially and frequently form an *aedeagal guide* (adminiculum, penis guard, phallosome) (Figs. 133, 135, 140). In some Tipulidae and Anisopodidae (Fig. 19.16) they form a complex, elongate, ventromedial process; in other Tipulidae they form a transverse plate. In the Tabanoidea the fused lobes appear to be united laterally with the fused parameres and thus form the anteroventral wall of the cone-shaped *aedeagal sheath* (penis sheath, tegmen) (Figs. 32.6, 33.14). In many Muscomorpha they are fused with the posterior median extremity of the hypandrium and project trough-like around the anteroventral surface of the aedeagus (Figs. 135, 140).

Much confusion exists concerning the interpretation and naming of the parts here called gonopods and parameres, the homologies of which are still disputed throughout the endopterygote orders (for reviews, see especially Scudder 1971 and Matsuda 1976). The crux of the dispute rests mainly on whether the pair of large, primitively two-segmented arms on the posterior margin of sternite 9, the gonopods of this manual, that occur in most pterygote insects including the Diptera, are homologous with the primitive two-segmented appendages (gonopods) on the posterior margin of sternite 9 in Thysanura (Apterygota) (Griffiths 1972). The two-segmented arms associated with sternite 9 (gonopods) in such endopterygote orders as Mecoptera, Trichoptera, Hymenoptera, and Diptera are generally thought to be homologous with each other, and most workers except Crampton (1938, 1941, 1942) and Snodgrass (1957, 1963) believe that they are homologous with the gonopods of Thysanura (Sharov 1966, Mackerras 1970, Matsuda 1976). Also, it is generally agreed that Coleoptera is one of a few orders in which the male does not have elements that can be referred to these gonopods (Snodgrass 1935, Lindroth and Palmén 1970, Matsuda 1976). The significance of this last statement relates to the application of the name paramere.

Interpretation of both the gonopods and the parameres in the Diptera is complicated by the fact that the name paramere was applied to the gonopods by such workers as Crampton (1938, 1941, 1942) and Snodgrass (1957, 1963). In these last papers, Snodgrass postulated that the primitive gonopods were lost not only in the Coleoptera but in all endopterygote insects and were replaced during ontogeny by parameres. As a result of this argument, he also concluded that these new para-
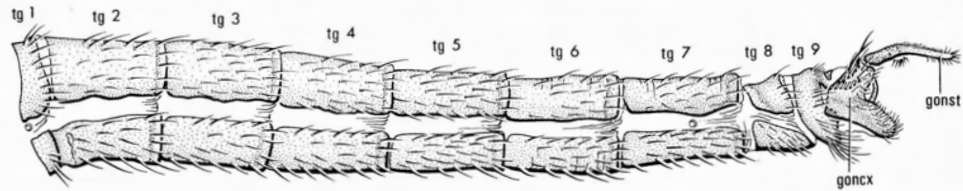
111 Trichocera garretti ♂
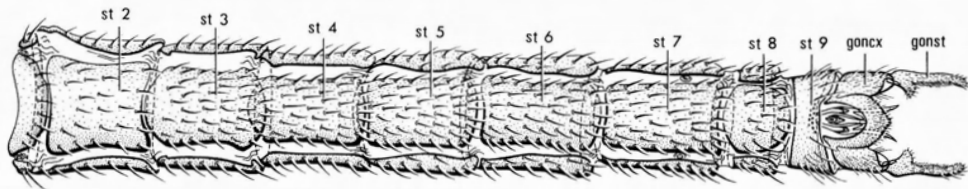
112 Trichocera garretti ♂
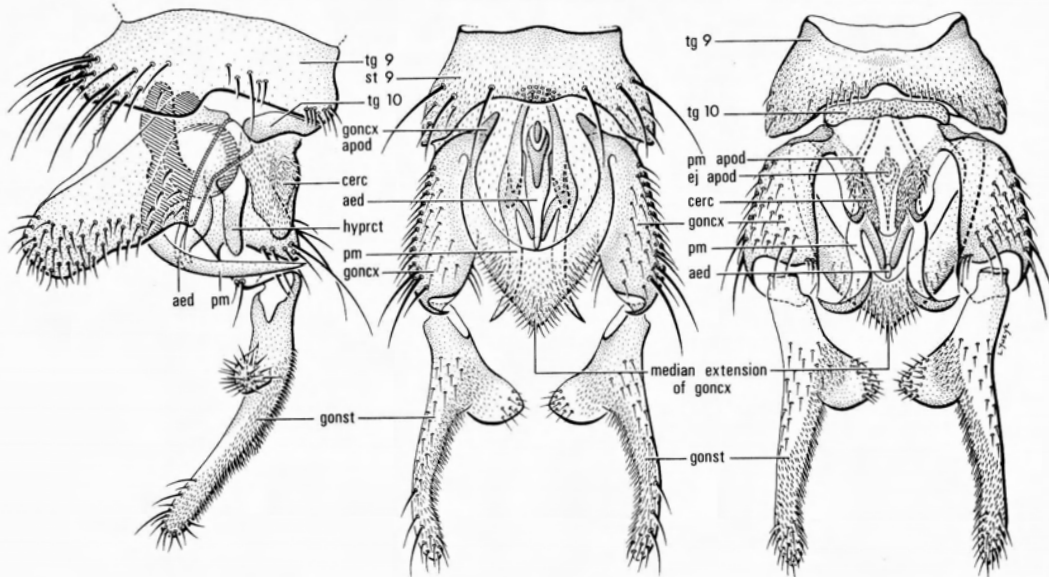
113 Trichocera garretti ♂   114 Trichocera garretti ♂   115 Trichocera garretti ♂

Figs. 2.111–115. Male abdomen and terminalia of *Trichocera garretti* (Alexander): (111) left lateral and (112) ventral views of entire abdomen; (113) left lateral, (114) ventral, and (115) dorsal views of terminalia.

Abbreviations: aed, aedeagus; cerc, cercus; ej apod, ejaculatory apodeme; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hyprct, hypoproct; pm, paramere; pm apod, parameral apodeme; spm pmp, sperm pump; st, sternite; tg, tergite.

meres became secondarily two-segmented, and that the pair of paraphallic lobes that are named parameres in our discussion and that occur at the base of the aedeagus in most endopterygote insects including the Diptera are paraphyses (parandrites of Crampton 1938) of secondary origin. This argument is a reversal of his previous conclusions (Snodgrass 1935), and it appears to be wrong for most endopterygote orders, including the

Diptera (Sharov 1966, Mackerras 1970, Matsuda 1976). Crampton himself (1938, p. 5) cautioned that, "The evidence thus far produced by those who maintain that the genital forceps (gonopods) of Hymenoptera represent the parameres of Coleoptera is not entirely satisfactory," and he only accepted it provisionally as a working hypothesis. It is unfortunate that he disregarded these reservations in his later papers. Mackerras
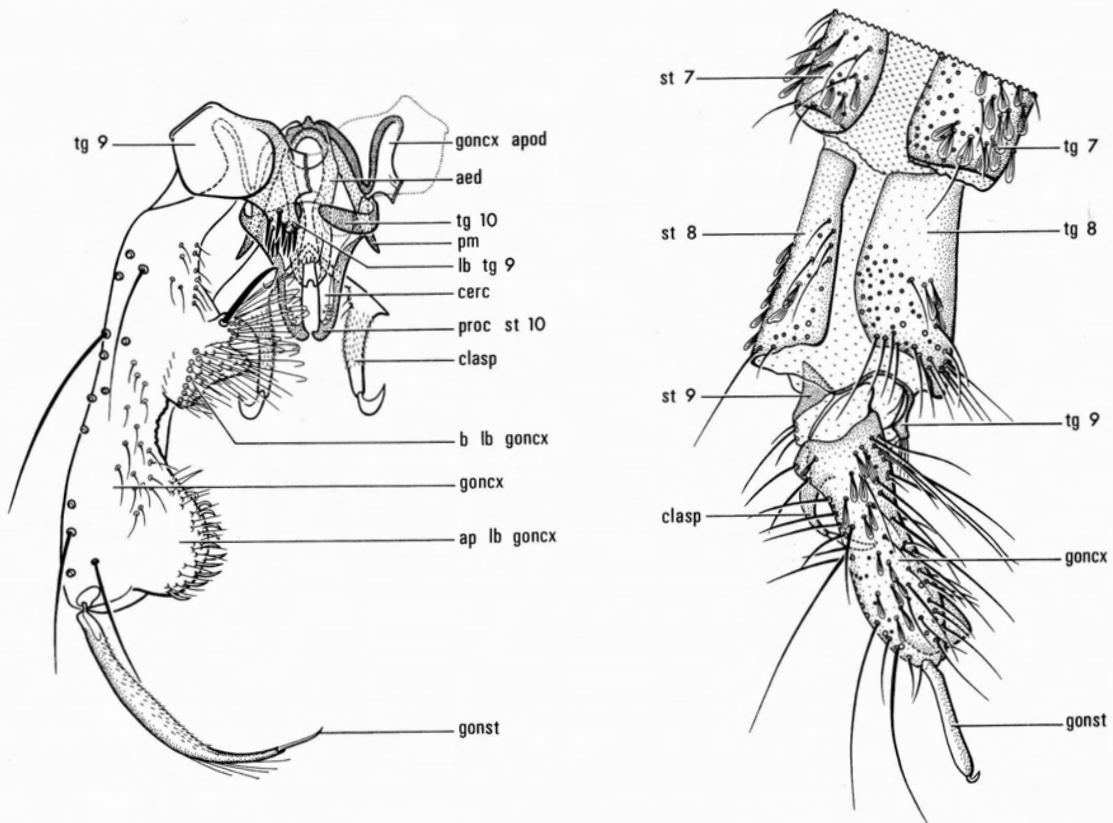
116 Aedes hexodontus ♂

117 Aedes grossbecki ♂
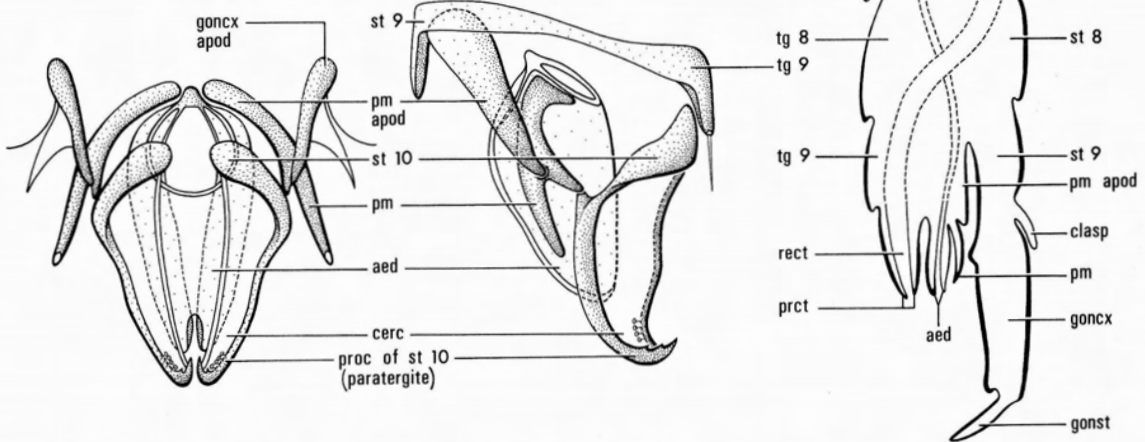
118 Aedes stimulans ♂ **119** Aedes stimulans ♂ **120** Aedes sp. ♂

Figs. 2.116–120. Male terminalia of Culicidae: (116) *Aedes hexodontus* Dyar, dorsal view (after Wood *et al.* 1979); (117) *Aedes grossbecki* Dyar & Knab, left lateral view, before rotation (redrawn from Knight and Laffoon 1971); (118) dorsal and (119) left lateral views (diagrammatic) (redrawn from Matheson 1944) of *Aedes stimulans* (Walker) showing details of aedeagus and associated parts; (120) longitudinal section (diagrammatic) through distal abdominal segments and terminalia of *Aedes* sp. subsequent to 180° rotation, with sclerotized areas indicated by thicker lines (redrawn from Edwards 1920).

Abbreviations: aed, aedeagus; ap lb goncx, apical lobe of gonocoxite; b lb goncx, basal lobe of gonocoxite; cerc, cercus; clasp, claspette; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; lb tg 9, lobe of tergite 9; pm, paramere; pm apod, parameral apodeme; prct, proctiger; proc st 10, process of sternite 10 (paratergite); rect, rectum; st, sternite; tg, tergite.
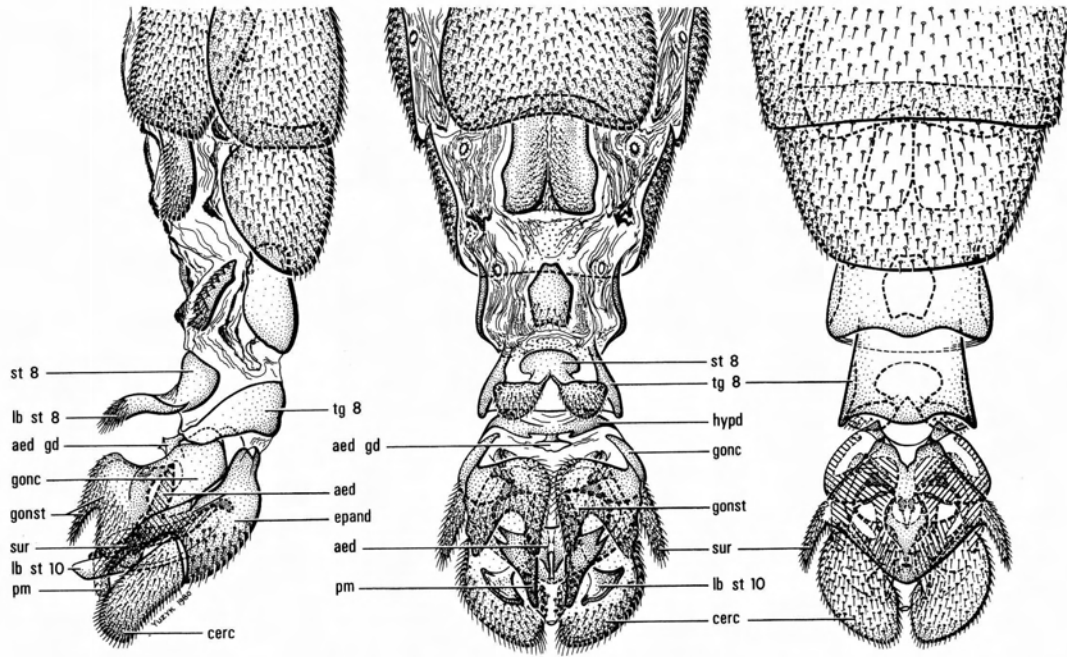
121 Xylomya tenthredinoides ♂   **122** Xylomya tenthredinoides ♂   **123** Xylomya tenthredinoides ♂
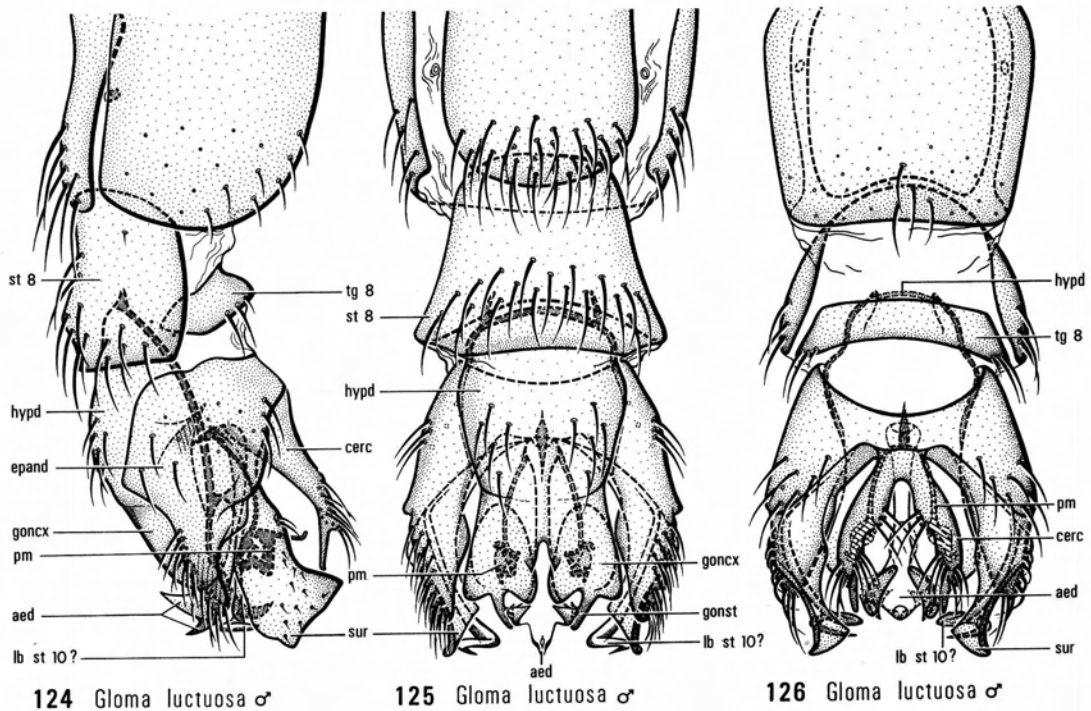
124 Gloma luctuosa ♂   **125** Gloma luctuosa ♂   **126** Gloma luctuosa ♂

Figs. 2.121–126. Male terminalia of Xylomyidae and Empididae: (121) left lateral, (122) ventral, and (123) dorsal views of *Xylomya tenthredinoides* (Wulp); (124) left lateral, (125) ventral, and (126) dorsal views of *Gloma luctuosa* Melander.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; a 1b sur, anterior lobe of surstylus; cerc, cercus; epand, epandrium; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; hypd, hypandrium; hyprct, hypoproct; 1b st, lobe of sternite; 1b tg, lobe of tergite; p 1b sur, posterior lobe of surstylus; pm, paramere; pm apod, parameral apodeme; st, sternite; sur, surstylus; tg, tergite.
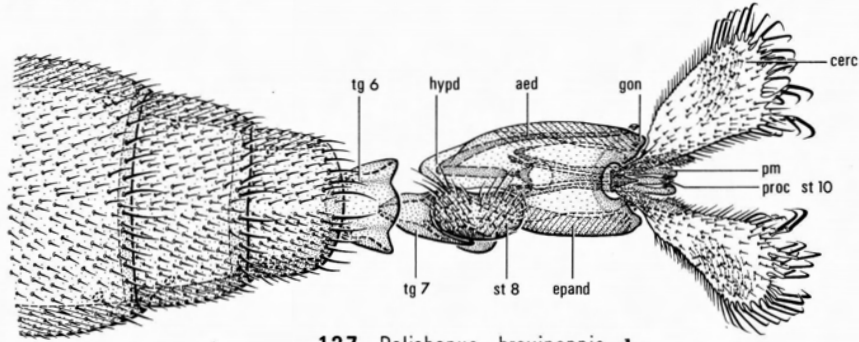
127 Dolichopus brevipennis ♂
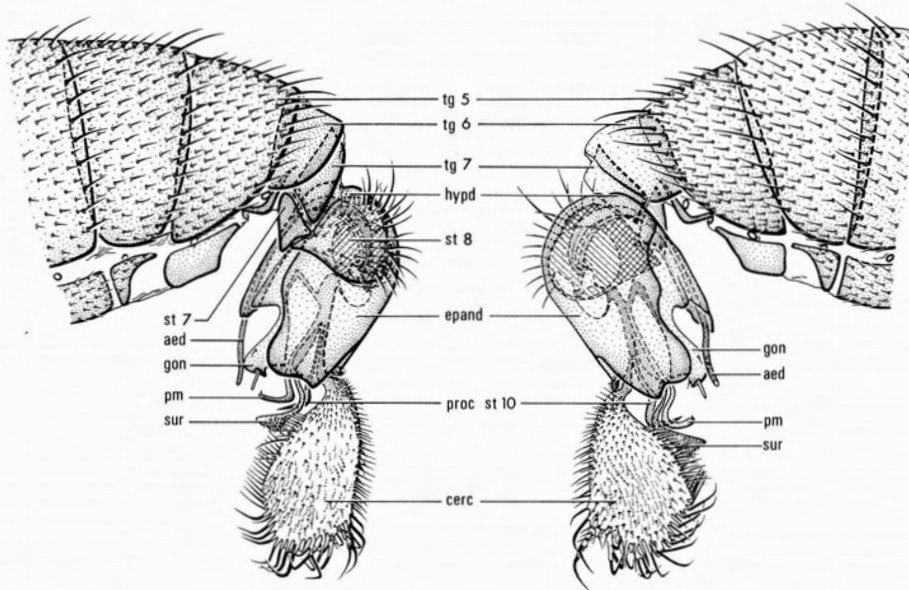
128 Dolichopus brevipennis ♂

129 Dolichopus brevipennis ♂
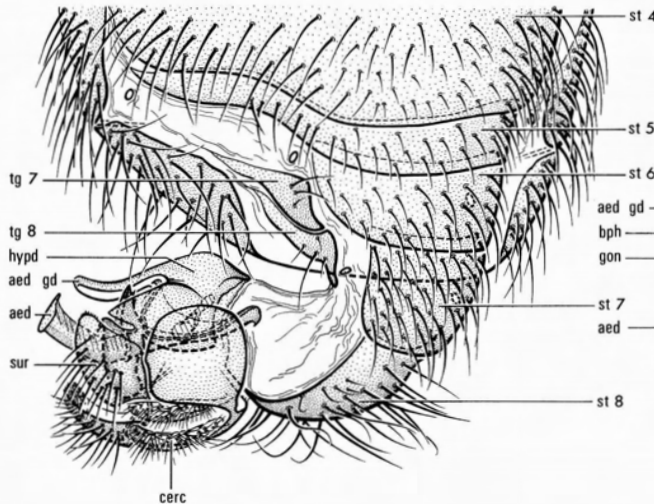
130 Syrphus ribesii ♂
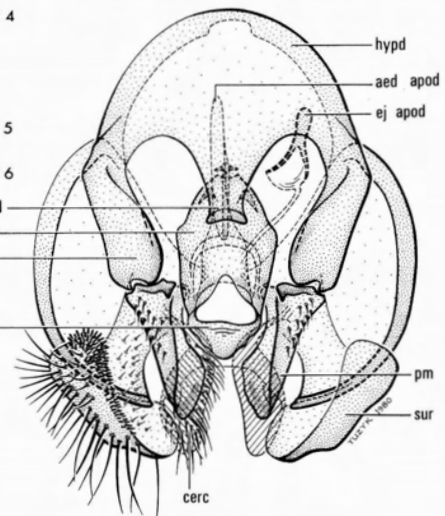
131 Syrphus ribesii ♂

Figs. 2.127–131. Male abdomen and terminalia of Dolichopodidae and Syrphidae: (127) dorsal, (128) left lateral, and (129) right lateral views of *Dolichopus brevipennis* Meigen; (130) *Syrphus ribesii* (Linnaeus), ventral view of apical portion of abdomen with terminalia in normal resting position; (131) *S. ribesii*, ventral view of terminalia.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; bph, basiphallus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; proc st 10, process of sternite 10; st, sternite; sur, surstylus; tg, tergite.
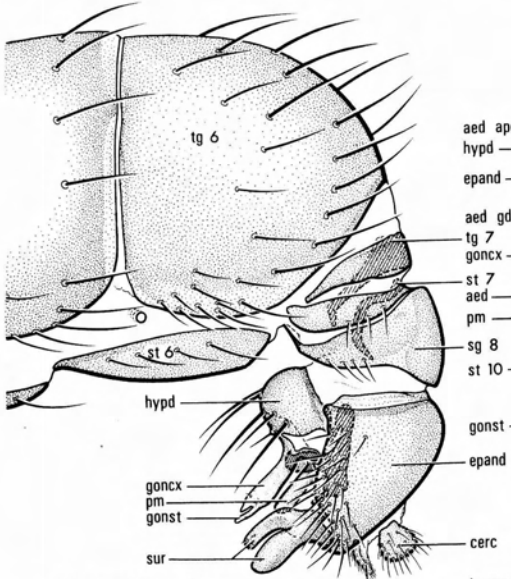
132 Callomyia sp. ♂
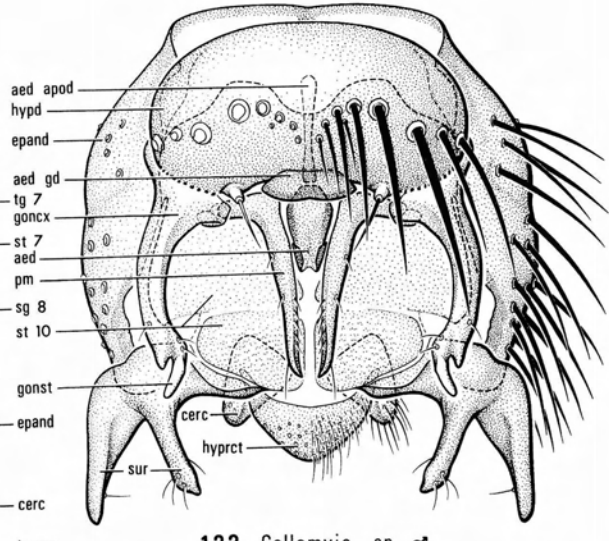
133 Callomyia sp. ♂
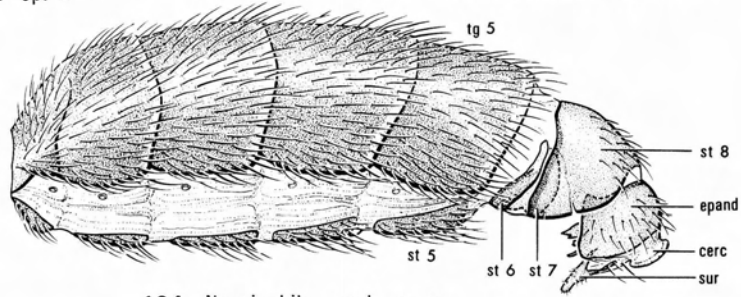
134 Neopiophila setaluna ♂
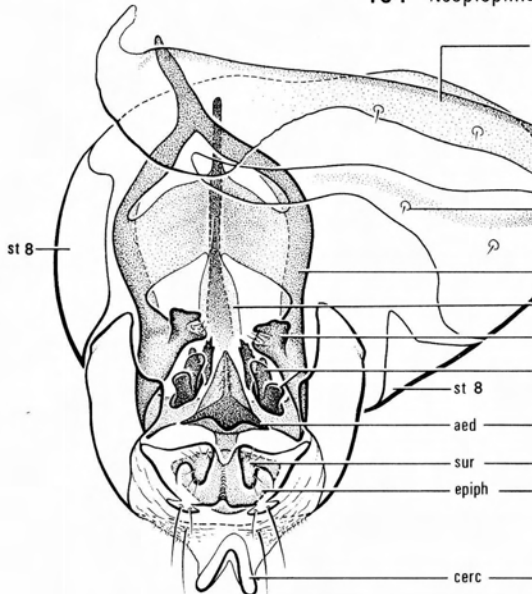
135 Neopiophila setaluna ♂
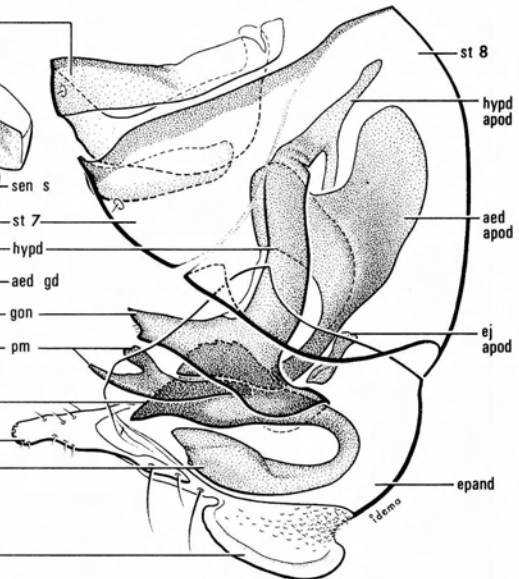
136 Neopiophila setaluna ♂

(1970, p. 27) summed up the matter as follows: "The weight of probability still lies with the gonocoxite theory for the endopterygotes, and it would seem undesirable to depart from it without further evidence." That conclusion is adopted here for the Diptera.

The gonocoxite articulates proximally with the posterior margin of the hypandrium and distally bears the gonostylus. In form, the gonocoxite may be relatively simple as in *Trichocera* (Figs. 113–115) or complex as in the Culicidae (Figs. 116, 117) with closely associated *claspettes* and with **apical, subapical,** and **basal lobes**; sometimes it is very large as in *Axymyia* (Figs. 11.4–5) and sometimes it is greatly reduced as in most Muscomorpha (Figs. 135, 138–141); it may be free from the hypandrium as in the Trichoceridae (Fig. 114), *Cramptonomyia* (Pachyneuridae (Figs. 12.3–4), and the Culicomorpha (Figs. 116, 117) or fused with the hypandrium as in *Axymyia* (Figs. 11.4–5) and many other Bibionomorpha and Muscomorpha. The so-called claspettes found in many Culicidae (Fig. 116) and somewhat similar lobes sometimes called by the same name among other Nematocera, e.g. Cecidomyiidae (Figs. 16.93), are among the most striking processes associated with the gonocoxite; in the Culicidae, at least, they arise proximally in the membrane between the bases of the gonocoxites, anteroventral to the base of the aedeagus (compare this position with that of the parameres below) and may be homologous with the aedeagal guide of other Diptera. Frequently, especially in the Nematocera and orthorrhaphous Brachycera, each gonocoxite has a conspicuous internal **gonocoxal apodeme**. The distal ends of the gonocoxal apodemes are usually widely separated from each other, but in some Ceratopogonidae (Fig. 28.101) and most if not all Chironomidae (Figs. 29.77–110) they are fused. The gonostylus may be simple as in most Trichoceridae (Figs. 113–115) or complex as in *Hesperinus* (Bibionidae) and many Tipulidae (Figs. 7.3–6); toothed or untoothed as in the Cecidomyiidae (Figs. 16.85, 16.87); and relatively large as in many Nematocera, much reduced as in *Callomyia* (Platypezidae) (Figs. 132, 133), or absent or combined with the gonocoxite as in all Schizophora (Figs. 135–141). In the Nematocera and orthorrhaphous Brachycera both the gonocoxite and the gonostylus are usually preserved, but it is not unusual for the gonostylus to be reduced and fused with the gonocoxite. In the Muscomorpha, however, the gonopod (pregonite) is usually reduced to a simple lobe on the

hypandrium (Figs. 135, 136, 138–141) and only rarely is the primitive two-segmented condition apparent, e.g. in *Callomyia* (Platypezidae) (Figs. 132, 133). In the Syrphoidea, however, no discrete gonopodal lobe is evident (Figs. 130, 131). Some workers (Crampton 1942, van Emden and Hennig 1970, Hennig 1976a) are reluctant to homologize these lobes in the higher Diptera with gonopods and refer to them by the noncommital term pregonites. The position, the sometimes two-segmented condition, and the general resemblance of them in the Platypezidae and certain orthorrhaphous Brachycera leave little doubt that they are, in fact, homologous structures throughout the Diptera (Hennig 1976b). It seems desirable to adopt the more explicit term, gonopod, for them in the Muscomorpha as in the Nematocera and orthorrhaphous Brachycera.

With regard to the true parameres, as defined in this manual, it is generally accepted that they are derived from secondary divisions of the primary phallic lobes, and that they are primitively unsegmented (Snodgrass 1935, 1957, 1963; Scudder 1971; Matsuda 1976). They are located between, and articulate with, the base of the aedeagus and the dorsomedial base of each gonocoxite. They occur regularly in most orders, and in the Diptera they constitute an important part of the genital complex. It is these lobes in the Coleoptera (in which gonopods are absent) that Verhoeff (1893) first named parameres, and it is these lobes that Snodgrass (1957) insisted are paraphallic lobes derived from the primary phallic lobes of segment 10. Unfortunately, in the Diptera they are sometimes confused with additional lobes or processes associated with the gonocoxite; for example, Scudder (1971) misinterpreted the claspette, which in the Culicidae arises near the proximal inner ventral surface of each gonocoxite, as a paramere.

The parameres (Figs. 113–115, 116, 118, 119, 121–126, 130–133, 135, 136, 140, 141) are surprisingly constant throughout the order and only rarely are they indistinguishable or absent. Normally the base of each paramere articulates with the basal posterolateral extremities of the aedeagus and with the base of the gonocoxal apodeme arising from the proximal dorsomedial rim of the gonocoxite. Usually each paramere is subtended by an internal **parameral apodeme** for muscle attachment. The parameres serve as accessory structures for supporting and directing the aedeagus, and perhaps also for protecting the aedeagus while it is

Figs. 2.132–136. Male abdomen and terminalia of Platypezidae and Piophilidae: (132) *Callomyia* sp., left lateral view of apical portion of abdomen with terminalia in normal resting position; (133) *Callomyia* sp., ventral view of terminalia; (134) left lateral view of entire abdomen with terminalia slightly unfolded from normal resting position, (135) ventral view of terminalia and adjoining sclerites, and (136) left lateral view of terminalia and adjoining sclerites of *Neopiophila setaluna* McAlpine.

Abbreviations: adv sut, adventitious suture; aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; a 1b sur, anterior lobe of surstylus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; goncx, gonocoxite; gonst, gonostylus; hypd, hypandrium; hypd apod, hypandrial apodeme; hyprct, hypoproct; p 1b sur, posterior lobe of surstylus; pm, paramere; sen s, sensory seta; sg, segment; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.
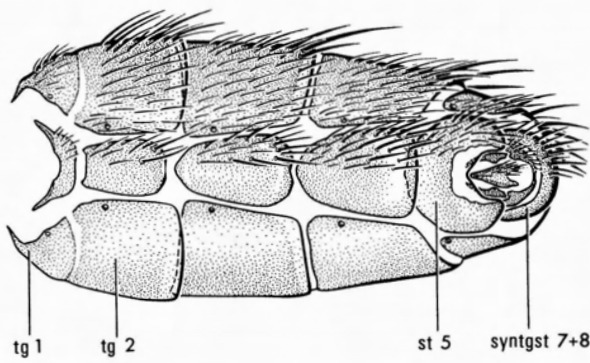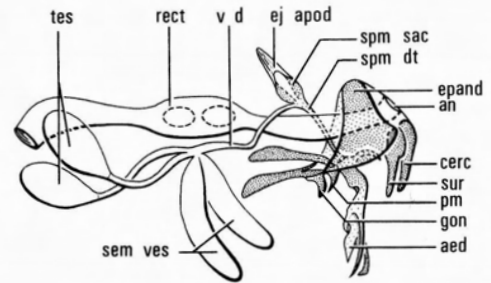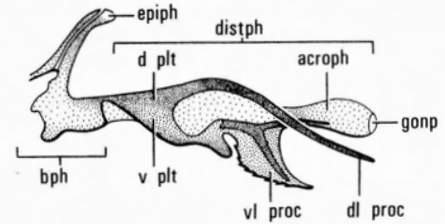
137 Melanophora roralis ♂

138 Phormia regina ♂

139 Pollenia rudis ♂
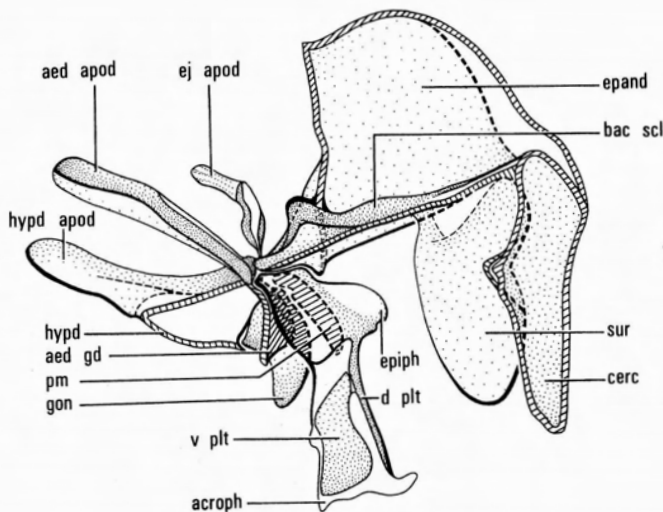
140 Masistylum arcuatum ♂
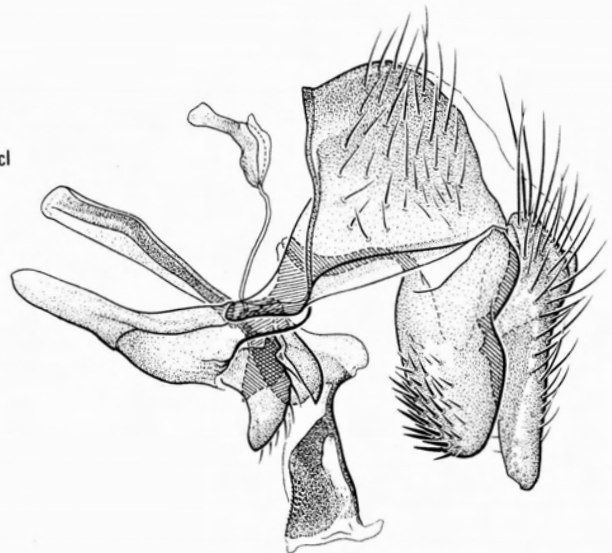
141 Masistylum arcuatum ♂

Figs. 2.137–141. Male abdomen and terminalia of Calyptratae: (137) *Melanophora roralis* (Linnaeus) (Rhinophoridae), ventral view of entire abdomen with terminalia in normal resting position; (138) *Phormia regina* (Meigen) (Calliphoridae), longitudinal section (diagrammatic) through distal abdominal segments and terminalia showing vas deferens and ejaculatory duct looped around rectum before reaching base of aedeagus (redrawn from Crampton 1942); (139) *Pollenia rudis* (Fabricius) (Calliphoridae), details of aedeagus and associated parts in left lateral view; (140) *Masistylum arcuatum* (Mik) (Tachinidae), longitudinal section of terminalia in left lateral view; (141) *M. arcuatum*, normal terminalia in left lateral view.

Abbreviations: acroph, acrophallus; aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; an, anus; bac scl, bacilliform sclerite; bph, basiphallus; cerc, cercus; distiph, distiphallus; dl proc, dorsolateral process; d plt, dorsal plate; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; gonp, gonopore; hypd, hypandrium; hypd apod, hypandrial apodeme; pm, paramere; rect, rectum; sem ves, seminal vesicle; spm dt, sperm duct; spm pmp, sperm pump; spm sac, sperm sac; st, sternite; sur, surstylus; syntgst, syntergosternite; tes, testicle; tg, tergite; vl proc, ventrolateral process; v d, vas deferens.

not in use (Hennig 1976a, 1976b). Usually they are relatively small, simple, and more or less triangular; they are lightly to heavily sclerotized and sometimes even bear strong setulae or spines, e.g. Simuliidae (Figs. 27.65–73). In some groups, especially in the Muscomorpha, they are rather complicated with several lobes, e.g. Microsania of the Platypezidae and Neopiophila of the Piophilidae (Figs. 135, 136). In other cases they are largely fused with the basiphallus, e.g. some Cecidomyiidae (Fig. 16.87). In most Tabanoidea they are somewhat membranous and fused to form at least the dorsal wall of a conical aedeagal sheath, which together with the fused aedeagal guides encloses the aedeagus (Fig. 33.14). In the Asilidae this sheath encloses only the base of the aedeagus (Theodor 1976). In the Syrphoidea, where the gonopods are atrophied, the parameres are often unusually exposed and prominent (Figs. 130, 131).

There has been a general hesitancy to accept the homology of the parameres throughout the Diptera. Although long recognized and called parameres in the Nematocera and certain orthorrhaphous Brachycera, the neutral term, postgonites, is the name most commonly applied to them in the Muscomorpha. Some workers (Hennig 1976b) postulated that the postgonites of the Muscomorpha may be derived from the gonostylus. However, their position and relationship to the gonopod and the aedeagus leave scarcely any doubt that they are homologous with the parameres of lower Diptera, as suggested by van Emden and Hennig (1970, p. 139). It seems timely to adopt a uniform terminology for them throughout the order.

The aedeagus exhibits a great variety of forms, and in many families it provides the best specific characters available. It develops from tissues behind sternite 9, and most authors regard it as a derivative of segment 10. Its primary function is to transfer sperm to the female reproductive system, usually by the direct transfer of free sperm into one or more spermathecae or to a site in the bursa near the spermathecal opening or openings. In the Chironomidae, Thaumaleidae, Ceratopogonidae, and Simuliidae, the sperm is transferred in a gelatinous envelope, the *spermatophore*, to the female genital chamber. In these four families the aedeagus is mainly membranous and nondistensible. In the Ceratopogonidae (Figs. 28.98–119) the sclerotized ventral portion, possibly a specialized aedeagal guide, is called the aedeagus; in the Simuliidae (Figs. 27.51–73) the same structure is called the *ventral plate*. The aedeagus is usually elongate in species that deliver free sperm and short and rather bursa-like in those that produce a spermatophore. It is exposed in most Diptera, but in some forms, e.g. most Tabanoidea, it is enclosed within the aedeagal sheath (Fig. 32.6). In some acalyptrates, e.g. Celyphidae, *Amiota* (Drosophilidae), *Dasiops* (Lonchaeidae), *Minettia* (Lauxaniidae), and some Piophilidae (Fig. 135), the aedeagus is greatly reduced or absent.

The external wall of the aedeagus is usually at least partially sclerotized and frequently consists of many different plates, processes, spines, and lobes (Fig. 139). It is not possible to homologize all the parts that have been distinguished and named by different authors in different families, but a number of basic elements can usually be distinguished, especially in higher Diptera. These include: a proximal *basiphallus* (phallobase, phallophore, theca); a distal *distiphallus* (juxta, phallus); one to three membranous internal tubes, the *endophallus*,[1] which unite proximally with the sperm ducts; and one or more distal openings, the *gonopores* (phallotremata).

The basiphallus is the sclerotized basal sector of the aedeagus. Usually it is relatively short and simple, but in many Schizophora, especially Tephritoidea, it is very elongate and convoluted or coiled. Internally it is usually subtended by an *aedeagal apodeme* (ejaculatory apodeme, phallapodeme, Tragplatte). When present in the Nematocera and most orthorrhaphous Brachycera (Fig. 125) the aedeagal apodeme is a simple internal extension of the aedeagus, and it lies more or less in the same plane as the aedeagus. In the Muscomorpha, however, it is separated from the basiphallus by a membranous articulation, and it joins the basiphallus at a distinct angle (Figs. 136, 140) (Hennig 1976b). Here it may be free and wedge- or Y-shaped, a condition referred to as *cuneiform*, or it may be at least partially fused with the median internal surface of the hypandrium (Fig. 136), namely *fultelliform*. Externally the contraction of the muscles attached to the aedeagal apodeme in the Nematocera and orthorrhaphous Brachycera results in compression of the closely associated *sperm pump* (ejaculator, ejaculatory bulb, ejaculatory pump). Contraction of the muscles attached to the aedeagal apodeme in the Muscomorpha results in exsertion of the aedeagus (Hennig 1976b). Externally the basiphallus also sometimes bears, especially in the Brachycera, an external process called the *epiphallus* (spinus), arising from its posteromedial surface (Figs. 135, 136, 140, 141).

The term distiphallus is usually applied to the relatively discrete apical section of the aedeagus of higher Diptera, but perhaps it may also be a useful term for the apex of the aedeagus in some lower Diptera. In the Tanyderidae, the Blephariceridae, and other primitive Diptera the apex of the aedeagus is three-branched (Downes 1968). Each branch carries a separate seminal duct, the endophallus, ending in an independent gonopore. This condition is correlated with three external spermathecal openings in the female, which are spaced to correspond to the three gonopores of the male (Edwards 1929, Downes 1968). In the Tabanoidea the aedeagus is distinctly three-branched (Fig. 32.6), but there is no stem-like section separating the basiphallus (endophallic hilt) and the distiphallus, and only the central branch contains an endophallic tube. The two lateral branches, called *aedeagal tines* (endophallic

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[1] It is unfortunate that Hennig (1976b) used this term for the entire aedeagus.

tines), arise directly from the basiphallus; at their bases they are directed anteriorly but they quickly curve dorsally and thence posteriorly on each side of the main central branch. During copulation they are forced through the opening of the aedeagal sheath together with the central branch that bears the gonopore. This condition is correlated with a single internal spermathecal opening in the female. The distiphallus of higher Diptera may also be trifid in representatives of many families, e.g. Asilidae, Empididae, Syrphidae, Pipunculidae, Platystomatidae, Sarcophagidae, and Tachinidae, and here also the corresponding spermathecal openings are located internally in the oviduct. Throughout the Diptera, many departures from the tripartite condition occur, namely from a bipartite condition in the Phlebotominae of the Psychodidae to a simple tube in most Cecidomyiidae (Figs. 16.83–110), and from a swollen structure, the *glans*, at the end of a long, coiled, or convoluted basiphallus such as is found in the Tephritoidea to the very complicated structure found in some Calyptratae (Fig. 140). Numerous terms have been created for the individual parts of the distiphallus, especially in the Muscomorpha (Roback 1954, Lopes 1956, and Lopes and Kano 1968, Sarcophagidae; Saltzer 1968, Calliphoridae; Nowakowski 1962 and Steyskal 1969, Agromyzidae; McAlpine 1973, Platystomatidae; Hennig 1974 and 1976a, Anthomyiidae). Although many of these terms are applicable only to particular families, a basic pattern is emerging (Hennig 1976a), and at least some of the parts, such as the *acrophallus* bearing the gonopores, are recognizable in different families. Some of these parts are shown in Fig. 140 and are labeled according to the terminology applied by Saltzer (1968) and Hennig (1976a). For a study on the function and relationships of various parts of the male and female terminalia in the Sarcophagidae, see Lopes and Kano (1968).

Some additional internal parts (Fig. 138) that function in the transfer of sperm and that are closely associated with the aedeagus are the sperm pump and one or more *sperm ducts* (ejaculatory ducts). A sperm pump occurs in all species that create a closed system for transfer of free sperm during copulation; it is undeveloped or absent in species that produce a spermatophore (Downes 1968). When present it is supplied by the common duct of the testes, the *vas deferens*, and it consists of a sac at the base of the aedeagus, the *sperm sac* (vesica, ejaculatory sac, Samenspritze). In the Nematocera and orthorrhaphous Brachycera it is closely associated with the aedeagal apodeme, and the muscles that operate it are sometimes attached directly to the aedeagal apodeme, which has been incorrectly labeled ejaculatory apodeme by some workers. In the Muscomorpha, however, the sperm pump is completely separate from the aedeagal apodeme and it has its own median unpaired process, the *ejaculatory apodeme*, for muscle insertions (Figs. 135, 140) (Hennig 1976b).

The epandrium is the principal dorsal sclerite, tergite 9, of the genital segment (andrium). It is always connected with its ventral sternite, the hypandrium, and with modified rudiments of tergite 10, posteriorly. Frequently, especially in higher Diptera, a pair of lateral lobes called the surstyli, now believed to be derived from tergite 10, project clasper-like from the posterolateral margins of the epandrium. These lobes have often been considered to be secondary processes of the epandrium (Crampton 1942, Hennig 1958) but, as postulated by Steyskal (1957) and McAlpine (1962, 1967) and as later shown by Hennig's (1976a, 1976b) detailed studies, they originate from laterally displaced portions of tergite 10.

In the Nematocera the epandrium is frequently reduced and fused laterally with the hypandrium to form a basal ring (Figs. 114, 119). Sometimes it occurs as a free, variously developed plate, e.g. Synneuridae (Fig. 21.5). In many cases it is extremely reduced and possibly combined with tergite 10, e.g. Anisopodidae (Fig. 19.14) and in other cases it is relatively large and free from tergite 10, e.g. most Bibionomorpha (Figs. 11.5, 12.4). In orthorrhaphous Brachycera the epandrium is usually relatively larger than in the Nematocera. In the Asilomorpha, e.g. Apioceridae (Figs. 41.15–16), the Asilidae, and the Empididae (Fig. 124), it is frequently deeply cleft dorsally, and its sides appear capable of clasper-like functions. Sometimes, especially in the Empididae, the epandrium has its own surstylus-like lobes, even though true surstyli are also present, as in *Gloma* (Figs. 124–126) and *Oreogeton* (McAlpine 1967).

In the Nematocera tergite 10 sometimes occurs as a simple, weakly sclerotized dorsal strip behind the epandrium, as in the Trichoceridae (Fig. 115) (Hennig 1973), but in a few cases it bears surstyli. Perhaps the most generalized surstyli observed in the order are those found in the family Ptychopteridae (Crampton 1942). In the genus *Bittacomorpha* they are directly attached to the lateral extremities of tergite 10 (not tergite 9 as indicated by Crampton 1942), which, though very narrow, is still complete on the dorsum. Similar surstyli also occur in other Ptychopteridae (Hennig 1973, Just 1973, called cerci), Blephariceridae, some Tipulidae (Byers 1961, called tergal arms), some Mycetophilidae, for example the genus *Symmerus* (Hennig 1973), and some Synneuridae (Figs. 21.4–5). In these cases tergite 10 is divided medially and appears as two more or less lateral lobes articulated with the posterolateral margins of the epandrium. In many Nematocera, however, tergite 10 is lost or indistinguishably fused with tergite 9. Likewise, in orthorrhaphous Brachycera tergite 10 sometimes varies in form. In the Rhagionidae, for example, it may be present as a free, transverse sclerite, or it may be divided on the midline into two variously reduced lateral sclerites, or it may be completely atrophied (Stuckenberg 1973). It takes the form of clasper-like surstyli in some Xylophagidae (Figs. 121–123), Stratiomyidae, Asilidae, Empididae (Figs. 124–126), and Dolichopodidae (Figs. 128, 129) (Crampton 1942).

In the Muscomorpha (Figs. 130–139) the epandrium is usually a strongly developed, more or less saddle-shaped sclerite, and the presence of articulated surstyli is a basic feature of practically all families (Hennig 1976b). Some authors (Hennig 1936, Griffiths 1972) have postulated that tergite 9 is lost in the Muscomorpha and that the epandrium in this group is the fusion product of the gonocoxites (periandrial theory of Griffiths 1972). However, Hennig himself (1976a, 1976b) presented detailed evidence to show that "this interpretation is certainly wrong." Matsuda (1976) declared that the periandrial idea is not acceptable because both the gonopods and the epandrium sometimes occur together, as shown in Fig. 10 of Griffiths' (1972) work, and Andersson (1977) also rejected it on several grounds. Occasionally in Muscomorpha two pairs of closely associated surstylar lobes are present (Steyskal 1957, McAlpine 1963). An *anterior surstylar lobe* is clearly evident as a separate entity in the conopid genus *Zodion* (Steyskal 1957, Fig. 4) and in the chamaemyiid genus *Cremifania* (McAlpine 1963, Figs. 11 and 12). This lobe appears to be a secondary lobe of the epandrium. The posterior lobe, or true surstylus, derived from tergite 10 and articulated with the epandrium, is much more common. In many acalyptrate groups, however, these two pairs of lobes become more or less integrated and give the appearance of a single divided surstylus, e.g. Dryomyzidae, Sciomyzidae, Heleomyzidae, and many Tephritoidea. Here the lobes can be distinguished as *inner* and *outer surstyli*, e.g. most Tephritoidea, or as *anterior, median*, and *posterior surstylar lobes*, e.g. Lonchaeidae. In a few cases, e.g. Tethinidae, the epandrium may even have additional surstylus-like lobes. In some families, e.g. most Sepsidae and the Chamaemyiidae, the surstyli are secondarily reduced and fused with the epandrium. The various lobes of the surstyli sometimes bear different types of hairs, spines, and processes. In many Tephritidae the distal end of the inner surstylus bears several strong teeth, the *prensisetae* (Munro 1947). These are probably homologous with the strong teeth on the posterior lobe of the surstylus in many Lonchaeidae and Otitidae.

Sternite 10, like tergite 10, is usually present in some form in Diptera (Steyskal 1957, McAlpine 1967, Hennig 1976a and 1976b), and it too is closely associated with the epandrium. Normally it is located in the ventral wall of the epandrium behind and dorsal to the aedeagus. Its evolution can be followed from primitive Nematocera, e.g. Blephariceridae, Ptychopteridae, and Anisopodidae, through the Brachycera into the Schizophora. In the Nematocera it is sometimes referred to simply as sternite 10, e.g. Anisopodidae (Fig. 19.18) and Synneuridae (Fig. 21.5), but often it is so reduced or membranous that it cannot be distinguished from the hypoproct, e.g. Cecidomyiidae (Figs. 16.87, 16.102, 16.113). In the Brachycera it has been given different names in different families, e.g. ventral lamella of the proctiger (Karl 1959, in Asilidae), sternite 10 (Vockeroth 1969, in Syrphidae), ventral proctigeral sclerite or second ventral proctigeral sclerite (Ulrich 1972, in

Empididae), bacilliform sclerites (Crampton 1942, in Calliphoridae), processi longi (German authors), inter-parameral sclerite (Griffiths 1972, in Muscomorpha), and ventral epandrial sclerite (Hennig 1976b, in Brachycera). Primitively it occurs as a simple plate that joins anteriorly with the posterior margins of the hypandrium, laterally with the inner margins of the surstyli when present or with the margins of tergite 10, and posteriorly with the hypoproct. It is relatively simple in the Synneuridae (Fig. 21.5), Ropalomeridae (Steyskal 1957), Ironomyiidae and Platypezidae (McAlpine 1967), and Rhagionidae, Empididae, Platypezidae, and Lonchopteridae (Hennig 1976b). Sometimes, e.g. some Anisopodidae (Fig. 19.16) and Xylophagidae (Fig. 122), it bears elongate processes. Commonly throughout the order it becomes more or less divided medially as in *Dioctria* (Asilidae), and in the Calyptratae, especially, it is divided into two rod-like struts, the *bacilliform sclerites* (processi longi), that connect the inner bases of the surstyli with the posterior arms of the hypandrium.

The proctiger is the anus-bearing region behind segment 10. Primitively in the Insecta it consists of a dorsal plate, the *epiproct*; a pair of lateral lobes, the *paraprocts*; a ventral plate, the *hypoproct*; and the cerci. All these are probably derived from the 11th and last true somite (Snodgrass 1935, 1963). True paraprocts have not been identified in the Diptera (Crampton 1942, p. 93). The processes, sometimes called paraprocts in the Culicidae, are derived from segment 10 and, therefore, are not true paraprocts. The epiproct is usually weakly developed or absent, but the hypoproct is a relatively constant feature. Frequently it is fused with sternite 10 and in many instances is indistinguishable as a separate sclerite. Embryologically the cerci arise as appendages of segment 11, between the bases of the paraprocts and the epiproct. They sometimes form a conspicuous and important part of the proctiger in the Diptera, e.g. in the Dolichopodidae (Figs. 127–129), but frequently, especially in the Nematocera (Figs. 111–120), they are weakly developed and practically indistinguishable. In their generalized condition they occur as a pair of hairy lobes on either side of the anus. In contrast to a primitive two-segmented condition in the female Diptera, the cerci in the male are only one-segmented, as in the Mecoptera (Hennig 1973). They are said to be absent in the male of all Tipulomorpha (Hennig 1973), but here they are probably incorporated in the proctiger or so-called anal segment, as in the Culicidae (Figs. 118, 119). In other nematocerous groups, e.g. Synneuridae (Figs. 21.5, 21.6), they are more sharply delimited from adjacent parts. In the Dolichopodidae (Figs. 127–129) they are frequently highly developed and ornamented. In most acalyptrate families, and no doubt in the basic pattern of the Muscomorpha, they are simple, relatively weakly sclerotized lobes (Figs. 135, 136). In the Calyptratae (Figs. 137, 138, 141), they form strongly sclerotized, elongate processes (mesolobes); here the two cerci are often fused at their bases but separated distally, and they articulate directly with the surstyli; in other groups, e.g. *Chaetolonchaea* of the Lonchaeidae and many Sar-

cophagidae and Tachinidae, they are sometimes completely fused together. The anus always opens between the cerci, behind and above the base of the aedeagus. Sometimes it is an important landmark.

Flexion and rotation. The apical portion of the male abdomen is frequently bent or folded forward ventrally, dorsally, or laterally (Figs. 142–146). Such bending is called *flexion*, and it may be categorized as *ventroflexion*, *dorsoflexion*, or *lateroflexion*, respectively. Flexion is termed *facultative* when it is voluntary and temporary, and *obligatory* when it is fixed and permanent.

In addition to being flexed, the male terminalia may be twisted through 90° to 360° about the long axis of the abdomen (Figs. 120, 138). Such twisting is called *rotation*, and it, also, is facultative when it is temporary, and obligatory when it is fixed permanently. Rotation through 180° (Fig. 120), best known in the Culicidae, results in true ventral structures coming to lie in a dorsal position. Such a condition is called *inversion*, and it can be recognized by reference to the relative positions of the aedeagus and the proctiger. When the terminalia are inverted the anus is ventral to the genital opening, whereas the reverse situation occurs when the terminalia are not inverted. Rotation through 360° (Fig. 138), which occurs in all Muscomorpha, is called *circumversion*. In all forms with circumverted terminalia the anus and the genital structures are restored to their original positions, but the main internal ducts of the genital system, the nervous system, and the tracheal system are twisted around the hind gut (Fig. 138).

Both flexion and rotation are adaptations for mating and for storing the terminalia when not in use, and both have evolved repeatedly in different ways in different groups within the order. An understanding of the various conditions now existing rests upon the following points.

Courtship and mating in the Diptera consists of a chain of sign stimulus–response reactions (Stich 1963), beginning with contact of the sexes and ending in sperm transfer. Plesiomorphically, the initial stages of mating (contact and coupling) are believed to take place during flight (McAlpine and Munroe 1968), and the final stages (ejaculation and sperm transfer) usually occur while the mating pair rests on a substrate. Apomorphically, the initial stages may occur on a substrate, and the final stages during flight.

The *initial coupling position* (pose of Lamb 1922) frequently differs from the *final mating position* (position of Lamb 1922, also see Richards 1927). For coupling, both sexes usually, if not always, face in the same direction and are said to assume a **unidirectional orientation** (Figs. 142–146), but for the final stages of mating, the two sexes of many species face in opposite directions and are said to assume a **tail-to-tail orientation** (Figs. 142b,c; 143b,c; 144a; 146a).

With regard to flexion of the terminalia, the simplest situation is found in groups such as the Chironomidae and the Simuliidae, in which the abdomen is relatively slender and tubular. During coupling the end of the abdomen is voluntarily ventroflexed to bring the ventral surface of the male terminalia in contact with the ventral surface of the female terminalia (Figs. 142, 142a). The aedeagus is then able to join with the spermathecal opening or openings. In all Diptera in which the one or more spermathecal openings are located internally in a bursa or common oviduct, the ventral surface of the aedeagus is placed adjacent to the dorsal surface of the bursa or oviduct (inverse correlation of genitalia, as opposed to direct correlation, according to Lamb 1922; see also Richards 1927, Griffiths 1972, Hennig 1973). In some Nematocera, however, the male terminalia are permanently dorsoflexed, e.g. Blephariceridae. This condition also occurs in some orthorrhaphous Brachycera, e.g. some Empididae, but in the Dolichopodidae the male terminalia are permanently lateroflexed (Figs. 127–129, 145, 145a). In the Muscomorpha, they are usually permanently ventroflexed. In the basic pattern of the Diptera the male terminalia were probably relatively unflexed during rest but were capable of being voluntarily flexed ventrally and forward during coupling.

With regard to rotation, the simplest situation is found in groups such as the Simuliidae and the Tabanidae, where the terminalia are unrotated and apparently incapable of facultative twisting. Here the initial coupling position is unidirectional as in all Diptera, with both sexes vertically upright, male above and female below (Figs. 142, 142a). The final mating position is tail-to-tail, and because there is no rotation of the terminalia, one of the pair, usually the male, must lie upside down (Fig. 142c). In this position the male is completely helpless, and locomotion of the coupled pair usually depends on the female. Therefore when exposed, both partners are vulnerable to predators and other

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Figs. 2.142–146. Copulatory positions of Diptera. In these sketches the sexes are distinguished by male and female symbols (♂ ♀), and the dorsal (posterior) surface of the aedeagus is indicated by a small black triangle. The sketches in the left column show positions taken by different groups during initial coupling of the pairs, and those in the right column show alternative positions taken during the final stages of copulation. Figs. 142 and 143 relate to groups in which there is no permanent rotation of the male terminalia. Figs. 144 and 145 relate to groups in which the male terminalia are permanently rotated through 180°, i.e. inverted; and Fig. 146 relates to the Muscomorpha (=Cyclorrhapha) in which the male terminalia are permanently rotated through 360°, i.e. circumverted. In Fig. 142b the terminalia of both the male and female are each facultatively rotated through 90°. In Fig. 142a the male terminalia are ventroflexed and those of the female are dorsoflexed; but the reverse is true in Fig. 143a. In Fig. 145a the male terminalia are permanently dextrally lateroflexed.

unfavorable environmental factors. This vulnerability probably explains, to some extent, why most Diptera have evolved various means, through rotation of the terminalia, to remain vertically upright during the final stages of mating. Because the rotation is effected in

different ways, at different ontogenetic times, and at different morphological points in different groups it is believed to have arisen independently many times within the order (Richards 1927). It begins with facultative inversion of the terminalia in which up to 180° of

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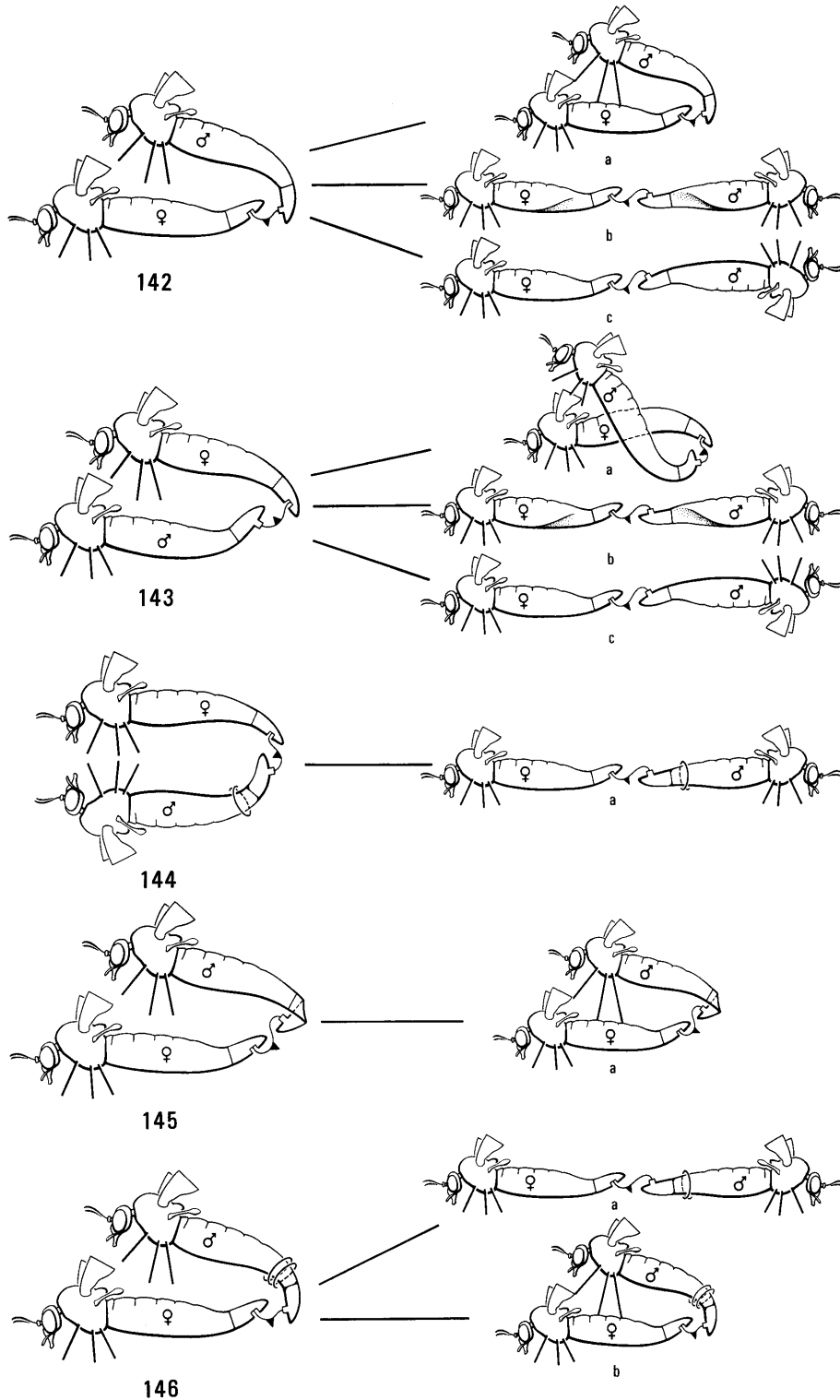
rotation is spread over a number of segments, as in certain Bibionomorpha, followed by obligatory inversion, as in the Culicidae, where the terminalia are permanently rotated 180° between segments 7 and 8, and culminating with circumversion (360° rotation) in the Muscomorpha.

Details on flexion and rotation are still unrecorded for most Diptera, but the information that is known permits the following summary.

In the Tipulomorpha permanent inversion occurs in some Tipulidae, e.g. some eriopterine tipulids (Richards 1927), including *Styringomyia*, *Molophilus*, *Amphineurus* (Crampton 1942), and *Erioptera* subgenus *Ilisia* (Alexander, Ch. 7); in the Tipulinae at least partial inversion occurs in *Macromastix* (Crampton 1942), *Brachypremna*, and *Megistocera* (Frommer 1963). However, it is uncertain when it occurs and what segments are involved. Permanent inversion of segment 9 and the proctiger takes place in the tanyderid *Protoplasa fitchii* (Crampton 1942); according to Hennig (1973), inversion is distributed over several segments in this family. In the Psychodomorpha permanent inversion of the male terminalia is a normal feature of Psychodidae (Feuerborn 1922b; Richards 1927; Quate, Ch. 17), but additional details are unknown. A full 180° rotation occurs in all *Sylvicola* (Anisopodidae). Inversion in both the Tipulomorpha and the Psychodomorpha probably occurs after the adults emerge. As already noted, inversion is perhaps best known and documented in the Culicidae and in a few marine Chironomidae with wingless females. In the Culicidae 180° obligatory rotation of all the parts of the male terminalia beyond segment 7 occurs after emergence but before copulation. Practically all of the twisting is effected between segments 7 and 8, with little or no dragging of the preceding sclerites out of their true ventral or dorsal positions. Internally the genital duct, at least, is crossed over the hind gut (Fig. 120). Rotation of 180° is recorded for the Dixidae (Feuerborn 1922a, Richards 1927, Crampton 1942) and the Chaoboridae (Cook 1956). In the Ceratopogonidae inversion may or may not occur depending on the genus, tribe, or subfamily (Richards 1927, Downes 1978), and it is usually facultative rather than obligatory. Inversion, when it occurs, always takes place after emergence, sometimes before and sometimes during copulation; when it occurs during copulation partial counter-rotation sometimes follows so that the terminalia of males that have mated show degrees of rotation between 0° and 180°. In this family most of the rotation occurs between segments 8 and 9, but one and sometimes two previous segments are also involved (Downes 1978). According to Tokunaga (1935) inversion of the terminalia in the marine chironomid *Telmatogeton* is accomplished during the pupal stage, but in most Chironomidae rotation occurs facultatively during copulation (Fittkau 1968, Dordel 1973). Sometimes it is spread over a number of segments and sometimes it is restricted to the more terminal ones. In the Culicidae, the Chaoboridae, and the Ceratopogoni-

dae, at least, permanent rotation may occur ***clockwise*** (dextral) or ***counterclockwise*** (sinistral).

In the Bibionomorpha 180° rotation is recorded for certain Mycetophilidae, e.g. *Diadocidia* (Lindner 1923), and at least 90° rotation is evident in the preserved males of many species of *Mycomya*. In the Pachyneuridae up to 90° rotation is present in pinned males of most species of *Pachyneura* and in *Cramptonomyia*. In one species of the sciarid genus *Bradysia*, all degrees of rotation from 0° to 180° are evident; here rotation obviously occurred after emergence of the adult, but whether it was before or during copulation is not known.

In orthorrhaphous Brachycera permanent inversion of the terminalia to 180° rotation occurs in most Acroceridae and Bombyliidae, but it is not known when it takes place. In the Asilomorpha 90° rotation is evident in some Scenopinidae, e.g. *Pseudotrichia* and *Belosta*. In the Asilidae 90° rotation is evident in the male of many Dasypogoninae, where inversion usually takes place during copulation. In the subfamily Laphriinae, however, the terminalia are permanently rotated 180° (Hull 1962), but whether it occurs before or after the adult emerges is unknown. A 90° rotation also occurs for many Empididae in the subfamilies Tachydromiinae, Ocydromiinae, and Hybotinae; here the terminalia are frequently permanently rotated 90° (Bährmann 1960, Kessel and Maggioncalda 1968, Griffiths 1972) and in most cases some of the sclerites are asymmetric (Smith 1969). Complete permanent inversion occurs in the empidid genus *Microphorus* (McAlpine 1967). In the Dolichopodidae, sternite 8 is rotated clockwise 90° to a more or less lateral position (Figs. 127, 128). The remainder of the terminalia is rotated an additional 90° in the same direction, and then lateroflexed to the right. The terminalia are therefore inverted and lie against a membrane in the right side of the abdomen, opposite the ventral surface of sternite 8, with the cerci and aedeagus directed anteroventrally (Figs. 127–128); the outer surface of sternite 8 is exposed on the left side. From the consolidated appearance of the terminalia throughout the family both inversion and lateroflexion probably occur during the pupal stage in the Dolichopodidae.

In male Muscomorpha (Figs. 130–141) rotation has proceeded beyond 180° to about 360°, resulting in circumversion of the terminalia. This condition appears to have occurred only once and is considered to be a synapomorphic character of the Muscomorpha. The first 180°, representing permanent inversion, always takes place in the puparium before emergence, but the final 180°, resulting in circumversion, may take place immediately after emergence from the puparium, and it is reversible during the final stage of mating in at least some Platypezidae (Kessel 1968). In most cases, however, circumversion is accomplished before emergence from the puparium and is irreversible. The first 180° of rotation always occurs in the vicinity of segment 8. Some dragging of sternites 6 and 7 into the left side of

the abdomen is usually apparent. Also, sternite 7, tergite 8, and sternite 8 usually become more or less fused into a single syntergosternite that occupies a more or less dorsal position. The final 180° of circumversion occurs between segments 8 and 9, restoring the genital and postgenital parts to their true dorsal and ventral positions. The sclerites of segments 6, 7, and 8, whether fused or not, are frequently asymmetric and partially to wholly atrophied. Where the vestiges of these segments appear symmetric as in some Drosophilidae and many muscoids, the symmetry is undoubtedly a secondary phenomenon.

Permanent ventroflexion is always correlated with circumversion and results in the terminalia being folded forward about 180° into a protective, more or less membranous genital pouch behind sternite 5 in the vicinity of sternites 6 and 7. In certain Aschiza, e.g. Syrphidae and Platypezidae, and perhaps also in some primitive Schizophora such as Lonchaeidae, ventroflexion may be completed immediately after the adult

emerges from the puparium. But in most Schizophora, and certainly in all Calyptratae, ventroflexion, like circumversion, is accomplished before the fly emerges from the puparium.

As mentioned above, many male Diptera in Empidoidea and Muscomorpha show pronounced asymmetries in the sclerites of abdominal segments 6–8 (Figs. 127–136). These conditions occur primarily in forms that have permanently rotated terminalia, but some workers (Griffiths 1972, Emmert 1972) believe they arose independently of rotation; according to them such asymmetries are primarily associated with flexion of the terminalia and the formation a genital pouch for protecting the genital apparatus. The relative reduction or retention of the tergites and sternites of segments 6–8 is particularly important in the Muscomorpha (Griffiths 1972). The presence or absence of spiracles 6 and 7, also of considerable taxonomic significance, especially in the Schizophora, appears to be partially correlated with the preservation or loss of these sclerites.

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H. J. TESKEY

INTRODUCTION

Diptera larvae are extremely variable. Head structures range from a well-developed exposed capsule with mouthparts adapted for biting and chewing, to variously reduced structures partially or completely retracted within the thorax with mouthparts altered for piercing and rasping. Rarely, the head skeleton is essentially absent. The segments of the larval body may be variously fused or subdivided, conspicuously swollen in portions, or cylindrical or compressed. Some or all segments may bear filamentous or tuberculous outgrowths of various kinds.

The variation is so great that no individual or concise combination of characters exists by which Diptera larvae can be distinguished from all other insect larvae. The only character common to all Diptera larvae, but also found in representatives of several other orders, is the absence of jointed thoracic legs. This feature, when coupled with the fact that the majority of free-living Diptera larvae are rather slender with active directional movement, serves to distinguish most Diptera larvae. Most legless larvae of other orders are rather swollen, with movements that appear slow and undirected.

HEAD

The great diversity in head structure can be systematized according to certain morphological trends that correspond somewhat with the phylogeny of the Diptera. Three broad categories of head structure have been distinguished based on the degree of reduction and the amount of retraction within the thorax of the head capsule, and on the structure and plane of movement of the mandibles. A well-developed, fully exposed head capsule with mandibles usually bearing teeth and operating in a horizontal or oblique plane is termed *eucephalic* (Brauer 1883) and typifies the larvae of most Nematocera. A *hemicephalic* head capsule is more or less reduced or incomplete posteriorly and partially retracted within the thorax, with sickle-shaped mandibles operating in a vertical plane. Such a head capsule is mainly found among the orthorrhaphous Brachycera. Further reduction and retraction of the head capsule within the thorax coupled with the development of an internal pharyngeal skeleton produces the *acephalic* condition, the term used to describe the characteristically shaped *cephalopharyngeal skeleton* that typifies larvae of the Muscomorpha (*see* "Muscomorpha").

Although these terms are useful in defining general trends, they are not entirely mutually exclusive. Exceptions to their application include the Tipulidae, a nematocerous family with a head capsule that is more or less extensively reduced posteriorly and partially retracted within the thorax. The tipulid mandibles vary from stout and toothed, adapted for chewing, to slender and sickle-shaped, for piercing. But they are almost always opposed to each other in a horizontal plane. The head capsule of some blepharicerid larvae is eucephalic except for a slight dissolution of the capsule dorsolaterally. Although the head capsule of the Cecidomyiidae is classed as hemicephalic or acephalic, the family is undoubtedly referable to the Nematocera. Another nematocerous family, the Synneuridae, essentially lacks any vestige of a head capsule and is the only truly acephalic example. On the other hand larvae of the brachycerous families Therevidae and Scenopinidae appear to have well-developed, fully exposed head capsules with the only brachycerous features being the slender, sickle-shaped mandibles operating in a vertical plane and the slender, sclerotized *metacephalic rod* (capsule rod, manubrium) (*see* "Cranium") articulated posteriorly to the head and extending into the prothorax.

Despite such exceptions these fundamental concepts form the basis of the following detailed discussion, showing how the three successive types of head capsules are derived. Trends in the evolution of head structures other than those already mentioned are also discussed. Because the acephalous condition represented by the cephalopharyngeal skeleton of the Muscomorpha constitutes such a major transition, it is treated separately from the Nematocera and orthorrhaphous Brachycera.

Nematocera and orthorrhaphous Brachycera

Cranium. The eucephalic head capsule consists mainly of the *cranium*. The cranium is the sclerotized external cuticle of the head to which the mouthparts are attached anteriorly and in which the muscles operating these mouthparts and the *pharynx* (*see* "Pharynx") originate. It comprises three sclerites, namely a middorsal *frontoclypeal apotome* (cephalic apotome) and a pair of lateral sclerites called the *genae* (Fig. 1). These sclerites are separated by lines of weakness termed *ecdysial lines*. The integument splits along these lines during molting. The ecdysial lines bordering the frontoclypeal apotome are normally rather prominent. Either they appear in the form of an inverted Y as in a few larvae of the Bibionoidea or, more commonly, they lack the stem line and resemble a U or a V with the two arms reaching the occiput separately although very close together. The ecdysial lines on the head are continuous with a single middorsal ecdysial line on the thoracic segments. Sometimes one median ecdysial line, or

rarely, as in the Ptychopteridae, a pair of such lines is present ventrally. Although these ventral lines rarely split at ecdysis, they sometimes function as a hinge permitting outward movement of the two halves of the head when the dorsal ecdysial lines split (Hinton 1963).

The ecdysial lines in the larvae have commonly been homologized with sutures that occur in the adult insect. The arms of the Y have been termed the frontal sutures, and the stem has been called the coronal suture; both together have been called epicranial sutures. In line with this terminology the area synonymous with the fronto-clypeal apotome has commonly been referred to as the frontoclypeus. Although there is some merit in retaining the sutural names for the ecdysial lines, Snodgrass (1947) has shown that the lines are not sutures in the strict sense but are simply lines of weakness and that the area enclosed by the ecdysial lines is not entirely homologous with the frontoclypeus of the adult form. Instead, Snodgrass applied the name apotome, meaning "part cut out", to this area. The name apotome alone, or cephalic apotome as is sometimes applied, is not fully descriptive, however. According to a generally accepted rule proposed by Snodgrass (1947), all muscles associated with the pharynx, cibarium, and epipharyngeal surface of the labrum originate on, and help define, the frontoclypeus. As these muscles originate on the frons and clypeus of most larvae it seems preferable to retain the name frontoclypeus in the form frontoclypeal apotome for the sclerite, despite the few known exceptions to the rule, for example larvae of the Tipulidae (Chiswell 1955).

A frontoclypeal suture between the frons and the clypeus is rarely evident in Diptera larvae. However, evidence of these two areas can often be obtained from muscle insertions. The clypeus bears the muscles dilating the *cibarium* (preoral cavity), which is the roof of the mouth, whereas the frons serves for attachment of the pharyngeal muscles and the muscles operating the *tormae* (*sing. torma*) and *premandibles* (messors) of the labrum (Snodgrass 1947) (*see* "Labrum").

The genae comprise the greatest area of the eucephalic head capsule. Because the frontoclypeal apotome narrows posteriorly and a ventral gular sclerite is lacking, the genae normally border the entire occipital foramen. The edges bordering the occipital foramen are normally thickened and strengthened to form a *postoccipital carina*, which may be delimited anteriorly by a slight groove, the *postoccipital sulcus* (postoccipital suture) (Fig. 2). Ventrolaterally on the postoccipital sulcus, or the area where the sulcus would be expected to run, a slightly more heavily sclerotized area, sometimes bearing a slight depression on each side, is often present. These depressions are the *posterior tentorial pits*. The anterior edge of each gena is also somewhat thickened to strengthen it for articulation of the mouthparts. This thickened border is called the *subgenal margin*.

The retraction of the head capsule within the thorax and the associated reduction in the extent of the cranial elements of the capsule characteristic of the hemicephalic condition occur to some degree in all families of the orthorrhaphous Brachycera as well as in the Tanyderidae, the Tipulidae, the Axymyiidae, and the Cecidomyiidae of the Nematocera (Figs. 7.66–67, 16.5, 31.51–54, 39.5, 42.76–77, 47.57). The retraction is permanent in these groups because the integument and some of the muscles controlling head movement have acquired new insertions, usually from near the middle of the cranium to immediately behind the mouthparts.

The extent of the reduction of the head capsule of orthorrhaphous Brachycera is quite variable. The reduction appears to begin with desclerotization of the posterior margin followed by disappearance of desclerotized cuticle. Thus, the head capsule of the Stratiomyidae is complete except for a relatively large occipital opening (Fig. 36.59). In the Tabanidae (Fig. 31.56) substantial reductions to the posteroventral areas of the head capsule occur. Here desclerotization has resulted in isolated small posterolateral lenticular sclerites. Although these appear detached from the rest of the capsule, they are united by a transparent cuticle that also extends somewhat ventrally to unite with the apical portion of a pair of *tentorial arms* (*see* "Tentorial Arms"). The cranium of the Rhagionidae and the Vermileonidae is reduced to a convex, posteriorly truncate dorsal plate leaving the entire ventral side of the head capsule open (Figs. 33.22, 39.4). In some representatives of the Rhagionidae a tendency to median longitudinal desclerotization of this plate can be seen. Similar desclerotization of the dorsal plate is carried even further in the Apioceridae, the Mydidae, and the Asilidae (Figs. 40.29, 42.78–79) where the posterior two-thirds or more of the dorsal plate is reduced to relatively broad, paired bars united for some or all of their length by a transparent cuticle. In the Dolichopodidae and the Empididae this trend has resulted in slender, disconnected, paired rods that in the Dolichopodidae are somewhat expanded caudally (Figs. 47.58, 48.41, 48.43). Division of the retracted elements of the cranium into paired structures does not occur universally, however. In the Therevidae and the Scenopinidae, for example, only a single rod is present (Figs. 37.24, 38.12).

The single rod-like retracted portion of the cranium in the Therevidae and the Scenopinidae is separated from the exposed portion of the cranium by a distinct suture. The beginning of this development possibly occurs in larvae of *Coenomyia* (Xylophagidae). Here, the retracted posterior portion of the head capsule is less heavily sclerotized than the exposed anterior portion, particularly along the median line, and it is distinctly notched laterally at the point of attachment with the thoracic integument where a pair of thoracic muscles are inserted (Fig. 34.15). In larvae of *Xylophagus* (Xylophagidae), the exposed portion of the head capsule is similar to that of *Coenomyia*, but the retracted portion consists of two relatively short, sublateral rods flexibly hinged to the

anterior portion of the cranium. A similar type of articulation (although in some cases involving only one median rod) exists in larvae of the Therevidae, Scenopinidae, Mydidae, Apioceridae, Asilidae, Empididae, and Dolichopodidae (Figs. 37.24, 38.12, 40.29, 42.78–79, 47.58, 48.41, 48.43). In all such cases the articulated rods are called metacephalic rods (capsule rod of Melin 1923, manubrium of Cook 1949).

A broad range of cranial reduction analogous to that described above occurs in the single family Tipulidae. The initial reduction consists of shallow dorsolateral incisions and loss of the thickened postoccipital margins (Figs. 7.67, 7.77). From this stage the head capsule becomes reduced to three or four slender rods (Figs. 7.76, 7.83, 7.88). However, in these cases none of the rods involve the tentorial arms.
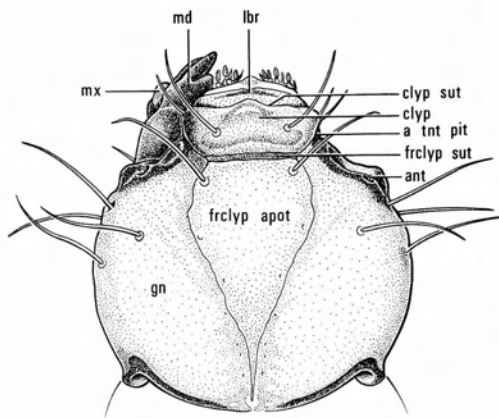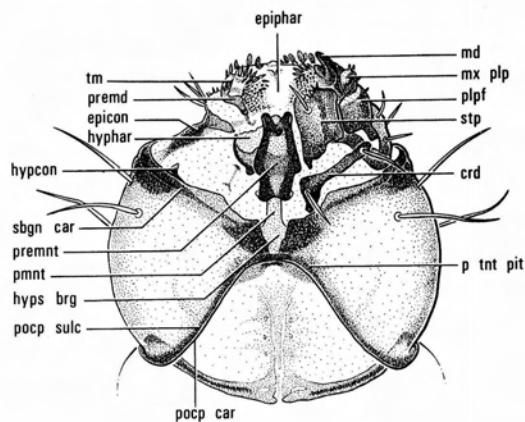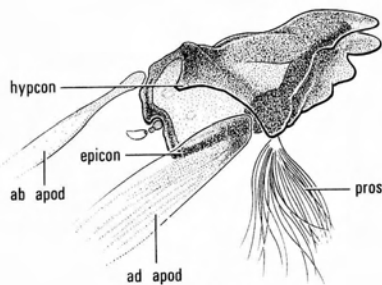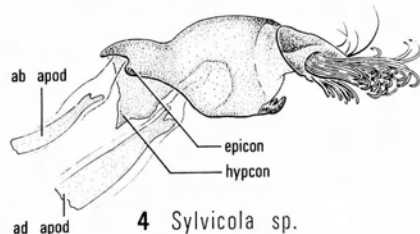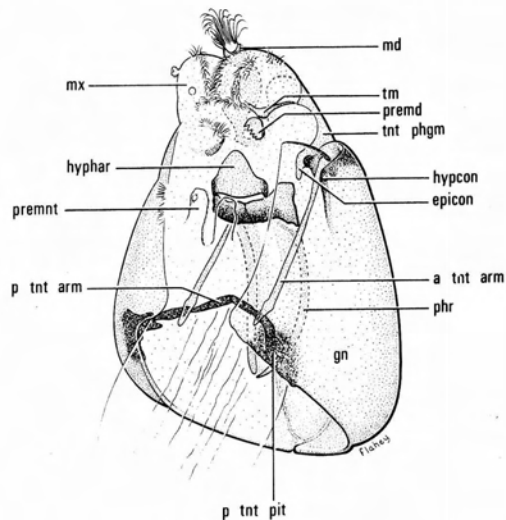
Figs. 3.1–5. Head capsule features: (1) dorsal and (2) ventral views of *Bibio* sp. (Bibionidae) with right mandible and maxilla removed; (3) right mandible of *Bibio* sp., ventromedial view; (4) left mandible of *Sylvicola* sp. (Anisopodidae), lateral view; (5) ventrolateral view of head capsule of *Sylvicola* sp. with left mandible and maxilla removed (*continued*).

Abbreviations: ab apod, abductor apodeme; ad apod, adductor apodeme; ant, antenna; a tnt arm, anterior tentorial arm; a tnt pit, anterior tentorial pit; clyp, clypeus; clyp sut, clypeolabral suture; crd, cardo; ecdys ln, ecdysial line; epicon, epicondyle; epiphar, epipharynx; frclyp apot, frontoclypeal apotome; frclyp sut, fronto-clypeal suture; gn, gena; hypcon, hypocondyle; hyphar, hypopharynx; hyps brg, hypostomal bridge; lbr, labrum; md, mandible; mx, maxilla; mx plp, maxillary palpus; phr, pharynx; plpf, palpifer; pmnt, postmentum; pocp car, postoccipital carina; pocp sulc, postoccipital sulcus; premd, premandible; premnt, prementum; pros, prostheca; p tnt arm, posterior tentorial arm; p tnt pit, posterior tentorial pit; sbgn car, subgenal carina; stp, stipes; tm, torma; tnt phgm, tentorial phragma.

The retraction of the head capsule in the Axymyiidae has not resulted in any weakening of the hind margin.

Tentorial arms. The *tentorium* is the internal skeleton of the head and it is present as a plesiomorphic structure in many larvae of the Nematocera and Brachycera (Hennig 1973, Anthon 1943*b*). However, it has become more or less extensively reduced or lost in several groups of Nematocera, e.g. Tipulidae, Sciaroidea, Psychodidae, Ptychopteridae, and Chironomoidea. With the notable exceptions of the Tipulidae and the Sciaroidea, the greater rigidity provided to the head capsule in these groups by a solid ventral connection between the genae, the hypostomal bridge (*see* "Ventral Region of Head Capsule"), seems to compensate for the loss or reduction of the tentorium. The tentorium in the eucephalic head consists basically of chitinized, rod-like invaginations from two pairs of *tentorial pits*. The posterior pair of pits is located ventrolaterally on the postoccipital sulcus (Figs. 2, 5) and the anterior pair is located behind the *anterior* (dorsal) *mandibular articulation* adjacent to the ecdysial lines (Figs. 1, 5). The invaginations from the posterior tentorial pits in the basic scheme extend transversely toward each other and unite to form a bridge-like *posterior tentorial arm*, while the paired *anterior tentorial arms* extend backward to meet the posterior arms (Fig. 5). The tentorium may also include a pair of short *dorsal arms* as outgrowths of the anterior arms to the cranial wall near the base of the antennae. This most primitive arrangement of the tentorium apparently exists among Diptera larvae only in some Anisopodidae (Anthon 1943*a*). The tentorium may be reduced, usually beginning with the failure of the posterior arms to unite, followed by complete loss of the posterior arms, and then by loss of the anterior arms. However, it has been suggested (Hennig 1973) that in the Sciaridae all that remains of the tentorium are the posterior arms forming the posterior of two ventral points of union or abutment of the genae (Fig. 15.33).

The internal structure of ridges and braces associated with or near the ends of the anterior tentorial arms is often very complex and has been described and illustrated at some length by Anthon (1943*b*) and Cook (1949). The development of a pair of internal *tentorial phragmata* (*sing. tentorial phragma*; vertical plates, pharynx supports) is of great importance because it constitutes a trend, possibly beginning among some Nematocera, further developed among the orthorrhaphous Brachycera, and culminating in the Muscomorpha. These tentorial phragmata are flattened, plate-like invaginations of the tentorial pits and of adjacent sutures. Cook (1944) called these sutures, in part, the paraclypeal folds in the Culicidae. He then initiated the name paraclypeal phragmata for the invaginations, which most subsequent authors have used for the tentorial phragmata. However, Hartley (1963) pointed out that the paraclypeal phragmata of orthorrhaphous Brachycera may not be homologous with those in the Nematocera. Indeed this seems to be the case, for in some Nematocera, e.g. Ble-

phariceridae, some Psychodomorpha, and some Culicomorpha, a portion of the lateral margin of the clypeus appears to fold or bend inwardly. This fold is anterior to and often more or less separated from the anterior tentorial pit and its incipient tentorial phragma (Fig. 5). It is to this structure that Cook gave the name paraclypeal phragma. The paraclypeal phragma commonly bears the anterior mandibular articulation, although in the Culicidae this articulation is on a slender extension of the fold to the hypopharynx called the *cibarial bar* (Cook 1949). The paraclypeal phragma apparently fuses with the tentorial phragma and the tentorial elements of the composite structure become dominant in the Brachycera. It therefore seems preferable to follow Roberts (1971*a*) in calling these structures in the Brachycera the tentorial phragmata, especially as the tentorium is undoubtedly a major part of the structure. The anterior tentorial arms project from the lower posterior margin of the phragmata and constitute a prominent feature of the head of most Brachycera (Figs. 6, 8, 12). The tentorial arms are especially well-developed in this group because they have assumed greater importance as major points of attachment for mandibular adductor muscles to compensate for the reduction of the cranium.

In those Asiloidea and Empidoidea in which the metacephalic rods have a basal line of weakening, the tentorial arms have a similar suture or weak point at their junction with the tentorial phragmata (Figs. 8; 47.58). Roberts (1969*b*) also reports such a weakening in the articulation point on the tentorial arms of *Rhagio* (Rhagionidae), but this weakened point is absent in the related genus *Chrysopilus* (Rhagionidae).

Ventral region of head capsule. The morphology of the ventral side of the head capsule of many nematocerous larvae is controversial. Specifically, the problem concerns the origin of a sclerotized, anteriorly toothed plate, the *hypostoma* (hypostomium, hypochilum, labial plate, maxillary plate, prementum), situated below the mouthparts in larvae of many Tipulidae, Psychodidae, and Culicomorpha. Some claim that the hypostoma is a derivative of the labium (Cook 1944), and others believe its origin is with the subgenal region of the cranium (Anthon 1943*b*). Until further detailed comparative morphological study provides an answer to this argument, the terminology of Anthon (1943*b*) is accepted here.

In the most primitive condition of the ventral region of the head capsule, as exemplified by the Bibionidae and the Anisopodidae, the genae are widely separated (Fig. 5) or a narrow, bridge-like extension between the genae is present in front of the occipital foramen (Fig. 2). This bridge is commonly referred to as the *hypostomal bridge* (subgenal bridge). In the membranous zone anterior to the hypostomal bridge unmistakable parts of the labium can be recognized. According to Anthon (1943*a*) these are most extensive in *Olbiogaster* (Anisopodidae) and include a *submentum*, a *mentum*, a *prementum*, *glossae*, and *labial palpi*. In representatives
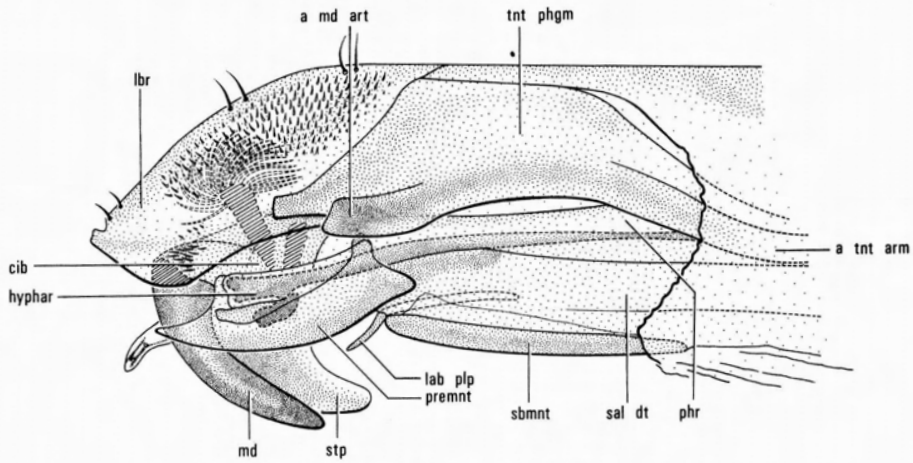
6 Tabanus marginalis
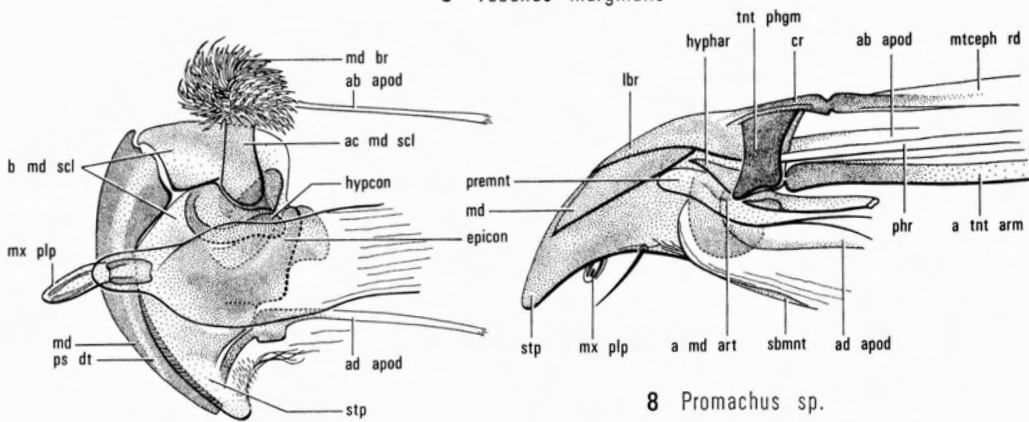
7 Tabanus marginalis
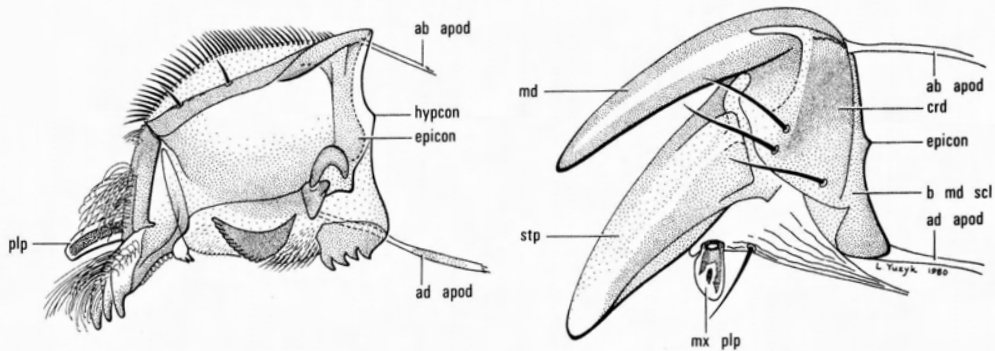
8 Promachus sp.

9 Odontomyia sp.

10 Promachus sp.

Figs. 3.6–10. Head capsule features (*concluded*): (6) lateral view of anterior portion of head capsule of *Tabanus marginalis* Fabricius (Tabanidae) with left mandibular–maxillary complex and portion of head capsule removed; (7) left mandibular–maxillary complex of *T. marginalis*, lateral view; (8) lateral view of anterior portion of head capsule of *Promachus* sp. (Asilidae) with left mandibular–maxillary complex and portion of head capsule removed; (9) left mandibular–maxillary complex of *Odontomyia* sp. (Stratiomyidae), lateral view; (10) left mandibular–maxillary complex of *Promachus* sp., lateral view.

Abbreviations: ab apod, abductor apodeme; ac md scl, accessory mandibular sclerite; ad apod, adductor apodeme; a md art, anterior mandibular articulation; a tnt arm, anterior tentorial arm; b md scl, basal mandibular sclerite; cib, cibarium; cr, cranium; crd, cardo; epicon, epicondyle; hypcon, hypocondyle; hyphar, hypopharynx; lab plp, labial palpus; lbr, labrum; md, mandible; md br, mandibular brush; mtceph rd, metacephalic rod; mx plp, maxillary palpus; phr, pharynx; plp, palpus; premnt, prementum; ps dt, poison duct; sal dt, salivary duct; sbmnt, submentum; stp, stipes; tnt phgm, tentorial phragma.

of the Bibionidae the labium is somewhat reduced, although usually *postmental elements* (a union of both submentum and mentum) and *premental elements* are present (Fig. 2). A similar situation exists in the Tanyderidae (Crampton 1930), the Blephariceridae (Anthon and Lyneborg 1968), and the Ptychopteridae. Among some other larvae of the Nematocera the hypostomal bridge is lengthened, correspondingly reducing the labium to only the premental elements. In the extreme condition, as exemplified by the Simuliidae and some Chironomidae (Figs. 27.80–81, 29.119–127), the hypostoma is well developed. It is apparently used for scraping food such as algae from submerged surfaces. Anthon (1943*b*) demonstrated the progressive development of the hypostomal bridge and the resulting displacement of the labium anteriorly, and finally somewhat internally, above the hypostoma until it becomes closely appressed to the hypopharynx. In these cases the prementum and hypopharynx appear to be combined as a single unit; the only means for differentiating the two is the position of the *salivary duct*, which opens in a pocket between the ventral wall of the hypopharynx and the prementum.

This hypothesis on the development of the hypostomal region seems to be supported by modifications of the region shown in the Tipulidae. In representatives of this family the hypostoma itself is often more or less divided medially, with each half quite obviously situated at the apex of an uninterrupted, sclerotized forward extension of the subgenal margin of the cranium (Figs. 7.76–77, 7.87).

Part of the difficulty with the hypothesis stems from Anthon's (1943*a*) own illustrations of *Olbiogaster* (Anisopodidae) and *Ptychoptera* (Ptychopteridae). The ventral sclerites lying between the genae appear to be homologous in the two genera and differ only in the degree to which they are separated from the genae. However, in *Olbiogaster* he names these sclerites the submentum and the mentum and in *Ptychoptera* the hypostomal bridge and the hypostoma.[1] The mentum in *Olbiogaster* and the hypostoma in *Ptychoptera* are apically toothed and look identical. Reduced premental elements lie above these toothed structures in close association with the hypopharynx.

Larvae of the Chironomidae bear other distinctive structures on the ventral surface of the head capsule that are important in the systematics of the family. On either side of the hypostoma in many members of the family are *paralabial plates* that may be marginally toothed (Fig. 29.118), striate (Figs. 29.119–120), or fringed with setae (Figs. 29.123, 29.125, 29.127). In larvae of the Tanypodinae the hypostoma is membranous and above it, apparently derived from the prementohypopharyngeal complex, is a sclerotized apically toothed plate called the *ligula* (Figs. 29.117–118).

A rather generalized labium is retained in most orthorrhaphous Brachycera. A large submentum and a smaller prementum often with labial palpi are found in the Tabanidae, some Stratiomyidae, and the Asiloidea (Figs. 6, 8; 37.26, 40.29). The submentum is lost but the prementum is retained, usually in a rather membranous condition, in other orthorrhaphous Brachycera. Like the Nematocera, it is closely bound to the hypopharynx. Again, the salivary duct is a useful landmark in distinguishing the hypopharynx.

Labrum. The labrum, or so-called upper lip, is continuous anteriorly with the frontoclypeal apotome, with no apparent separation in many cases. However, a clypeolabral suture may be present (Fig. 1). The basic form of the labrum in nematocerous larvae is a relatively broad, dorsoventrally compressed lobe. However, in the larvae of several families of Nematocera and in all of the orthorrhaphous Brachycera the labrum assumes a rather slender, laterally compressed, wedge-like appearance, probably in conjunction with rotation of the plane of movement of the mandibles toward a vertical axis (Figs. 5, 11). The ventral surface of the labrum is called the *epipharynx* (palatum). It usually bears a variety of setae, hairs, or spines that are sometimes generally distributed or, commonly, grouped into brushes or combs. These structures play an important part in the feeding process. They serve either by directing food materials toward the mouth as is done, for example, by the highly evolved labral brushes or fans of the Culicidae (Figs. 25.23, 25.26–27) and the Simuliidae (Fig. 27.76), or by cleaning the mandibles. The movement of the brushes and fans is mediated by muscles inserted on one or two pairs of small sclerites set in the mainly membranous surface of the epipharynx (Figs. 5; 29.119–122, 29.131–133). Chief among these is a flat, trapezoidal or triangular sclerite called the *torma (pl. tormae)*, on each side at the lateral angle between the labrum and the clypeus; the torma sometimes embraces the basal corners of the labrum where it either articulates with, or is fused with, a *dorsal labral sclerite* (labral plate). The median end of the torma usually projects anteromedially on the epipharynx. A second sclerite, the *premandible*, is sometimes present and articulates posteriorly with each torma. It is often incorrectly considered a part of the torma. The free end usually bears one or more teeth or spines sometimes resembling a comb. The motion that these sclerites impart to the labral brushes is produced by one or two pairs of labral retractor muscles originating on the frontoclypeal apotome. Another sclerite on the epipharynx with an associated brush of setae is a median *epipharyngeal bar* (palatal bar) that lies between the premandibles and behind the median ends of the tormae. This sclerite is usually V or U shaped or is sometimes divided medially. Paired labral compressor muscles are inserted on this sclerite and are attached to the median dorsal labral sclerite. The epipharyngeal bar is present in larvae of many Nematocera (Fig. 29.119) but is absent in others such as the Tipulidae (Matsuda 1965).

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[1] Originally spelled hypostomium and used incorrectly as such by many subsequent authors.
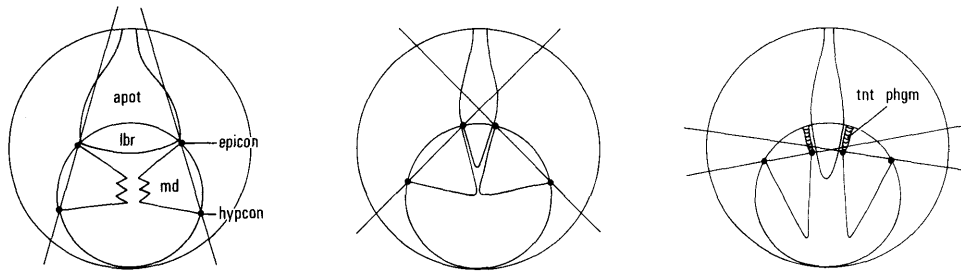
Fig. 3.11. Diagrammatic representation of rotation of plane of mandibular movement resulting from narrowing of labrum, shift of mandibular articulations, and development of tentorial phragmata.

Abbreviations: apot, apotome; epicon, epicondyle; hypcon, hypocondyle; lbr, labrum; md, mandible; tnt phgm, tentorial phragma.

The development of all of these sclerites and the hairs and spines associated with them among the Nematocera is extremely varied and of great taxonomic importance. A variable number of cibarial dilator muscles are also inserted on the epipharynx, on the postlabral portion. They usually have their opposite attachment on the clypeus.

All of the above sclerites and associated spines and brush-like groupings of hairs are absent in larvae of the orthorrhaphous Brachycera. However, hairs apparently used for cleaning the mandibles and, in some cases rather numerous but more generally distributed, are normally present in representatives of this group.

Mandible. Anthon (1943b) and Hennig (1973) considered the larval mandibles to be primitively two segmented. This condition exists most conspicuously in larvae of two genera of the Tipulidae (*Ulomorpha* and *Pilaria*) (Fig. 7.89), the Trichoceridae, the Anisopodidae (Fig. 4), the Ptychopteridae, and most orthorrhaphous Brachycera. The subdivision of the brachycerous mandibles is probably a secondary condition and therefore unrelated to that in the Nematocera.

The mandibles of several families of the Nematocera, especially those families in which the mandibles operate in a horizontal plane in opposition to one another, appear to retain some biting and chewing function. Accordingly, there is often a distal toothed incisor lobe and a proximal molar lobe (Fig. 3). One or both lobes may bear tufts of hairs. The hair tuft nearest the molar surface on the upper paralabral surface is called the *prostheca*. These hair tufts apparently function in cleaning the epipharynx and the maxillae just as the hairs on the epipharynx clean the mandible as it moves in and out. The hairs are directed inward so that food particles are forced toward the mouth.

Mandibles of some other Nematocera, e.g. some Tipulidae and Chironomidae, are claw-like, with a reduction in the number of teeth on the incisor surface and a loss of the molar grinding area (Figs. 7.83, 7.89,

29.117–118). This alteration in form appears to be associated with a major trend in the Nematocera, culminating in the Brachycera, to rotation of the mandibles from a horizontal plane through movement first in an oblique direction and finally to a vertical plane with the mandibles parallel to one another (Cook 1949, Schremmer 1951).

The mandible has two points of articulation, an anterior **epicondyle** and a posterior **hypocondyle**. The hypocondyle articulates laterally on the subgenal margin of the cranium, whereas the point of articulation of the epicondyle is normally closely associated with the proximal end of the anterior tentorial arm near the anterior angle of union of the genae and the frontoclypeal apotome. Rotation of the mandible is due to a shifting of its points of articulation. This shift apparently takes place in two steps (Fig. 11). The first is a movement of, at least, the epicondyle higher on the curve of the cranium. This repositioning is normally accompanied by a narrowing of the labrum and the frontoclypeal apotome, and it is characteristic of the larvae of all Psychodomorpha. The second step is displacement downwardly or inwardly of the anterior articulation on the developing tentorial phragma. This conformation is the case in many Psychodomorpha and in all orthorrhaphous Brachycera. In the Culicidae, however, the anterior articulation is on the cibarial bar.

In many families of the orthorrhaphous Brachycera there is a strong tendency for the mandibles and maxillae to become fused. Cook (1949) discussed this development in the Tabanidae, the Stratiomyidae, and the Therevidae. De Meijere (1916) and Bischoff (1924) also treated the subject extensively. The fusion is most extensive in the Stratiomyidae where the respective structures cannot be clearly differentiated except for the maxillary palpi (Fig. 9). Extensive modifications have taken place here involving membranization and the addition of complex groups of hairs apically. The apical portion of the mandible appears also to have been lost. The whole structure functions in sweeping food materials into the mouth (Cook 1949, Roberts 1969b). In most other

representatives of the orthorrhaphous Brachycera the fusion has not progressed to the point where the mandible and maxilla cannot be distinguished. They are, however, very closely linked both spatially and in movement. The inner membranous surface of the maxilla is attached to the **basal mandibular sclerite**.

With the exception of the Bombylioidea, the mandible of the orthorrhaphous Brachycera is basically subdivided with a slender, pointed, heavily sclerotized, usually curved apical blade that articulates dorsally to an inner basal mandibular sclerite (Figs. 7, 10). The basal mandibular sclerite bears two condyles in the Tabanomorpha as in all Nematocera, namely an inner epicondyle, articulating with the tentorial phragma, and an outer hypocondyle, which articulates with the anterolateral margin of the cranium. However, the hypocondyle has been lost in many Asiloidea and in the Empidoidea. This loss is the first appearance of a condition that is normal to all Muscomorpha. The reduction of the mandible to a single articulation in the Asiloidea is probably associated with the much larger, more heavily sclerotized maxilla that is present in these larvae (Figs. 10; 40.29, 42.78–79). The maxilla has its own connection with the sides of the cranial plate through the *cardo* (*see* "Maxilla") and inwardly has a membranous connection with the basal mandibular sclerite. The mandible is thus wedged between a solidly mounted maxilla and the labrum so that it cannot stray from its vertical movement and has little need for the hypocondyle.

The corresponding situation in the larvae of the Empididae and the Dolichopodidae is clouded by the reduction and skeletonization of their head capsules (Figs. 47.58, 48.41, 48.43). In these families a V- or U-shaped sclerite occurs on either side of a median labrum. The outer arm of this sclerite is probably the cardo of the maxilla and the inner arm is the mandible. In addition, one or more maxillary sclerites lie anterior to this V- or U-shaped sclerite, and one of them bears the maxillary palpus. The median portion of the cardo is connected dorsally to the basal mandibular sclerite. A similar formation is seen in the larval head capsule of *Vermileo* (Vermileonidae) (Fig. 39.4).

The basal mandibular sclerite of the Tabanidae comprises three closely linked sclerites (Cook 1949, Teskey 1969). Two of these are apparently subdivisions of the normal basal sclerite but the third is a bar-like **accessory mandibular sclerite** that connects with a group of dorsolateral spines (Fig. 7). These spines, called **mandibular brushes**, are present in most, if not all, Tabanoidea and are unique to this group. They apparently function for anchoring the head capsule within the host, but Roberts (1969*b*) sees their role in *Rhagio* (Rhagionidae) as assisting in locomotion. When the mandible is at rest, the mandibular brush is retracted beneath a fold of integument. But when the mandible is adducted the mandibular brush is pulled from beneath the covering integument by means of its connection with the accesso-

ry sclerite, and the spines become erect and lie in a recurved anchoring position. Another feature of some significance in tabanid larvae is a hollow mandible traversed by a poison duct opening subapically on the anterior edge of the blade. The duct runs through the basal sclerite to an inner pore near the hypocondyle and then to a poison gland within the head capsule.

In all Diptera larvae the **mandibular abductor muscles** perform the retractive movement of the mandibles and the **mandibular adductor muscles** control the closing or downward movements of the mandibles. These muscles are inserted by means of **apodemes** on either side of the fulcrum for mandibular movements. When a basal mandibular sclerite is present, the muscle insertions are near the proximal and distal ends of the sclerite (Fig. 10). In tabanid larvae the abductor insertion is on the accessory mandibular sclerite (Fig. 7). Both sets of muscles normally originate on the posterior and lateral walls of the genae and the tentorial arm, when present. With the reduction of the head capsule in the Brachycera, only a few of the mandibular adductor muscles are retained on the remnants of the cranium (in some cases the metacephalic rods) and the origins of the majority of muscle bundles are shifted to the tentorial arms.

Maxilla. The basic structure of the larval maxilla as it exists, for example, in some Tipulidae, the Bibionidae, the Mycetophilidae, the Sciaridae, the Anisopodidae, and the Ptychopteridae consists of a basal cardo and a distal *stipes*, bearing a one-segmented **maxillary palpus** (Figs. 2; 14.99–100, 15.33). The distal extremity of the stipes may be slightly differentiated into two endite lobes, the **galea** and the **lacinia**. The maxillary palpus is sometimes borne on what appears to be a secondary lobe of the stipes called the **palpifer**. The cardo commonly can be recognized by the two to four well-developed setae that it bears. But very often, with the exception of the palpus which is normally very evident, the homologies of the parts of the maxillae in nematocerous larvae are obscure.

The maxilla of nematocerous larvae is often mostly membranous, perhaps in line with its normal, rather passive role in feeding; aside from a sensory function, it serves to form a ventrolateral margin for the mouth opening within which the mandible can push food particles into the oral cavity. A notable exception to this passive function of the maxilla is found in the larvae of the Sciaroidea. Here the maxilla, especially the stipes, is heavily sclerotized and flattened with a toothed margin (Figs. 14.99, 15.33). It appears to have a function similar to the mandibles in actively rasping the food substrate.

The maxilla of the Asilidae also diverges from the passive role and seems to be specially adapted for a fossorial existence. Here the maxilla is enlarged, well sclerotized, and often somewhat shovel shaped or spatulate apically for digging (Figs. 10; 42.78–79). It also

serves to protect the blade-like mandible, which lies in a concavity on its median face. This surface is densely haired, apparently for cleaning the mandible. Distinctive also of the maxilla of larvae of all families of the Asiloidea is the retention of a well-defined cardo which, as mentioned above, bears several hairs. In the Asilidae three hairs are present, judging from the above figures and all the illustrations of Melin (1923). The sclerotized cardo in larvae of the Asilidae is flexibly fused to the dorsal edge of the basal mandibular sclerite. A similar but narrower fusion is seen in the larvae of the Empididae and the Dolichopodidae.

No more than two maxillary muscles have been retained in Diptera larvae. These are inserted in the stipes and have their origin on the genae. Maxillary muscles are reduced to one in some Tipulidae and apparently in all orthorrhaphous Brachycera (Cook 1949). The reduced musculature of the maxilla of the orthorrhaphous Brachycera appears to be associated with the partial fusion of the maxilla with the mandible whereby the inner membranous surface of the maxilla is continuous with the basal mandibular sclerite. The two structures move essentially as a single unit, mediated primarily by the mandibular muscles, thus decreasing the need for well-developed maxillary muscles.

Antenna and eye. The antennae and eyes are borne on the genae. The antenna is normally located near the anterodorsal corner of the sclerite in the vicinity of the anterior mandibular articulation. The maximum number of antennal subdivisions is six in some Chironomidae (Hennig 1973), although this number is very rare. Normally one to three subdivisions are present and they are commonly very short, sometimes no more than a pimple-like projection as in the Bibionidae, many Mycetophilidae, some Psychodidae, the Anisopodidae, and the Ptychopteridae. However, the antenna of the larvae of some Blephariceridae and the Deuterophlebiidae is elongate, and in the Deuterophlebiidae, conspicuously biramous (Figs. 8.7, 9.3). The antenna of the Chaoboridae has evolved into a prehensile structure with apical spines and is used for capturing prey (Figs. 24.9–10). The antenna usually bears various sensory organs whose sensory functions in larvae are poorly understood.

Eyes have been described for only a few larval Diptera, namely *Tipula* (Tipulidae), *Ptychoptera* (Ptychopteridae), the Culicomorpha, *Rhagio* (Rhagionidae), and the Stratiomyidae (Roberts 1971*b*, Hennig 1973). However, they are obviously more widely present judging from published illustrations of many other taxa. Even in their apparent absence, light-sensitive cells are probably present in most larvae. Bolwig (1946) and Hartley (1963) have shown the presence of such cells in a depression on the anterolateral margin of the tentoropharyngeal sclerite of certain cyclorrhaphous larvae (Fig. 12). The eyes in the Nematocera and orthorrhaphous Brachycera are simple *stemmata* (*sing. stemma*) consisting at most of a lens or crystalline sphere in the surface of the head capsule beneath which are bundles of elongate visual cells shielded by a cup of black pigment granules. The pigment provides for directional perception of light. In many cases the lens is absent. A precocious adult eye with numerous ommatidia commonly occurs anterior to the larval eye in some larvae of the Chaoboridae and the Culicidae.

Pharynx and associated parts. According to Snodgrass (1935), the cibarium is the food pocket of the preoral mouth cavity, between the base of the hypopharynx and the undersurface of the clypeus. It is followed by the pharynx and then by the esophagus. All three parts are evident in most Nematocera. The dorsal walls of the cibarium and pharynx bear dilator muscles that are inserted on the frontoclypeal apotome. The cibarium or the pharynx, or both, can therefore act as a pumping mechanism. The pharynx of some nonpredacious nematocerous larvae that feed on waterborne particles has a complex filtering apparatus for straining the suspended food particles from the water and then for ejecting the excess water from the mouth. Anthon (1943*b*), Cook (1944), and Snodgrass (1959) described some variations of the *pharyngeal filter* and indicated that it occurs in some Tipulidae, the Psychodidae, the Trichoceridae, the Anisopodidae, the Scatopsidae, the Ptychopteridae, and the Culicidae. Anthon and Lyneborg (1968) illustrated the pharyngeal filter of the Blephariceridae. In all these larvae it has the same general form as is shown in Fig. 5.

Contraction of the dilator muscles inserted on the dorsal walls of the cibarium and pharynx, together with closure of the esophagus, enlarges the pharynx, thereby creating a negative pressure that sucks in the water which contains the food particles. The opening to the pharynx is then constricted and the intrinsic muscles in the pharynx are contracted. This action creates sufficient pressure to force the water back through the constriction. During expulsion, the water passes through a filter formed by dense, comb-like fimbriations that retain the very fine food particles.

In larvae of orthorrhaphous Brachycera the pharynx is an elongate tube. This tube has been called, at least in part, the cibarium or the cibarium–pharynx by Cook (1949) and Roberts (1969*b*), even though the portion so named extends well behind the hypopharynx. These writers have perhaps been following a later interpretation by Snodgrass (1947) that the frontal ganglion is situated at the boundary between the cibarium and the pharynx. It seems preferable, however, to maintain in the orthorrhaphous Brachycera the distinction between the cibarium and the pharynx that is based on morphological features of the food canal itself, as is done for the Nematocera at the beginning of this section.

The pharynx is often more or less sclerotized ventrally and membranous dorsally in many brachycerous larvae. A series of muscles inserted in this membranous upper

surface and attached to the cranium dorsally serves to dilate the tube so that it can function as a pump, like that described above for nematocerous larvae. The elasticity of the upper membrane and the sclerotized ventral and lateral walls suffices for contraction of the tube. Efficient pumping action is aided by a flaplike valve at the opening of the pharynx, as described for larvae of the Tabanidae (Olsufjev 1936), and by the ability to constrict the esophageal opening. The sclerotization of the pharynx is accompanied, at least in larvae of the Stratiomyidae, the Vermileonidae, the Empididae, and the Dolichopodidae, by fusion of the pharynx with the tentorial phragmata. This condition may be a precursor to the situation that occurs in larvae of the Muscomorpha (see description of head under "Muscomorpha"). Sclerotization of the pharynx and its fusion with the tentorial arms are particularly well developed in the Stratiomyidae, possibly in conjunction with the evolution of a *pharyngeal grinding mill*. This mill and a similar structure in some Syrphidae, patterned on the principles of a mortar and pestle, is shown in Figs. 36.58–59 and is described by Robert (1969a).

A pharyngeal filter is absent in larvae of most orthorrhaphous Brachycera, apparently because most larvae of the group are predatory. Their food, although mainly liquid, is highly concentrated and filtering would serve no real purpose. An exception is found in some Stratiomyidae, which have a pharyngeal filter bearing some similarity to the filter of the larvae of some Muscomorpha. The pharyngeal filter in *Stratiomys* (Stratiomyidae) consists of two lateral, longitudinal grooves in the floor of the pharynx covered by a dense, comb-like series of transversely oriented filaments. The grooves communicate to the exterior anteriorly on either side of the prementum. Excess water is forced through the filaments and along the grooves to the exterior while suspended food particles are retained by the sieving action of the filaments.

Muscomorpha

The larval head of the Muscomorpha departs radically from the heads of more primitive Diptera. The muscomorphan head capsule is difficult to homologize with the more primitive Diptera because a series of connectant groups showing the gradual evolution of the cephalopharyngeal skeleton and associated structures is lacking. This difficulty is evidenced by the differences of opinion expressed in older literature (as summarized by Ludwig 1949 and Hennig 1973). Many workers resorted to postulating completely new structures to explain some of the modifications. However, the muscomorphan head is considered here to represent a logical further development of the features of the head capsule of larvae of the orthorrhaphous Brachycera. The major evolutionary sequences in its development can be interpreted as an extension of trends pointed out by Cook (1949) and repeated above, particularly as they occur in the larval head of orthorrhaphous Brachycera. Chief among these trends are the further reduction, including complete

desclerotization, of all external elements of the maxillae and the head capsule, together with loss of all direct connection of the tentorial phragmata with the external body cuticle; complete fusion of the tentorial arms with the pharynx; and additional phragmatal growth posteriorly to the tentorial phragmata and to the fused tentorial arms and pharynx.

In the Muscomorpha the head comprises an outer membranous *cephalic segment* (pseudocephalic segment), which anteriorly bears the antennal and maxillary sensory papillae, and the internal *cephalopharyngeal skeleton* (Figs. 12, 13). Most descriptions of larvae of the Muscomorpha either make no mention of the cephalic segment being part of the head or they include it with the description of the body segments; this treatment indicates a misunderstanding of its derivation. Such misinterpretation is obviously the case where 12 segments are attributed to the body of muscomorphan larvae. Schremmer (1956) pointed out that the cephalic segment probably originated from the maxillae and from small anterior portions of the head capsule that have become membranous; these membranous portions fuse dorsally over the mandibles and enclose them in a deep atrium (oral pocket). This interpretation explains why the sensory organs of the maxillary palpi and the antennae are in such close proximity. Without such rationalization, this proximity could be explained only by a complex migration. The modification of the maxillae as a sheath for the mandibles occurs among larvae of the orthorrhaphous Brachycera, in particular in some species of the Mydidae and the Asilidae where the median face of each maxilla has a concavity in which the mandible is recessed. The progressively skeletonized appearance of the maxillae in larvae of the Vermileonidae, the Empididae, and the Dolichopodidae indicates that membranization does in fact occur.

The cephalic segment is bilobate anteriorly, with an antennal and a maxillary sensory papilla at the apex of each lobe. These two lobes are referred to as the *antennomaxillary lobes*. Whereas the two papillae are separated in most larvae, Roberts (1970) showed them both present at the apex of a relatively large two-segmented protuberance in *Myathropa florea* (Linnaeus) (Syrphidae). A second, but much smaller pair of sensory organs, enervated from the maxillary nerve, is present behind the primary pair in *Calliphora* (Calliphoridae) and other larvae (Ludwig 1949, Roberts 1971a). This secondary pair is normally located among a series of *oral ridges* that radiate from the preoral cavity, and these sensory organs are therefore usually difficult to detect. Homology of the antennal and maxillary sensory papillae has been demonstrated from studies of the nervous system by the above authors and Hartley (1963).

The oral ridges are situated on the antennomaxillary lobes on either side of the preoral cavity. Their function is apparently similar to that of the pseudotracheae of the adult; they serve to direct food-carrying liquids toward

the atrium (Figs. 12, 13). They vary widely in structure, although this aspect has apparently not been studied much. The configuration of the ridges has been used diagnostically in some of the European literature but has been generally ignored on this continent. The ridges are, at least in some larvae, made up of rows of minute spicules. They are apparently best developed in some saprophagous syrphid larvae of the tribe Eristalini, which inhabit putrid or stagnant water rich in organic matter. Hartley (1963) and Roberts (1970) described the cephalopharyngeal skeleton of these larvae. Their mandibles are greatly reduced and the cephalopharyngeal skeleton is further retracted within the thorax; the antennomaxillary lobes are thus partially invaginated so that the ridges line an internal cavity. Here they are very pronounced, and each bears a fringe of bristles forming a comb that touches the adjacent ridge. The ridges thus no longer channel food toward the mouth but serve as a coarse filter to separate some of the solid particulate matter from the liquid carrier. The oral ridges and spicules are sometimes used as rasping devices, particularly when the spicules are well developed as in some Platypezidae (Fig. 5.45).

The cephalopharyngeal skeleton normally comprises three main parts: the *tentoropharyngeal sclerite* (basal sclerite, pharyngeal sclerite, pharyngosinusal theca), the *hypopharyngeal sclerite* (hypostomal sclerite, H-shaped sclerite, intermediate sclerite, labial sclerite, labiohypopharyngeal sclerite), and the *mandibles* (mouth hooks) (Figs. 12, 13).

The tentoropharyngeal sclerite consists of a pair of reclining, somewhat U-shaped sclerites on either side of the pharynx. The two arms of each U-shaped sclerite are called the *dorsal* and *ventral cornua* (*sing. cornu*; wings). The two ventral cornua are fused on each side with the pharynx. The bases of the U-shaped sclerites involving the anterolateral walls represent, at least in part, the tentorial phragmata; the two ventral cornua, which are fused with the pharynx, apparently include the two anterior tentorial arms. In contrast, in the orthorrhaphous Brachycera the tentorial arms project from the ventral edges of the tentorial phragmata; here any fusion with the pharynx involves only the phragmata, and the tentorial arms are always free apically. In the Muscomorpha the ventral cornua are normally somewhat expanded apically to provide an adequate surface for attachment of mandibular and labial muscles. The dorsal cornua probably represent an additional posterior expansion of the tentorial phragmata. Roberts (1971a) and Hartley (1963) called the dorsal cornua the clypeal or clypeofrontal phragmata, but this derivation seems doubtful because there is no evidence of such phragmatal growth in larvae of the orthorrhaphous Brachycera from which the Muscomorpha are apparently derived. Both dorsal and ventral cornua may bear conspicuous, clear, unpigmented areas or windows that sometimes continue to the posterior margin and thus appear like sinuses or incisions in the cornua (Fig. 5.79). The dorsal margin of each ventral cornu often has a distinctively shaped projection.

The tentoropharyngeal sclerites may be joined anterodorsally by a dorsal bridge (Fig. 12), which Hartley (1963) and Roberts (1970) derived from the labrum. This bridge is often weak, with a fenestrated appearance. The anterior margins of the tentoropharyngeal sclerite below the dorsal bridge is concave and part of the sclerite behind this concavity is often depressed. In this depression lie visual cells. This depression provides a dark background so that these cells can obtain a directional perception of illumination (Roberts 1971b).

The hypopharyngeal sclerite is a more appropriate name morphologically for the sclerite lying between the mandibles and the tentoropharyngeal sclerite than other names that have been applied to it. This sclerite is apparently a fusion product of several structures, of which the hypopharynx is almost certainly a part. A combined name for the components of the sclerites would be too unwieldly. The most commonly used name, hypostomal sclerite, is inaccurate morphologically and could be confused with the postlabial sclerite of the same name in larvae of some Nematocera. It comprises two lateral, more or less longitudinal bars joined ventrally near the middle by a transverse bar; thus, from above and from below, this sclerite resembles the letter H (Fig. 13). The cibarium runs through this supporting structure to connect with the pharynx. The lateral bars articulate with the mandibles anteriorly and are continuous posteriorly with the anteroventral margin of the tentorial phragmata in most if not all Aschiza and in several Schizophora (Figs. 5.3, 5.45, 5.50–51, 5.74); they are separated from the tentorial phragmata by a narrow line of cleavage in all other Schizophora. Therefore the lateral bars may be derived from the tentorium as considered by both Hartley (1963) and Roberts (1970). They are perhaps, at least in part, anterior extensions of the points at which the tentorial phragmata articulate with the mandibles in the orthorrhaphous Brachycera. The salivary duct enters the cibarium just behind the transverse bar. Because this duct opens at the base of the labium, between it and the hypopharynx, in all more primitive Diptera larvae, the transverse bar can reasonably be assumed to be partially derived from one or both of these structures. Traxler (1977) suggested that the entire hypopharyngeal sclerite is of labial and hypopharyngeal origin whereas Ludwig (1949) considers it solely of labial origin; but neither of these proposals have been substantiated. Several small labial sclerites sometimes occur anteriorly, below the hypopharyngeal sclerite, in larvae of at least the Schizophora. These sclerites support the ventral membranous wall of the atrium. The more anterior of these sclerites is sometimes in the form of a transverse bar supporting the labial lobe at the hind margin of the mouth (Fig. 13). Miller (1932) showed this sclerite (his liguloid arch) to have small spines along its leading edge in *Calliphora* (Calliphoridae). The strong, dentate, ventral arch that is a characteristic feature of larvae of the Sciomyzidae (Fig. 5.57) is possibly homologous with this labial sclerite. A pair of labial muscles is attached to the anterior labial sclerite. These muscles serve to dilate the atrium.

Dilation of the atrium creates a negative pressure that draws food-carrying liquids into the cavity. The stream of nutrient-rich liquid is then moved along through the cibarium and pharynx by a similar muscle action.

The labium is commonly much more well developed in larvae of the Aschiza than the Schizophora. In some Phoridae and Platypezidae it consists of a solid, sclerotized continuation of the hypopharyngeal sclerite; its apex is modified to form a rasping structure that functionally may replace the mandibles (Figs. 5.45, 5.50–51). An apically pointed extension from the hypopharyngeal sclerite, similar to the pointed labrum above it, is figured by Hartley (1963) and Roberts (1970) in larvae of *Syrphus* (Syrphidae). However, in *Syrphus* highly modified mandibles are present that articulate with a short dorsal spur from near the middle of this hypopharyngeal-labial sclerite.

A pair of slender sclerotized rods called *parastomal bars* project from each side of the anterior margin of the tentoropharyngeal sclerite above the hypopharyngeal sclerite in some Muscomorpha, both in the Aschiza and the Schizophora (Figs. 12; 5.50, 5.58). In some Syrphidae, particularly Syrphinae, and also in first-instar larvae of some Schizophora, these bars converge and fuse anteriorly and have been homologized with the labrum (Hartley 1963, Roberts 1970). This interpretation has some support in such orthorrhaphous Brachycera as the Tabanidae where the epipharyngeal margin of the slender, wedge-shaped labrum is shown by Teskey (1969) to have a narrow band of heavier sclerotization on either side. Because the epipharynx is continuous with the dorsal wall of the pharynx at the point where the tentorial phragmata fuse with the pharynx, it is reasonable to assume that these narrow, sclerotized bands have also fused with the phragmata. The sclerotized bands have remained intact in the higher Diptera, both in their role of supporting the labrum when it is present and in supporting the dorsal wall of the epipharynx. When the free end of the labrum is absent, the parastomal bars may connect with a fenestrated *epipharyngeal sclerite* (epistomal sclerite) lying above the anterior extremity of the hypopharyngeal sclerite (Fig. 5.58). Labral sensory organs pass through these fenestrations (Roberts 1971a).

The *mandibles* (mouth hooks) of the Schizophora are commonly strongly sclerotized, curved, and tapered apically from a widened squarish or triangular base (Fig. 12). They are hollow, and a small pore laterally on the basal portion is the external opening of the lumen. A similar pore occurs in the basal mandibular sclerite of tabanid larvae (Teskey 1969). This similarity, plus the general similarity of the form of the base of the muscomorphan mandible to that of the orthorrhaphous Brachycera, suggests that the structures are homologous and that the two parts of the mandible have become solidly fused. The apical, hooked portion sometimes has accessory teeth along the ventral margin.

The mandibles are articulated proximally with the lateral bars of the hypopharyngeal sclerite, and muscles inserted on the base of the mandible above and below the point of articulation control the up-and-down movement. The upper abductor insertion is directly on the mandible, whereas the lower adductor insertion is on a small sclerite called the *dental sclerite* below the base of the mandible, according to Ludwig (1949) and Roberts (1971a). If such muscle attachment does occur on the dental sclerite, the sclerite must be attached firmly to the mandibular base. However, Miller (1932) stated that in *Calliphora* (Calliphoridae) the adductor muscle insertion is directly on the mandible. He described a very complex dental sclerite but offered no explanation of its function.

Associated with the mandibles of some Muscidae are accessory oral sclerites below the mandibles (Fig. 5.101). Roberts (1971a) illustrated these sclerites in *Limnophora* (Muscidae) and explained their operations, but he suggested nothing about their origin.

Another oral sclerite of a different type is also illustrated by Roberts (1971a) and Miller (1932) in larvae of *Calliphora*. This slender, rod-like sclerite, which is slightly expanded at its posterior end, lies in the membranous ridge between the two atria in which the mandibles retract. The function of this sclerite is unknown and it apparently occurs only in *Calliphora* and some close relatives.

The various sclerites of the cephalopharyngeal skeleton described above are found in many shapes and sizes throughout the Muscomorpha, and they provide excellent characteristics for the identification of the various taxa.

Hartley (1963) and Roberts (1971a) considered the foregut, or that part of the alimentary canal lying within the cephalopharyngeal skeleton, to comprise three regions: the preoral cavity, the atrium, and the cibarium–pharynx. The *preoral cavity* is bounded by the mandibular lobes that bear the ridges converging on the mouth. The *atrium* is internal. Its floor bears the labial sclerites and is supported by the transverse bar of the hypopharyngeal sclerite. Its roof bears the epipharyngeal sclerite supported by the parastomal bars. Behind the atrium is the cibarium–pharynx, sometimes bearing longitudinal ridges of the pharyngeal filter.

The above definitions of the terms preoral cavity and atrium are adopted here. However, this interpretation of the cibarium–pharynx does not correspond to Snodgrass' (1935) original definition of the terms that was adopted earlier in this work. In Snodgrass' definition the hypopharynx forms the floor of the cibarium. It is therefore more accurate to call this region the cibarium rather than the cibarium–pharynx and restrict the term pharynx to the portion of the alimentary tract traversing the tentoropharyngeal sclerite that sometimes bears the pharyngeal filter. Moreover, the region is morphologically well defined and can be readily related to the condition

in larvae of the Nematocera and orthorrhaphous Brachycera. The term atrium can be retained for the region between the functional mouth and the cibarium. The atrium is essentially unique to the Muscomorpha and was created by the additional retraction of the head, including the mandibles, within the cephalic lobe and the thorax.

As a rule the pharyngeal filter is present only in those larvae of the Muscomorpha that are saprophagous and consume solid food materials suspended in liquid (Keilin 1912). The filter is absent in predatory larvae, as explained previously. The filter is effectively described by Hartley (1963) and Roberts (1971a). The lower surface of the pharynx has a series of longitudinal ridges; the free edge of each ridge bears lateral rows of short filaments projecting laterally to meet the filaments of the next row, as shown in Fig. 14. The pharynx is thus divided into a series of ventral channels and one dorsal channel. This filter functions analagously to those of the Nematocera and the Stratiomyidae. Liquid in which food particles are suspended is drawn into the dorsal channel. Then by appropriate pressures and valve closure the liquid is forced through the filamentous sieve into the ventral channels, where it is regurgitated through the mouth.

The musculature of the cephalopharyngeal skeleton has been mentioned here only to the extent needed to explain the operation of certain structures. The complete musculature and nervous systems as they exist in larvae of some Syrphidae and the *Calliphora* (Calliphoridae) is described and illustrated by Hartley (1963), Ludwig (1949), and Roberts (1970, 1971a). These descriptions almost certainly can be applied to all larvae of the Muscomorpha.

BODY

Body shape. The body shapes of Diptera larvae are diverse. Most nematocerous larvae, as exemplified by the Tipulidae, the Bibionidae, most Sciaroidea, the Trichoceridae, the Anisopodidae, and the Chironomidae, are subcylindrical (Figs. 7.66, 13.12–14, 14.97, 18.7, 19.19, 29.114–116). Larvae of the Cecidomyiidae, the Tabanidae, and several Muscomorpha such as the Canacidae and the Ephydridae have a fusiform body (Figs. 5.37, 5.62–63, 16.8–9, 31.51–52). Larvae of certain Ceratopogonidae, *Glutops* (Pelecorhynchidae), the Therevidae, and the Scenopinidae have an elongate, serpentine body (Figs. 28.132–134, 30.5, 38.11). Some larvae, for example the Xylophagidae and many Muscomorpha, have a body form that is markedly narrowed anteriorly (Figs. 5.73, 5.76, 5.98, 5.102, 34.11–12). Many Diptera larvae have dorsoventrally flattened bodies. These include the Xylomyidae, the Stratiomyidae, the Lonchopteridae, the Platypezidae, and *Fannia* (Muscidae) (Figs. 5.40–41, 5.47, 5.53, 35.6–7, 36.71–73). The larvae of many Syrphidae and many parasitic forms are very stout (Figs. 5.1, 5.17, 5.33, 5.38, 43.28, 44.4). Part of the body may be conspicuously

swollen. The thorax of larvae of the Chaoboridae and the Culicidae is characteristically swollen (Figs. 24.10, 25.33–34). Larvae of the Simuliidae are swollen toward the posterior end (Fig. 27.77). Larvae of *Goniops* (Tabanidae) and the Conopidae are pear shaped (Figs. 5.11, 31.54). The larva of *Microdon* (Syrphidae) is hemispherical (Fig. 5.12).

Body segmentation. The number of recognizable body segments is most commonly 12 in the Nematocera and 11 in the Brachycera. Of these, three are always thoracic and the remainder abdominal. Any variance from these numbers is to decrease the number of abdominal segments in the Nematocera and to increase it for the Brachycera. Thus the larvae of the Tipulidae, the Deuterophlebiidae, some Psychodidae, the Trichoceridae, the Anisopodidae, the Ptychopteridae, and the Simuliidae have eight recognizable abdominal segments, whereas the number is further reduced to seven in the Blephariceridae and the Axymyiidae. On the other hand larvae of the Asiloidea commonly have nine recognizable abdominal segments. The ninth abdominal segment is sometimes small and displaced onto the ventral side of the body, as in many Cecidomyiidae and the Scatopsidae.

In all cases where nine abdominal segments are present, the anus is located on the ninth segment. Therefore when only eight abdominal segments are present and the anus is situated ventrally on the terminal segment, a fusion of the eighth and ninth abdominal segments is indicated.

One of the abdominal segments in the Blephariceridae is included in a compound fusion segment involving the head capsule, the three thoracic segments, and the first abdominal segment. The entire larva therefore appears to comprise only seven segments, the first being quite large (Fig. 8.7).

In the embryos of Blephariceridae and several other Nematocera investigated, 13 body segments are initially recognizable but later the above-mentioned fusion, plus fusion of the last four body segments, occurs to produce the apparent seven-segmented condition (Matsuda 1976, Craig 1967). Fusion of the three thoracic segments with each other is an important diagnostic feature of the Chaoboridae, the Culicidae, and the Simuliidae (Figs. 24.10, 25.33–34, 27.77).

Conversely, subdivision of the segments is a feature of the larvae of several taxa. A narrow intercalary pseudosegment is inserted in front of the prothorax and each of the abdominal segments of *Sylvicola* and *Mycetobia* (Anisopodidae) (Fig. 19.19). The three thoracic and first abdominal segments of larvae of the Psychodinae are commonly divided into two subdivisions, and the following six abdominal segments are each divided into three (Figs. 17.14–15). These subdivisions can usually be differentiated from the true segmental boundaries by slightly less prominent folds in the integument, but the sclerotized plaques present dorsally on many or all

12 Phormia regina

13 Phormia regina
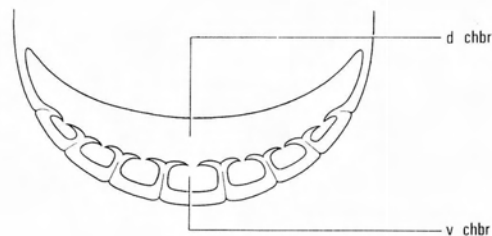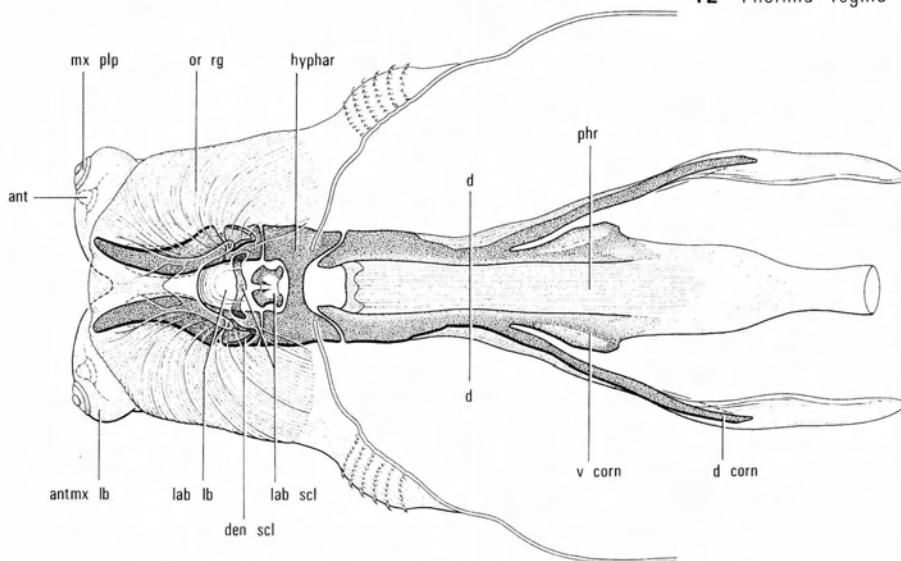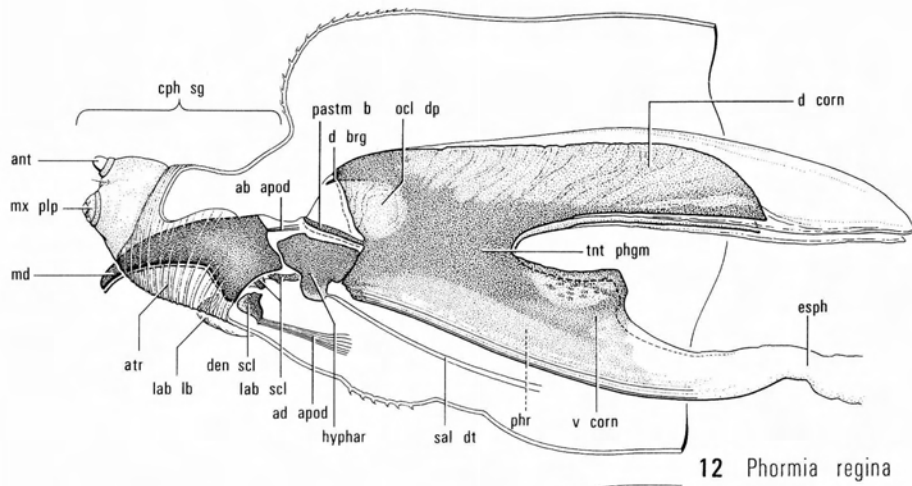
14 Phormia regina

Figs. 3.12–14. Cephalic segment and cephalopharyngeal skeleton of *Phormia regina* (Meigen) (Calliphoridae): (12) left lateral view with left antennomaxillary lobe removed; (13) ventral view, entire; (14) diagrammatic cross section (d-d) of pharyngeal filter.

Abbreviations: ab apod, abductor apodeme; ad apod, adductor apodeme; ant, antenna; antmx lb, antennomaxillary lobe; atr, atrium; cph sg, cephalic segment; d brg, dorsal bridge; d chbr, dorsal chamber; d corn, dorsal cornu; den scl, dental sclerite; esph, esophagus; hyphar, hypopharynx; lab lb, labial lobe; lab scl, labial sclerite; md, mandible; mx plp, maxillary palpus; ocl dp, ocular depression; or rg, oral ridge; pastm b, parastomal bar; phr, pharynx; sal dt, salivary duct; tnt phgm, tentorial phragma; v chbr, ventral chamber; v corn, ventral cornu.

subdivisions are a better indication. Larvae of *Trichoc-era* (Trichoceridae) have a similar pseudosegmentation (Fig. 18.7).

Larvae of the Therevidae and the Scenopinidae, which closely resemble each other, are unique in having 20 segmental divisions, most of which are so similar as to make the pattern of division difficult to interpret (Fig. 38.11). Slight size and shape differences in alternate units of the 12 segmental divisions beyond the anterior three (thoracic) segments indicate that these comprise six true abdominal segments that have each become subdivided once. The posterior spiracles, which typically occur on the true eighth abdominal segment (*see* "Respiratory System"), are located on the 14th abdominal subdivision; this positioning indicates that the preceding 13th subdivision is probably an undivided seventh abdominal segment. There is no clear guide as to how the true eighth and ninth abdominal segments are divided to produce the terminal four subdivisions.

Similar difficulties in interpreting the true body segmentation occur in some Bibionidae (*Bibio* and *Plecia*), where the posterior spiracles lie on the ninth abdominal division (Figs. 13.12, 13.14). Are these two segments actually subdivisions of the eighth abdominal segment (as suggested by Hennig 1948), or have the posterior spiracles shifted their normal location? A study of the internal anatomy of these segments might answer this question and might also provide an explanation of the odd sequence of subdivisions of the abdomen of larvae of the Therevidae and the Scenopinidae.

Except where obvious fusion occurs, the segments or their subdivisions are usually clearly differentiated from each other. However, sometimes the borders are indistinct, usually because of general integumental wrinkling as in some Syrphidae (Fig. 5.17), which obscures segmental lines. In these cases the true segmentation can often be distinguished by studying the repetitions of the setal patterns of the cuticle.

Cuticle. The cuticle of most Diptera larvae is non-pigmented, weakly or not at all sclerotized, flexible, and elastic. The usual lack of pigment and general sclerotization is perhaps explained by the concealed way of life of most Diptera larvae. The thickness and durability of the cuticle vary considerably among Diptera larva. At one extreme is the very thin membranous cuticle that is characteristic of aquatic Culicomorpha. Larvae of the Sciaroidea and many Muscomorpha living exclusively in concealed niches surrounded by a near-saturated atmosphere, where abrasive forces are at a minimum, also have a thin cuticle. At the other extreme are larvae of the Asilidae, living and moving in relatively dry soil. They have a tough, leathery cuticle that protects them from abrasion and water loss. All gradations are found between these extremes, and the thickness and durability of the cuticle are usually good indicators of the potential stresses found in the habitat occupied by the larva.

Sclerotization of the cuticle is most conspicuous in larvae of *Xylophagus* (Xylophagidae) and related genera. In these larvae, the dorsal surface and, to a lesser extent, the ventral surface of the thorax, as well as the dorsal surface of the terminal segment surrounding the spiracles, bear sclerotized plates (Figs. 34.11–13). Partial or complete sclerotization of the posterior spiracular disc (*see* "Number and Distribution of Spiracles") or structures associated with the spiracles or anus is a feature of many Tipulidae, Scatopsidae, Synneuridae, Culicidae, Psilidae, and others (Figs. 5.86, 7.78–81, 21.6, 25.34). In the Scatopsidae a pair of lobes called adanal lobes, or a shelf above and behind the anus, are sclerotized as well as the tubular processes bearing the posterior spiracles (Fig. 20.26). A variety of sclerotized structures may occur on larvae of the Culicidae; the most prominent of these are usually the subconical respiratory siphon and the so-called saddle covering the dorsal surface of the ninth abdominal segment bearing the anus (Figs. 25.28–32). Additionally, sclerotized tergal plates sometimes occur on other posterior abdominal segments of culicid larvae, and the setal clusters that are so conspicuous a feature of these larvae may also arise from sclerotized plaques.

Some or all of the segmental subdivisions of larvae of the Psychodinae bear sclerotized plates dorsally (Figs. 17.14–15). A ventral, variously shaped sclerite on the prothorax, called the *sternal spatula* (breastbone, spatula sternale), is characteristic of many larvae of the Cecidomyiidae (Fig. 16.7). According to Milne (1961) the sternal spatula is used primarily to construct the pupal chamber in soil.

Larvae of the Stratiomyidae and the Xylomyidae have a particularly distinctive armored cuticle. Its rough, reticulate appearance is caused by the deposition of calcium carbonate.

Few Diptera larvae are conspicuously colored. The rather general, greenish or brownish coloration of some Tabanidae and the red of some Chironomidae is imparted by the coloring of the hemolymph. The reddish hemolymph takes on its coloration from hemoglobin (Keilin 1944). The larvae of many of the Cylindrotominae (Tipulidae) and the Syrphidae that live on the surface of plants are greenish. More commonly the color is arranged in surface patterns that change with age of the larvae, for example, many Mycetophilidae and Culicomorpha. The color is bestowed by pigment granules contained in chromatocyte cells of peripheral fat bodies (Hinton 1958, 1960). The coloration of the body sometimes depends on the character and density of cuticular pubescence. Dense microtrichia give a grayish tinge to the body of tipulid larvae. The cuticular microtrichia of some Limoniinae are golden colored.

Generally, larvae that live deep within soil and wood are uniformly whitish or yellowish. Color varies most in larvae that live in litter, under bark, or in water and especially in those larvae that develop on plants or amidst moss.

Cuticular outgrowths on the body surface of Diptera larvae range from minute, fine microtrichia or spicules, to scale-like projections, to simple or greatly modified hairs or setae, through to strong spines and fleshy processes in various combinations. The incidence of such outgrowths on segments preceding the terminal one are reduced among representatives of the schizophorous Muscomorpha. The characteristics of these outgrowths and their distribution provide valuable diagnostic features. The great diversity of arrangement, size, and character of these cuticular structures is indicated below.

When small microtrichia and spicules are present they often cover extensive areas of the integument, as in larvae of some Tipulidae, Bibionidae, Platypezidae, Syrphidae, Aulacigastridae, Sciomyzidae, Drosophilidae, and Ephydridae (Figs. 5.15, 5.41, 5.56, 5.63–64, 7.74–75, 13.12). In these larvae, the microtrichia are evenly distributed and relatively uniform in size. In *Ptychoptera* (Ptychopteridae) the microtrichia are of various sizes; the smaller ones are unevenly distributed and the larger setulae are arranged in multiple transverse and longitudinal rows (Fig. 22.5). The microtrichia in larvae of some Scatopsidae are arranged in a transverse band on each segment; these segments sometimes also bear a secondary pattern of slightly longer setulae arranged in longitudinal rows (Fig. 20.24). Microtrichial pubescence is restricted to areas usually bordering the prolegs (*see* "Locomotory Structures") in larvae of the Tabanidae (Figs. 31.51–52) and constitutes one of the most important diagnostic features of these larvae (Teskey 1969). Stout, thorn-like or scale-like spines are prominent features on all or most segments of larvae of the Oestridae (Figs. 5.33, 5.35).

Large, fleshy processes are the most prominent of cuticular outgrowths. They may occur on all segments or only on the terminal segment. Normally when such projections are present on several segments they become progressively larger toward the caudal end (Figs. 5.14, 5.19, 5.53, 5.55). The projections are sometimes stronger laterally that elsewhere on the body. The occurrence of this feature on several larvae that are dorsoventrally flattened greatly accentuates the flattened condition, as in Lonchopteridae, some Platypezidae, *Periscelis annulata* (Fallén) (Periscelididae), and *Fannia* (Muscidae) (Figs. 5.40–41, 5.47, 5.53, 5.55). The adaptive advantage of having tubercles on more than the terminal segment is sometimes difficult to understand. However, with larvae of the Cylindrotominae (Tipulidae) (Fig. 7.65) one only has to see them in their natural habitat among moss and other vegetation to see how perfectly camouflaged they are.

Tubercles restricted to the terminal segment commonly surround or are adjacent to the posterior spiracles. The number, size, and position of these tubercles is relatively constant for each taxon. In aquatic larvae these tubercles are often fringed with hydrophobic hairs (Figs. 7.72, 7.78–81, 23.10, 36.74, 36.86) that spread

out over the water surface. These hairs prevent water from entering the spiracles when the larva takes in air, and they enclose a bubble of air over the spiracles when the larva submerges.

Many larvae bear a few symmetrically arranged setae occurring either alone (Fig. 7.70) or interspersed among a general body covering of microtrichia (Figs. 7.74–75). The setae are usually simple and hair-like, and they vary greatly in size; but sometimes they are club-shaped, stellate, pectinate, plumose, or otherwise variously shaped (Figs. 17.16, 25.33, 28.130). The setae may be present on all segments including the head or, as in larvae of the Scenopinidae, the Therevidae, and the Asilidae, they may be present only on the thoracic and terminal abdominal segments (Figs. 38.11, 42.76–77). The number and distribution of setae are usually similar on the mesothorax and metathorax but this pattern normally differs from the pattern repeated on each of the first seven abdominal segments. The setal pattern on the prothorax differs widely from that on the terminal segment or segments and from that on the mesothorax, the metathorax, and the first seven abdominal segments. A system of setal nomenclature for comparative purposes can often be devised, based on the dorsal, lateral, and ventral locations of specific setae, exclusively differentiated with various modifiers such as inner, mid, outer, pre-, and post-. Such systems are also applicable for naming tubercles. However, the complex setal patterns of some groups cannot be satisfactorily described in this way, and other methods have been devised in some families such as the Culicidae (Knight and Laffoon 1971) and the Phoridae (Schmitz 1938).

Locomotory structures. Diptera larvae lack segmented thoracic limbs. The most common replacements for these limbs are different types and sizes of projections, usually bearing locomotory spinules, on the anterior margins of one or more body segments. These projections are held extended by turgor pressure and are retracted by the action of muscles inserted in the projections. The form and distribution of the projections and the configuration and structure of their spinous covering are of great systematic importance.

Hinton (1955) suggested that the locomotory structures of Diptera larvae have evolved *de novo* many times and he gave to all such structures the name proleg. However, the appendages are basically of two types, and only one of these is called a **proleg** here; the other type is called a **creeping welt** (locomotory ridge, ambulatory ridge). A third very different type of structure, called a **suction disc**, occurs in larvae of the Blephariceridae and some Psychodinae. The terms pseudopodia and parapodia have often been applied to fleshy locomotory structures of the abdominal segments in larvae of the Tabanidae, the Athericidae, and the Syrphidae, but not in other larvae bearing such appendages. This differentiation is not justified, however, because such structures do not differ significantly from those structures that are

Number and distribution of prolegs in various groups of Diptera (modified from Hinton 1955)

	Thorax			Abdomen								
	1	2	3	1	2	3	4	5	6	7	8	9
Dixidae				2	0–2							
Chironomidae	2											2
Ceratopogonidae	0–2											1–2
Thaumaleidae	1											1
Simuliidae	1											1
Blephariceridae					2	2	2	2	2	2		
Nymphomyiidae				2	2	2	2	2	2	2		2
Deuterophlebiidae				2	2	2	2	2	2	2		
Tanyderidae												2
Ptychopteridae				2	2	2						
Tipulidae (*Dicranota*)					2	2	2	2	2			
Tabanidae				6–8	6–8	6–8	6–8	6–8	6–8	6–8		
Athericidae				2	2	2	2	2	2	2	2	
Asilidae												
Lasiopogon				2	2	2	2	2				
Leptogaster					2	2	2	2	2	2		
Laphria				6–8	6–8	6–8	6–8	6–8				
Empididae												
several genera					2	2	2	2	2	2	2	
several genera				2	2	2	2	2	2	2	2	
Syrphidae	2			2	2	2	2	2	2			
Ephydridae (*Ephydra*)				2	2	2	2	2	2	2	2	
Muscidae												
Limnophora					2	2	2	2	2	2	2	
Graphomya					2	2	2	2	2	2		

always called prolegs which occur on the prothorax and the terminal segment.

Prolegs are typically round or oval fleshy tubercles usually located in pairs ventrally on the prothorax and terminal segment, on the terminal segment alone, or on one or more of the intermediate abdominal segments (Figs. 9.3, 10.7, 23.10, 29.114–116). In all cases they bear one or more curved locomotory spinules near their apices. In those cases where more than one pair of prolegs occur on the abdominal segments, the additional pairs are situated on the dorsal, lateral, and ventrolateral aspects (Figs. 31.51–52). The number and distribution of prolegs among the Diptera are shown in the accompanying table. The prolegs are sometimes modified from the typical form. In *Dasyhelea* (Ceratopogonidae) (Fig. 28.132) the terminal proleg comprises paired, sublateral clusters of a few curved spinules. These spinules are capable of complete retraction within the apex of the terminal segment, together with the anal papillae (*see* "Anus, Anal Papillae, and Tracheal Gills"). Prothoracic and terminal prolegs of larvae of the Thaumaleidae and the Simuliidae appear to be unpaired. This condition probably represents a fusion of paired prolegs. The proleg on the terminal segment of larvae of the Simuliidae appears as numerous concentric rows of spinules encircling the apex of the segment (Figs. 27.89–92).

The locomotory spinules of the prolegs are varied in form. They are sometimes very small, showing little organization on the apex of the proleg; the only pattern evident is that most of the spinules are commonly inclined posteriorly, with only a few spinules on the anterior margin of the proleg directed anteriorly. The spinules are often in the form of relatively large, strongly hooked crochets arranged in one or more partially or completely encircling rows at the apex of the proleg, as in *Atrichopogon* (Ceratopogonidae), the Chironomidae, and *Atherix* (Athericidae) (Figs. 28.131, 29.136, 32.7). The crochets on the prothoracic proleg of the Thaumaleidae are arranged in a linear transverse row (Fig. 26.4). Different kinds of locomotory spinules may be combined on a proleg. Only a single, hooked spinule occurs on each abdominal proleg of the Ptychopteridae (Figs. 22.5–6), the spinule being much larger in *Bittacomorpha* than in *Ptychoptera*.

Creeping welts are typically transverse swollen ridges on the anterior ventral margins and sometimes the anterior dorsal margins of usually the first seven abdominal segments (Figs. 5.59, 5.72, 7.74, 7.82, 14.97). They are most common among larvae of the Schizophora but are also present in some larvae of the Nematocera and orthorrhaphous Brachycera, e.g. Tipulidae, Mycetophilidae, Rhagionidae, Xylophagidae, Empididae, and Dolichopodidae. Creeping welts normally bear spinules that are commonly arranged in transverse rows. The spinules in a few of the anterior rows may be inclined anteriorly, but most of the spinules covering the remainder of the creeping welt are inclined

posteriorly (Fig. 5.102). When the welt involves the posterior portion of the preceding segment, the anteriorly inclined spinules are usually on this portion. Sometimes spinules are present laterally and dorsally on the abdominal segments, even though raised welts are not evident; such spinules may partially or completely encircle the anterior margins of the thoracic segments (Figs. 5.59, 5.76, 5.98). Spinules may be present on both dorsal and ventral anterior segmental margins without evident ridges, as in *Synneuron* (Synneuridae) (Fig. 21.6). Raised welts or ridges that lack spinules as are present in *Cramptonomyia* (Pachyneuridae) and *Lutzomyia* (Psychodidae) (Figs. 12.5, 17.16) probably have some use in locomotion. A locomotory function can also be attributed to other body tubercles of some larvae, even if only acting as an anchor against backward slippage.

A third very different type of foot-like structure, the suction disc, occurs in larvae of the Blephariceridae and some Psychodidae (e.g. *Maruina*). Suction discs are adaptations used by the larva for maintaining its position in swiftly flowing water. Suction discs have been thought to be modified prolegs (Hora 1933); however, this suggestion appears unlikely. Tonnoir (1933) has shown rather convincingly how these structures may have evolved in the Psychodidae and by analogy also in the Blephariceridae. Furthermore, larvae of the Blephariceridae have musculated lateral conical projections on the abdominal segments (Fig. 8.8), quite separate from the suction discs, which are believed to be homologous with the prolegs (Hinton 1955). The suction disc has a fleshy rim bearing marginal hairs. A hole in the center of this rim opens into a large internal chamber. Muscles are inserted in the roof of this chamber which contract to elevate the roof and increase the volume of the chamber. When the fleshy rim is closely applied to a smooth substrate such as a rock, the increased volume of the chamber creates a negative pressure within, which holds the larva firmly in position.

Other body parts also may assist in larval movement. The mandibles are important in this regard, especially in brachycerous larvae. They are used to provide an anchoring point against which contraction of the larval body results in forward motion. Transverse rows of backwardly directed setae called ambulatory combs (Fig. 23.10) are present on the venter of abdominal segments five to seven in larvae of the Dixidae. Preanal and postanal ridges on many brachycerous larvae appear to function in the same way as creeping welts. They sometimes bear spinules similar to those on the creeping welts, e.g. Micropezidae and Milichiidae (Figs. 5.70, 5.91). In *Ephydra* (Ephydridae), these spinules take the form of nearly typical crochets (Fig. 5.63). A single, rather large spicule is present on the preanal ridge of *Canace macateei* Malloch (Canacidae) (Fig. 5.37).

RESPIRATORY SYSTEM

The respiratory system includes the internal system of tracheae and the external spiracles. Although no discus-

sion of internal anatomy has been given here, except for the head, comparative studies of the tracheal system of Diptera larvae (Keilin 1944; Whitten 1955, 1960, 1963; Tatchell 1960) are highly significant in larval systematics and must be at least briefly discussed.

Internal tracheal system. The general plan of the structure of the tracheal system of Diptera larvae, as given by Whitten (1955), is shown in Fig. 15. There are two dorsal and two lateral *longitudinal trunks*. The dorsal trunks are united by ten segmental *anastomoses* (*sing. anastomosis*). Eight *transverse connectives* join the dorsal and lateral trunks on each side. Two dorsal and two ventral *cervical tracheae* and two *supraesophageal ganglionic tracheae* project into the head; the dorsal cervical tracheae and the ganglionic tracheae are united by a *cervical anastomosis*. A series of *ventral ganglionic tracheae* and *visceral tracheae* project from the lateral trunks, and the first three ganglionic tracheae form *midventral anastomoses*. Ten pairs of *spiracular tracheae* may be present, although all may not be functional. Although this arrangement is subject to variation in detail, the full complement of tracheae and anastomoses are present in larvae of the Bibionidae, the Psychodidae, the Trichoceridae, the Anisopodidae, and the Brachycera (Whitten 1960). Deviations from this plan by reduction of one or more of the tracheal anastomoses or connectives occur in larvae of at least some Tipulidae, Mycetophilidae, Sciaridae, Cecidomyiidae, Dixidae, Culicidae, Thaumaleidae, Simuliidae, Ceratopogonidae, and Chironomidae. The Scatopsidae follow the general plan but have an extra 11th dorsal anastomosis. The tracheae of larval Blephariceridae also follow the general plan except that the tracheae associated with the eighth abdominal segment (terminal portions of dorsal and ventral longitudinal trunks and the dorsal connectives) are absent (Whitten 1963).

The tracheal system of larvae that live freely in water fulfills a hydrostatic function as well as a respiratory function. The dorsal tracheal trunks of larvae of some Chaoboridae and some Culicidae are widened into tracheal vesicles, which help the larvae maintain their position in the water (Damant 1924, Keilin 1944). Some larvae of *Hybomitra* (Tabanidae) have swollen dorsal tracheal trunks, which allow them to float on the surface of the water where they can move by lashing the terminal portion of the body back and forth.

Number and distribution of spiracles. More important in the systematics of larval Diptera has been the individual characteristics and location of the *spiracles*. The basic number of spiracles on Diptera larvae is 10 pairs, although this number is present only in the Bibionidae and the Palaearctic genus *Pachyneura* (Pachyneuridae). These paired spiracles are located on the prothorax, the metathorax, and each of eight abdominal segments. The spiracles have often been named after the segment on which they are located.

However, the spiracles on the prothorax are apparently the mesothoracic spiracles that have migrated forward (Hinton 1947). Thus, it is more accurate and convenient to refer to them as the *anterior spiracles*. Similarly the eighth pair of abdominal spiracles, although usually located on this segment, is situated on the apparent ninth segment in larvae of *Plecia* and *Bibio* (Bibionidae), presumably as a result of backward migration. Therefore, this terminal eighth pair of spiracles is best referred to as the *posterior spiracles*. The metathoracic spiracles are referred to as the *posterior thoracic spiracles*, but the intermediate *abdominal spiracles* are differentiated by the number of the segment on which they occur.

Various degrees of reduction in the number of spiracles has taken place among Diptera larvae, and a convenient terminology has been devised for the resulting spiracular arrangements. This system is explained diagrammatically in Fig. 16. The *holopneustic* system is the basic arrangement discussed above for the Bibionidae and *Pachyneura* (Pachyneuridae). Loss of the posterior thoracic spiracles yields the *peripneustic* system, which is characteristic of the larvae of the Pachyneuridae (except *Pachyneura*), the mycetophilid subfamily Ditomyiinae, the Cecidomyiidae, the Scatopsidae, and the Synneuridae. In this system, as in the holopneustic system, the anterior spiracles and the posterior spiracles are normally larger than the intermediate abdominal spiracles. The *hemipneustic* system, characterized by the loss of the posterior spiracles, has usually been considered as a variation of the peripneustic system. Representative of this system are the larvae of most Mycetophilidae and Sciaridae. The *amphipneustic* spiracular system has only the anterior and posterior spiracles. This type is the most common and is characteristic of larvae of the Tanyderidae, the Axymyiidae, most Psychodidae, the Trichoceridae, the Anisopodidae, the Thaumaleidae, and most Brachycera. The presence of anterior spiracles only, the *propneustic* condition, appears to be confined to some Mycetophilidae (*Diadocidia* and some Sciophilinae). The presence of posterior spiracles only, the *metapneustic* system, is found in larvae of several families, most of which live in aquatic or semiaquatic habitats, such as the Tipulidae, the Ptychopteridae, the Dixidae, the Culicidae, and the Tabanidae. Larvae of the Tabanidae have anterior spiracles that are extruded just before pupation, but it is not known if they are functional. Finally, spiracles are absent in larvae of some families; such forms are said to be *apneustic*. All apneustic larvae are aquatic and include the Blephariceridae, the Deuterophlebiidae, the Nymphomyiidae, some Chaoboridae (e.g. *Chaoborus*), the Simuliidae, the Ceratopogonidae, most Chironomidae, the Athericidae, some Empididae, and representatives of several other families. Although they have no spiracles, they all have well-developed tracheae.

The spiracular system may change from one larval instar to another. For example, in the Mycetophilidae first-stage larvae are metapneustic, with the posterior spiracles occurring on the eighth abdominal segment; second- and third-stage larvae are propneustic; and fourth-stage larvae are hemipneustic (the eighth pair of abdominal spiracles are not regained) or peripneustic (Madwar 1937). First-stage larvae of the Muscomorpha are metapneustic, whereas the second- and third-stage larvae are usually amphipneustic.
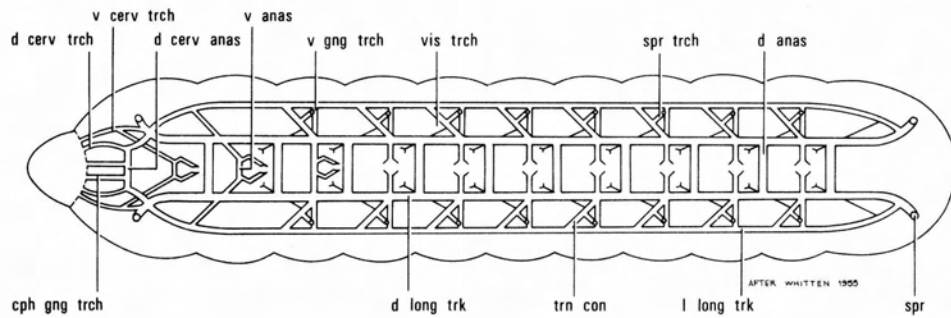
When spiracles are absent, remnants of the spiracular tracheae remain in the form of internal *spiracular filaments* that connect the tracheal trunks to the integument where the spiracle would normally occur. Although external evidence of the attachment of the spiracular filaments is usually not apparent, vestigial, nonfunctional spiracles can be seen in larvae of the Culicidae, the Simuliidae, the Mydidae, and the Asilidae (Figs. 27.76, 40.28, 42.76–77).

All spiracles are most commonly located laterally in the holopneustic, peripneustic, and hemipneustic systems. Only in a few Cecidomyiidae and the Scatopsidae are the posterior spiracles situated posteriorly. However, in larvae having the amphipneustic and metapneustic spiracular systems, the posterior spiracles most commonly assume a posterior or dorsal position. Often the posterior face of the terminal segment which bears the spiracles is flattened and is referred to as the *spiracular disc* (spiracular field). Of those larvae with the amphipneustic and metapneustic spiracular systems, only in the Tanyderidae, *Phlebotomus* and *Trichomyia* (Psychodidae), *Olbiogaster* (Anisopodidae), the Therevidae, the Scenopinidae, the Mydidae, and the Asilidae are the terminal spiracles situated laterally. The anterior spiracles are usually situated laterally, but they are in a subdorsal position in the Agromyzidae.
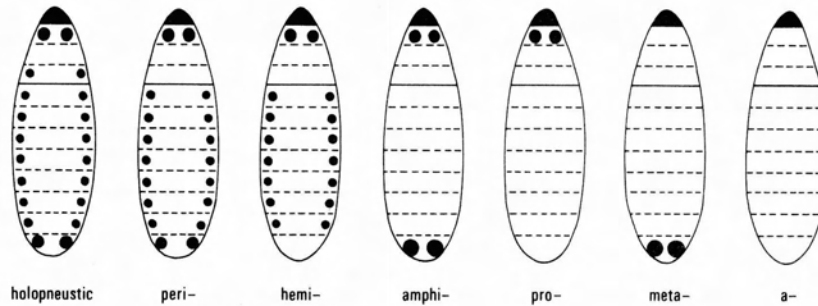
Structures of spiracles. The structure of larval spiracles is diverse. This diversity is exhibited not only among species but between the instars of species and between spiracles on the same larva. The anterior spiracles often differ from the abdominal spiracles, sometimes quite markedly; likewise the posterior spiracles may differ from others on the abdomen. Common to all spiracles of Diptera larvae is the absence of an internal mechanical closing device.

The variations of Diptera larval spiracles have been discussed by Keilin (1944) and Krivosheina (1969). Their discussions and that given here are based almost exclusively on mature larvae. There is an acute lack of detailed information on earlier instars. However, spiracles of the earlier stages that are presently known conform in most respects to the following description with the exception of the number of *spiracular openings* in each spiracle, which normally increases with maturity of the larva.
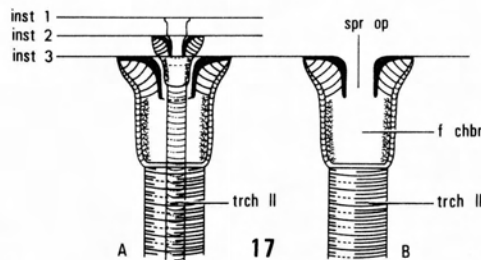
Keilin (1944) differentiated three types of spiracles based on the molting process of the spiracle. In spiracles of type I (Fig. 17), as seen in the Culicidae, the opening
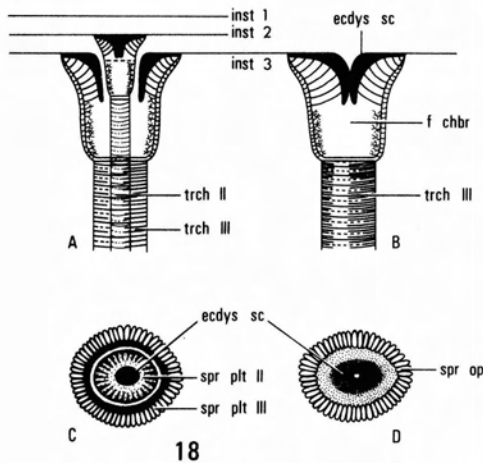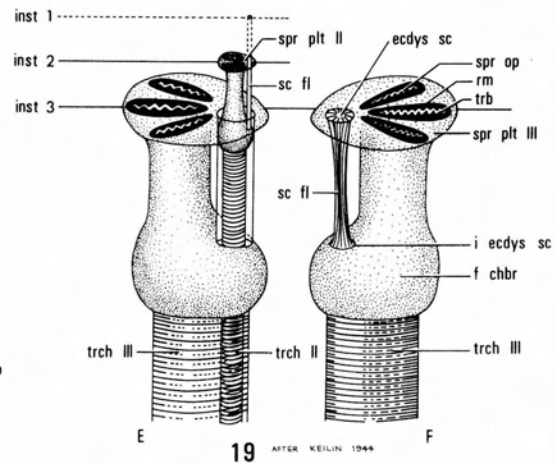
d cerv trch   v cerv trch   v anas

d cerv anas   v gng trch   vis trch   spr trch   d anas

AFTER WHITTEN 1955

cph gng trch   d long trk   trn con   l long trk   spr

15

holopneustic   peri-   hemi-   amphi-   pro-   meta-   a-

16

inst 1
inst 2
inst 3

spr op

f chbr

YUEYK 1950

trch II   trch III

A   **17**   B

inst 1
inst 2

ecdys sc

inst 3

inst 1

spr plt II   ecdys sc

inst 2

sc fl   spr op
rm
trb

inst 3

spr plt III

f chbr

trch II   f chbr

trch III

sc fl

A   trch III   B

i ecdys sc

f chbr

ecdys sc

spr plt II

spr plt III

spr op

trch III   trch II   trch III

C   **18**   D   E   **19**   AFTER KEILIN 1944   F

Figs. 3.15–19. Respiratory features of Diptera larvae: (15) diagrammatic dorsal view of generalized tracheal system; (16) diagrammatic representation of spiracular systems; (17–19) three basic types of spiracles—*A* before ecdysis, *B* after ecdysis, *C* and *D* anterior view before and after ecdysis.

Abbreviations: cph gng trch, cephalic ganglionic trachea; d anas, dorsal anastomosis; d cerv anas, dorsal cervical anastomosis; d cerv trch, dorsal cervical trachea; d long trk, dorsal longitudinal trunk; ecdys sc, ecdysial scar; f chbr, felt chamber; i ecdys sc, inner ecdysial scar; inst, instar; l long trk, lateral longitudinal trunk; rm, rima; sc fl, scar filament; spr, spiracle; spr op, spiracular opening; spr plt, spiracular plate; spr trch, spiracular trachea; st, sternite; trb, trabecula; trch, trachea; trn con, transverse connective; v anas, ventral anastomosis; v cerv trch, ventral cervical trachea; v gng trch, ventral ganglionic trachea; vis trch, visceral trachea.

through which the spiracular trachea of the previous instar is withdrawn becomes the spiracular opening (air inlet) of the next instar. The posterior spiracles of the Tabanidae are apparently also of this type. The spiracular opening in larvae of the Tabanidae is not associated with the exposed, vertically linear element of the spiracle (Fig. 31.55) homologous to that found in other larvae on which are located the spiracular openings; rather, the spiracular openings are situated on either side of these elements beneath a loose fold of integument, and they communicate with simple lateral apertures in the tracheal trunks (Teskey 1969). In the type II spiracle (Fig. 18), found in most Nematocera and the orthorrhaphous Brachycera, the ecdysial opening is closed and forms a central *ecdysial scar*. Perforated oval or linear areas providing new means of air intake are usually arranged around this scar more or less radially. The spiracular openings and ecdysial scar are located on a more or less well-defined *spiracular plate*. But of greatest significance in type II as well as in type I spiracles is the fact that the *felt chamber* of successive larval instars is developed around the felt chamber of the previous instars. The felt chamber lies between the spiracular plate and the trachea. The chamber may bear on its walls various filamentous outgrowths that sometimes ramify to form a maze of passages. The chamber functions as a filter. The type III spiracle (Fig. 19), characteristic of the Muscomorpha, has the ecdysial scar situated near the margin of the spiracular plate. The number of spiracular openings are usually greatly reduced, commonly to only three on each of the posterior spiracles. The ecdysial scar is displaced because the felt chamber develops beside, not around, the felt chamber of the previous instar. The trachea of the previous instar is withdrawn through a hole at the base of the newly developed felt chamber.

In Diptera larvae, Krivosheina (1969) distinguished two types of spiracles, radially symmetric and asymmetric. This distinction appears to coincide with Keilin's observations in that he emphasized the symmetry of the encircling arrangement of the spiracular openings and the central position of the ecdysial scar on the type II spiracle. The type III spiracle is asymmetric. However, the spiracles of several families of lower Diptera are decidedly asymmetric, as in the Mycetophilidae, the Sciaridae, the Anisopodidae, the Thaumaleidae, the Therevidae, the Scenopinidae, and the Asilidae, with the spiracular openings only partially encircling the spiracular plate (Figs. 19.21–22, 38.13–14). The intermediate abdominal spiracles of some Mycetophilidae have only one spiracular opening. Yet there is little doubt that the spiracles of these larvae are of type II. Keilin (1944) showed this to be the case in larvae of *Thereva* (Therevidae) and *Laphria* (Asilidae). Madwar (1937) illustrated the central position of the ecdysial scar filament within the felt chambers of several species of Mycetophilidae and Sciaridae.

The symmetry of the arrangement of the spiracular openings on the type II spiracle is greater than that of the type III spiracle, particularly in relation to the terminal spiracles. In nearly all type II spiracles a uniform, linear, semicircular or circular arrangement of the spiracular openings occurs, and the spiracular openings usually number more than three. If more than three spiracular openings occur in the type III spiracles, they are rarely, or never, similar in shape or symmetrically organized.

The spiracular openings are associated with a few to many variously shaped (oval, linear, lenticular, curved, serpentine), sometimes elevated areas (Figs. 5.8–10, 5.13, 5.16, 5.18, 5.20–30, 5.34–35, 7.86, 13.15–17, 21.8). The longer spiracular openings each sometimes bear a marginal supporting sclerotization called a *rima* (*pl. rimae*); the rima on each side of the spiracular opening may be further strengthened by cross struts or serrations called *trabeculae* (*sing. trabecula*) (Figs. 18; 5.80). The margin of the spiracular plate itself, called the *peritreme*, is also usually sclerotized. Hypodermic *spiracular glands* that secrete a hydrofuge substance open on the surface of the spiracular plate. These glands can normally be detected only under special circumstances. In most larvae of the Schizophora the glands are associated with variously branched *spiracular hairs*. Normally four such hairs are located near the outer end of each spiracular opening (Figs. 5.39, 5.104). In larvae of the Coelopidae a fringe of spiracular hairs encircles the spiracle inside the peritreme (Fig. 5.85). An area or areas of scar tissue marking the point of withdrawal of the spiracle and trachea of the previous instar is prominent on most spiracular plates. Normally only one such ecdysial scar is present, but in *Bibio* and *Dilophus* (Bibionidae) two and three scars, respectively, are present (Figs. 13.16–17). Major branching of tracheae occurring at the spiracle has resulted in these multiple scars.

The spiracles are usually sessile in larvae of the Nematocera, whereas they are commonly more or less elevated above the body surface on short supporting structures in larvae of the Brachycera. However, in the Scatopsidae each posterior spiracle occurs at the end of a sclerotized cylinder that is at least three times longer than its diameter (Fig. 20.24). Any greater elevation of the posterior spiracles than this is apparently an adaptation to living in liquid media. In these cases the posterior spiracles occur together at the end of a *respiratory siphon*. Such siphons may be relatively short as in representatives of the Psychodidae, the Culicidae, the Tabanidae, the Stratiomyidae, and the Ephydridae (Figs. 5.62–63, 17.15, 25.28–32, 31.51–52, 36.84), or slender, elongated, and sometimes retractable as in the Axymyiidae, the Ptychopteridae, some Syrphidae, and the Aulacigastridae (Figs. 5.15, 5.64, 11.6, 22.5).

Another adaptation to an aquatic existence is seen in some Stratiomyidae, where the terminal spiracles lie within a *spiracular atrium* (Fig. 36.86). The opposing edges of this atrium normally bear fringes of hydropho-

bic hairs that surround a bubble of air when the larva submerges. Lobes surrounding the posterior spiracles can achieve the same effect as a spiracular atrium, especially when these lobes are fringed with hydrophobic hairs as in the Tipulidae and the Dolichopodidae (Figs. 7.78, 7.81, 7.84, 48.40). The bubble of air may act as a gill (Hennig 1973). Larvae of the Sarcophagidae (Fig. 5.84) have a spiracular atrium that almost certainly offers protection to the posterior spiracles in both wet and dry environments even though it is not fringed and cannot be completely closed. Larvae of *Gasterophilus* (Gasterophilidae), living much of their lives in the stomachs of horses, can completely cover their posterior spiracles with two transverse folds of integument.

The posterior spiracles of some larvae, e.g. some species of *Chrysops*, *Merycomyia*, and *Tabanus* (Tabanidae), *Chrysogaster* (Syrphidae), and *Notiphila* (Ephydridae) (Figs. 5.61–62, 31.58–59), are modified to form a **respiratory spine**. Hinton (1957) suggested that such spines are used to penetrate the air spaces in aquatic plants. However, the respiratory spines of tabanid larvae do not constitute the point of air intake. Spines or pointed projections having no known function are present on the margin of the spiracular plate of some larvae of the Micropezidae, the Psilidae, the Lonchaeidae, and the Clusiidae (Figs. 5.86–89, 5.91).

In the larvae of the Muscomorpha the anterior spiracles exhibit a widely varied appearance, in most cases quite different from the posterior spiracles. They are almost always elevated or projecting and involve several to many spiracular openings. Among the Aschiza these openings are most commonly sessile on a spiracular stalk. They are either randomly arranged along the sides of the stalk (Fig. 5.64) or arranged in a row near to or at its apex (Figs. 5.16, 5.42). In the Schizophora the openings are most commonly at the ends of papillae of various lengths projecting from the stalk. The branching of these papillae is diagnostically important. This branching may be characterized as fan-like, with the papillae more or less arising from a common point (Figs. 5.68, 5.77, 5.103); semicircular (Figs. 5.92, 5.96); tree-like, with the papillae arising laterally on a central axis (Figs. 5.66, 5.71, 5.93, 5.97); bicornuate, a rather distinctive modification of the fan form that is distinctive of larvae of some Tephritidae, *Tanypeza* (Tanypezidae), and the Scathophagidae (Fig. 5.81); brush-like (Figs. 5.22–23, 5.26); or dendritic, with numerous long, slender filaments having a common point of origin and capable of retraction within the body (Fig. 5.60). Although these are the basic configurations, there are many intergrades between the fan-like and tree-like forms.

Anus, anal papillae, and tracheal gills. The *anus* is located ventrally or posteriorly on the terminal body segment. A terminal position is found only among some Nematocera, e.g. *Bibio* (Bibionidae) and Lestremiinae (Cecidomyiidae). The anus may be situated in a transverse or, more commonly, a longitudinal (Figs. 13.12–14, 16.10) cleft. This cleft is usually bordered or surrounded by the **perianal pad**, an area of distinctive size, shape, and surface contour.

The perianal pad is a prominent feature of many Diptera (Figs. 5.59, 5.70, 5.91, 7.71, 19.19–20). Stoffolano (1970) described some of the variations in the pad, referring to its very thin cuticle and large epidermal cells containing polytene chromosomes; but he provided no evidence as to its function.

Outgrowths of distinctive shape and size, called **anal papillae** (Figs. 7.72, 7.75, 11.6, 25.32, 27.90, 29.114), are found arising from the perianal pad or from within the anus in many aquatic or semiaquatic larvae of the Nematocera. The anal papillae are delicate, thin-walled structures, which in the resting state are sometimes retracted within the anus. One to three pairs of anal papillae are normally present, although these are sometimes secondarily branched.

The anal papillae are commonly considered to have a respiratory function. This theory is valid when the papillae are especially well tracheated, for example, in some Culicidae (Lewis 1949); however, they are primarily used as osmoregulatory organs (Wigglesworth 1938, Brindle 1952, Strenzke and Neumann 1960).

The term tracheal gills has sometimes been used for the anal papillae, but because the respiratory function of these structures is of minor importance, this term is inappropriate. However, there are other structures ventrally on the preanal segments in some Chironomidae and Blephariceridae (Figs. 8.8, 29.115) that apparently have only a respiratory function and can rightfully be called **tracheal gills** (Harnisch 1954, Whitton 1963).

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