Manual of Nearctic Diptera

Volume 1

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MORPHOLOGY AND TERMINOLOGY—ADULTS 2

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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 (1970*a*, 1970*b*, 1970*c*, 1971), and Laffoon and Knight (1971).

Orientation and relationship of parts. A fly is basically a bilaterally symmetric, horizontally oriented, forwardly 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

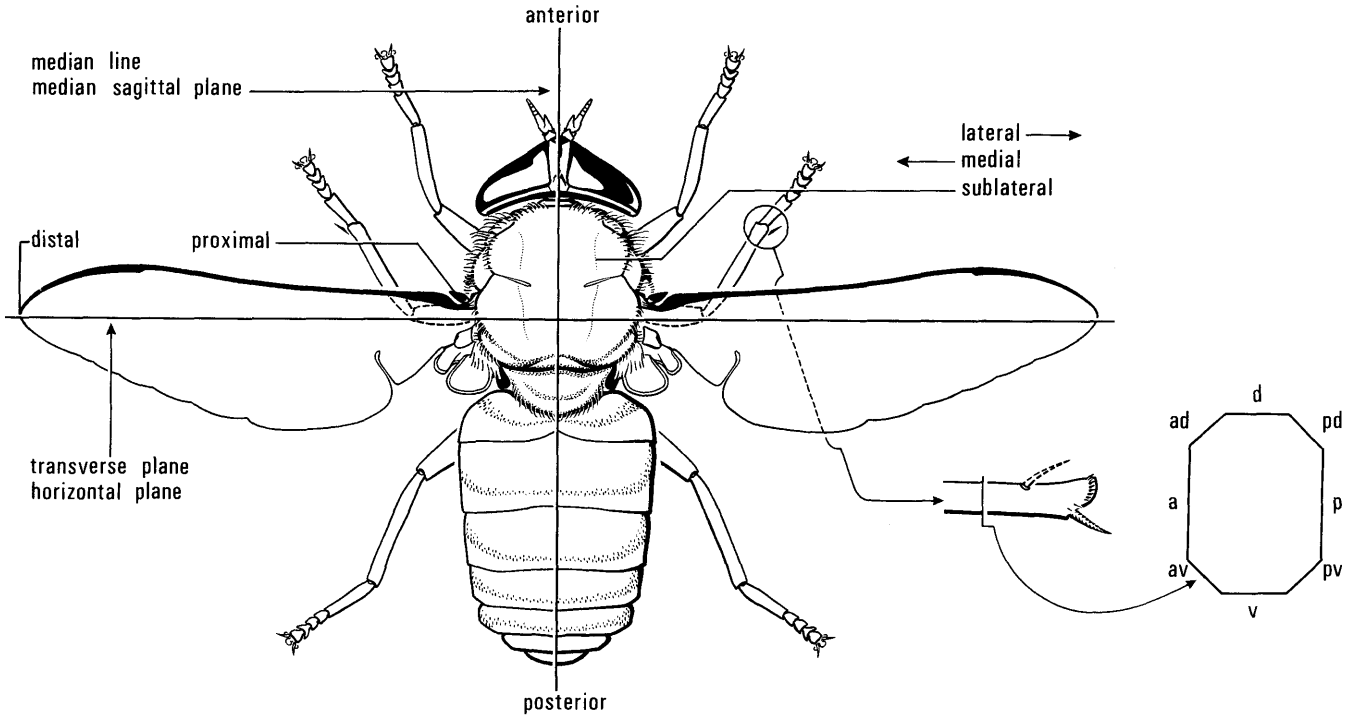


Fig. 2.1. A generalized fly, *Tabanus americanus* Forster, to show orientation and anatomical planes. *Inset:* Vertical section through distal portion of right mid tibia to show external surfaces.

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

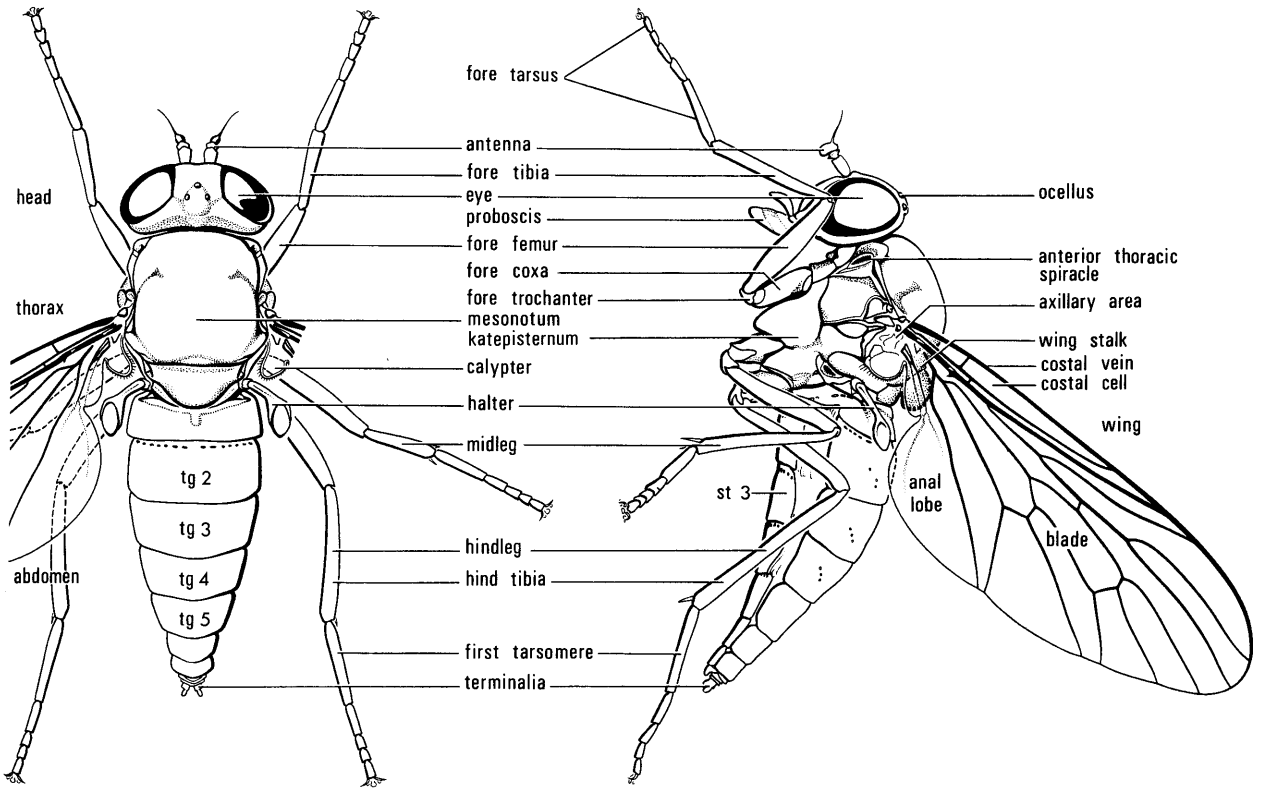
commonly used almost synonymously with tergum and sternum. The unsclerotized part of the segmental ***cuticle*** between two adjacent tergal or sternal plates is the ***intersegmental*** or ***conjunctival membrane*** (Figs. 4, 5); it usually folds inwardly, and portions of it sometimes become sclerotized. 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***.

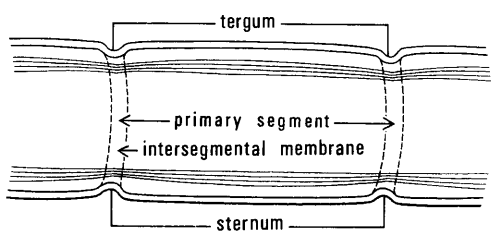
Most appendages such as ***antennae, palpi***, and ***legs*** are paired structures consisting of segmented tubes with flexible joints called ***articulations*** between the segments; the ***wings*** and ***halteres*** are specialized outgrowths of the thorax. The ***tracheae*** of the respiratory system 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 ♀



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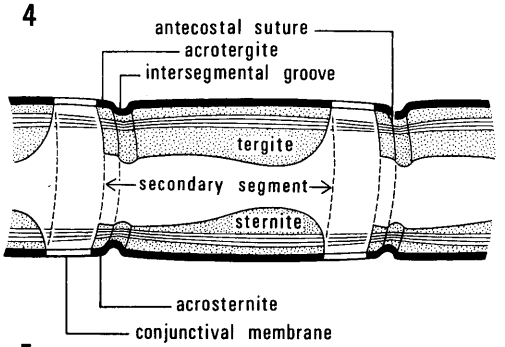

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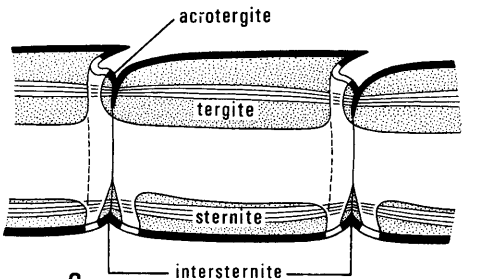

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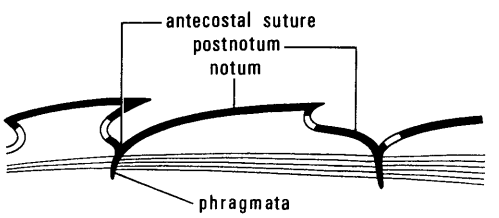

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Figs. 2.2–7. Main divisions and parts of Diptera: (2) dorsal and (3) lateral view of *Symphoromyia montana* Aldrich, to show main anatomical divisions and parts; (4–7) diagrams of primary and secondary segmentation, based on Snodgrass (1935) and Matsuda (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.

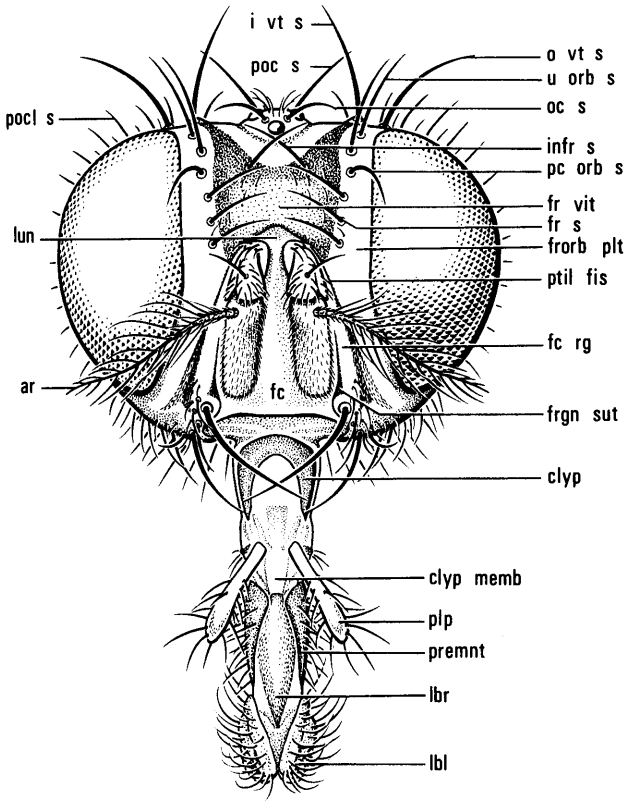
appendages. The parts of the head are defined principally by reference to the ***occipital foramen*** (through which pass the nerve cords, esophagus, aorta, and salivary ducts), the ***ocelli*** (*sing.* ***ocellus***), the insertions of the antennae, the margins of the eyes, the ***subcranial cavity*** (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***.

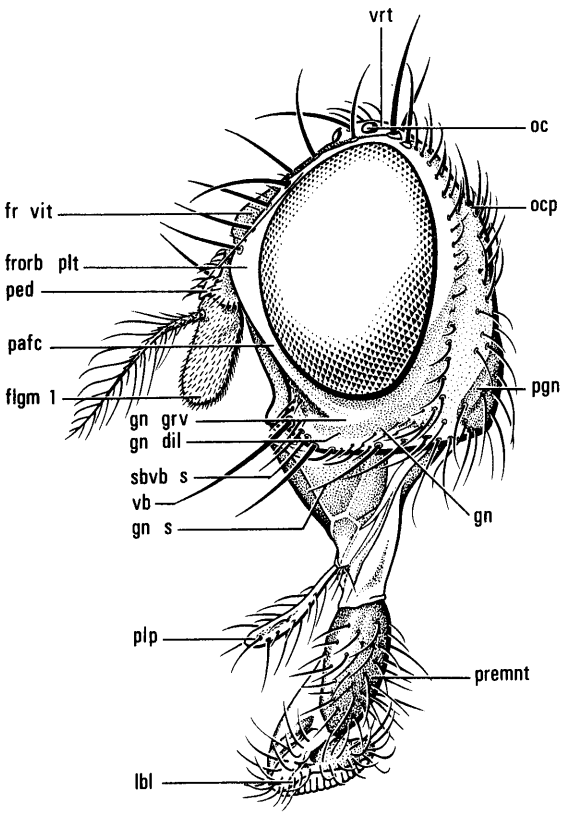
Vertex. The median portion of the upper extremity of the head, bounded by the eyes laterally, the occiput posteriorly, and the frons anteriorly, is called the vertex (Figs. 9, 65). It is a relatively indefinite area, containing the ocellar triangle medially and, at least in the Mus-

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).

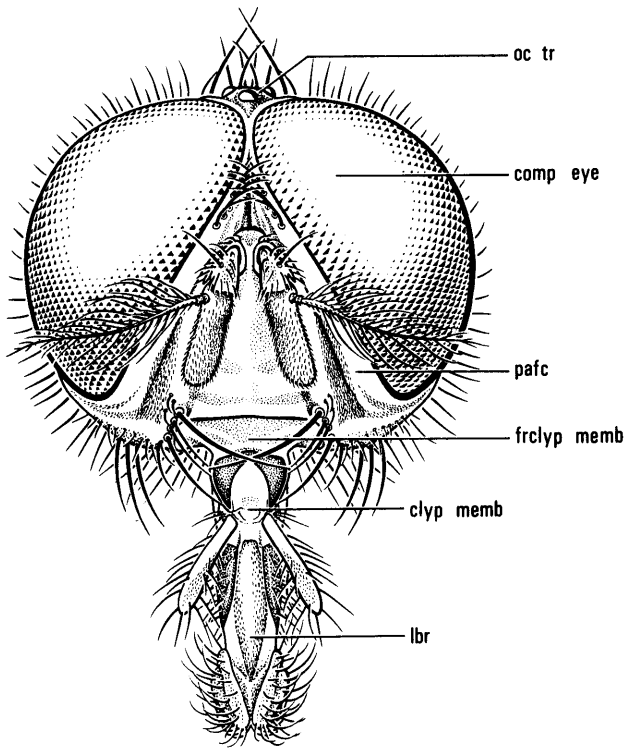
ar, arista
clyp, clypeus
clyp memb, clypeolabral membrane
comp eye, compound eye
fc, face
fc rg, facial ridge
flg, flagellum
flgm, flagellomere
frclyp memb, frontoclypeal membrane
frgn sut, frontogenal suture
frorb plt, fronto-orbital plate
fr s, frontal seta
fr vit, frontal vitta
gn, gena
gn dil, genal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



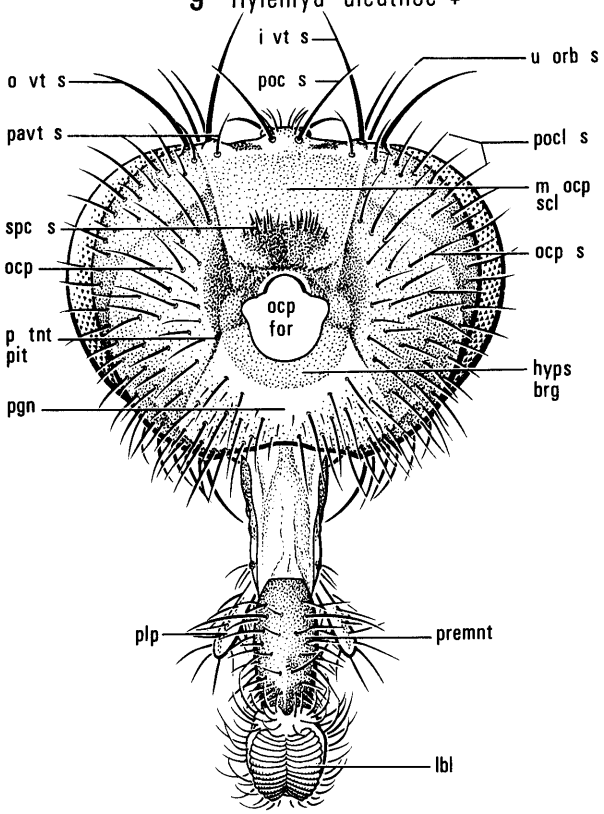
8 Hylemya alcathoe ♀



9 Hylemya alcathoe ♀



10 Hylemya alcathoe ♂



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