

Comparative Structure of the Labiohypopharynx of Fourth Stage
Mosquito Larvae (Diptera: Culicidae), with Comments on
Larval Morphology, Evolution and Feeding Habits*

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ABSTRACT. The labiohypopharynges of 62 species of fourth stage culicid larvae representing 3 genera of the Dixinae, 2 of the Chaoborinae and all but one (*Ficalbia*) of the 34 genera recognized by Knight and Stone (1977) have been studied with the light and scanning electron microscopes. The structure of the labiohypopharynx is described and illustrated for at least one species of each genus examined. Phylogenetic relationships are discussed in regard to larval morphology and feeding behavior.

INTRODUCTION

This paper concludes a series of comparative studies on the mouthparts of fourth stage culicid larvae. Knight (1971) examined the anatomy of the mandibles, determined the homologies of the mandibular substructures and developed a structural terminology "suitable for use in taxonomic studies." A similar study was conducted on the maxillae by Knight and Harbach (1977).

The comparative examination of the labiohypopharynx made by Harbach and Knight (1977b) paved the way for the present paper. Although the structural interpretation presented herein is basically the same as that given by these authors, a new terminology has been devised which reflects a more refined interpretation of structure and conforms more closely to that applied to other insects. The references cited by Harbach and Knight should be consulted for a comprehensive introduction to the literature on the morphology of the labiohypopharynx.

Although Montschadsky (1936), Surtees (1959) and Harbach (1977) have outlined certain evolutionary trends based on correlations between mouthpart structure and feeding habit, the evolution of culicid larvae is still a much vexed question. In order to shed additional light on larval phylogeny, evolutionary relationships which I have derived from the aforementioned series of studies, as well as observations made on other aspects of larval morphology, are set forth in the discussion.

MATERIALS AND METHODS

Light and scanning electron microscope investigations were conducted on the labiohypopharynges of alcohol-preserved fourth stage larvae. Material for

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examination under the light microscope was prepared and mounted on glass slides according to the procedures of Wirth (1961) and Knight (1971). For the scanning electron microscope, heads were Freon critical-point-dried and mounted anterior end up on aluminum stubs. Once secured, the median labral plate, palatum, antennae, mandibles and maxillae were carefully removed from each head in order that the topography of the labiohypopharynx could be examined without obstruction. The labiohypopharynges of one to several larvae were prepared for both the light and scanning electron microscopes.

Concerning the figures, each drawing depicts an anterior or near anterior aspect of a labiohypopharynx with its dorsal extremity uppermost. All scale lines are equal to 0.05 mm. The species are grouped into subfamilies and tribes, otherwise the linear order of the taxa has no phylogenetic import. Species studied in addition to those illustrated are listed in an appendix.

Following Edwards (1932), the family Culicidae is considered to include the Dixinae and Chaoborinae. The taxa constituting Edwards' subfamily Culicinae, however, are recognized here as belonging to the subfamilies Anophelinae, Culicinae and Toxorhynchitinae of Knight and Stone (1977). The tribes are those of Belkin (1962).

OBSERVATIONS

The labium of generalized insects is divided into a proximal postlabium comprising the submentum and mentum and a distal prelabium comprising the prementum, glossae, paraglossae and the labial palpi. In most nematoceros larvae the postlabium has been largely incorporated into the ventral surface of the head capsule (nematoceros larvae are basically prognathous) with only the distal portion of the mentum projecting beyond the anterior margin as a dentate lobe or ridge. The prelabium has united with the hypopharynx to form the composite *labiohypopharynx* (LbHy). In culicid larvae the labiohypopharynx is attached to the head between the mouth and the *dorsomentum* (Dm), a transverse subdivision of the mentum found in both culicid (Laffoon and Knight 1973) and chironomid larvae (Saether 1971), where it forms the protruding posterior wall of the preoral cavity (Figs. 1,2). The component parts of the labiohypopharynx, the dorsal *hypopharynx* (Hy) and the ventral *prelabium*, are joined and supported dorsally by the *cibarial bars* (CB) extending from lateral areas of the cranium. Ventrally the labiohypopharynx is reflected into the mentum at the base of the dorsomentum (Figs. 1,2).

Hypopharynx

The fleshy hypopharyngeal lobe, often strengthened internally by a sclerotized *hypopharyngeal bar* (HyB) (see e.g., Fig. 16), is separated from the sclerotized prelabium by a slitlike *salivary meatus* (SM) (Figs. 3,4,39) which is readily visible only with the scanning electron microscope (see the equivalent salivary slit in the lateral aspects of the labiohypopharynges figured by Harbach and Knight 1977b). The *salivary orifice* opens into the floor of the salivary meatus and is often seen in light microscope preparations.

In most Culicinae the hypopharynx bears a pair of earlike lobes, the *superlinguae* (Sl) (see e.g., Figs. 9,13,28,31). These are often imperceptible when observed with the light microscope owing to their membranous nature. As in generalized insects, the superlinguae have united with the median *lingua* (L) to form the definitive hypopharynx.

The adoral surface of the hypopharynx of *Zeugomyia* bears a row of branched cuticular processes (Fig. 23) not unlike the "dichotomous bristles" which occur on the hypopharynx of certain simuliid larvae (Craig 1977). The labiohypopharynx of dixine larvae is unique in that the lateral sides of the hypopharyngeal component support a pair of denticulate tritural surfaces, the *hypopharyngeal malae* (HyM) (Figs. 3,4).

Prelabium

The prelabial component of the labiohypopharynx is comprised chiefly of the labial *prementum*, and it is probable that a pair of extrinsic muscles which originate on the ventral cranial wall and insert laterally on often indistinguishable *premental apodemes* (PAp) (see e.g., Figs. 5,14,24,34) is one of two pairs of tentorio-premental muscles found in generalized insects. The central region of the prementum is commonly elevated and bears a variously developed collection of usually strongly sclerotized toothed or toothlike projections which encompass a pair of oval membranous areas. As has been suggested by other authors (Christophers 1960; Chaudonneret 1962), the membranous areas represent vestigial *labial palpi* (LP). Separating the palpi in the Anophelinae and certain Culicinae is a cusped tonguelike structure which seemingly corresponds to the fused glossae and paraglossae, the *ligula* (Lg), of many other insects.

Ligula. The anopheline ligula (Figs. 5-7) strongly resembles the "ligula" (Saether 1971) of certain chironomid larvae (see the figures of Johannsen 1937). In many culicine larvae, notably those of the genera *Culex* (Fig. 11) and *Aedes* (Fig. 27), the ligula is a recumbent troughlike structure which bears resemblance to the "ligula" of simuliid larvae (Craig 1977). In *Paradixa*, toxorhynchitine, and some culicine larvae, including most Sabethini, the ligula is unrecognizably fused with some of the toothlike elements of the prementum (see below).

Labial palpi. Each labial palpus commonly bears four sensory peglike structures (Yin 1970), *labial palpal sensoria* 1-4 (LPS₁, LPS₂, LPS₃, LPS₄), which are structurally similar to chemoreceptors known to have a gustatory function in other insects. Sensoria 1 and 2 often arise from a common pedicel (see e.g., Figs. 25,37).

Located on each side of the ligula in anopheline larvae is a scale- or leaflike process. These processes correspond exactly to the "paraglossae" (Saether 1971) of certain chironomid larvae. Das (1937), however, maintains that the paraglossae and glossae "generally form a single lobe" in larval insects. Since the structures arise from the labial palpi and appear to have an ill-defined socket, they are considered here as *labial palpal sensoria* 5 (LPS₅) (Figs. 5,6).

Prementum. In general, the most conspicuous feature of the culicid prementum is the intricate assemblage of toothlike processes which subtend the dorsal and lateral margins of the labial palpi. In the generalized condition exemplified by *Opifex fuscus* (Fig. 21), these processes can be conveniently subdivided into three groups: 1) the bilaterally paired *premental teeth* comprising (a) an interconnected group of *lateral premental teeth* (LPT) which flank the labial palpi, and (b) a *premental dental arch* (PDA) which curves around the dorsal margin of each palpus and is united with the base of the ligula; 2) a cluster of *premental cusps* (PCu) located centrally between the premental dental arches; and 3) a patch of numerous peglike processes, a *premental mala* (PM), borne on each sloping dorsolateral surface adjacent to the lateral premental teeth.

The premental teeth are weakly developed in dixine and anopheline larvae where they are typically represented by a pair of heavily sclerotized cusped ridges which bend laterally around the dorsal margins of the labial palpi. The premental teeth of culicine larvae are normally well developed but vary widely in specific form. Except in most sabethines, the lateral premental teeth of culicine larvae generally consist of three interconnected groups which from dorsal to ventral are designated *lateral premental teeth 1-3* (LPT₁, LPT₂, LPT₃). These are quite distinct in *Hodgesia* (Fig. 15) and Mansonini larvae (Figs. 18, 19), but in certain other genera LPT₁ are weakly developed and difficult to distinguish. In these cases the LPT₁ of each side appear to be reduced and coalesced with the lateral portion of the premental dental arch (see e.g., Figs. 11, 12, 16, 24). In toxorhynchitine (Figs. 39, 40) and most sabethine species (Figs. 32, 34-38), the lateral premental teeth of each side consist of a crescentic mass of dentate or dentate-serrate projections.

The trend in culicines is for the premental dental arches to separate from the lateral premental teeth and to fuse with the premental cusps and the ligula (see e.g., Fig. 26). In the more complex state exhibited by many sabethine species, these structures are unrecognizably fused with the latter to form the toothed triangular to T-shaped mass of *prementoligular teeth* (PLT) (Figs. 30-38). The ridge of prementoligular teeth which separates the labial palpi of *Paradixa* (Fig. 4) probably consists largely of a highly modified ligula.

In anopheline larvae, an elevated median longitudinal row of *premental ridge teeth* (PRT) extends dorsally from the premental teeth and separates a pair of broad, slanting, denticulate tritural surfaces (Figs. 5-7). These are seemingly homologous for the most part with the culicine premental cusps. The expansive tritural surfaces are largely homologous with the premental malae of *Opifex* although some of the ventromedial denticles of each may be homologous with a portion of the premental cusps.

The culicine premental cusps are evidently homologous with a somewhat larger group of similar structures borne centrally on the labiohypopharynx of dixine larvae (Figs. 3, 4). The anopheline premental malae correspond functionally to the hypopharyngeal malae of dixines.

In most culicines, the area lying between the salivary meatus and the premental teeth is somewhat membranous and is believed to correspond to the

adoral wall of the generalized insect prementum. This area commonly bears a pair of *premental sensoria* (PS) (see e.g., Figs. 19,29) which are innervated by branches of the labial nerve and have the structure of typical insect chemoreceptors (Yin 1970). The premental sensoria of anopheline larvae (Figs. 5-7) are quite small and sometimes difficult to distinguish from the denticles of the premental malae which border them. They give the impression of having been displaced dorsally by the well developed premental malae.

On the sloping lateral surfaces of the prementum immediately adjacent to each aggregate of lateral premental teeth is a group of *lateral premental processes* (LPP). These occur principally in aedine species (Figs. 21,22,24,27) but are also found in species of *Culex* (Fig. 11), *Culiseta* (Fig. 16) and *Orthopodomyia* (Fig. 20). The dixine homologues (Figs. 2,3) are located at the lateral margins of the labial palpi (these were incorrectly considered as lateral prelabial [= premental] teeth by Harbach and Knight 1977b). Equivalent structures in *Eucoethra underwoodi* (Fig. 41) are located dorsolateral to the cluster of labial palpal sensoria.

A group of *ventral premental processes* (VPP) arises near the ventral margin of the labiohypopharynx. In aedine (Figs. 21-25,27,28) and *Culiseta* species (Fig. 16) these are generally numerous and scalelike whereas in most other culicines they are usually few in number and spine- or lobelike. The processes are weakly developed in species of *Anopheles* (Fig. 6) and *Chagasia* (Fig. 7). They are absent in both the *Bironella* (Fig. 5) and *Toxorhynchites* species (Figs. 39,40) examined. The corresponding structures of *Eucoethra* (Fig. 41) and dixine larvae (Figs. 2,3) resemble those of certain aedine species.

A peculiar heart-shaped flap, the *premental cordate process* (PCP), arises immediately ventral to the ligula in anophelines (Figs. 5-7). The structure dorsally opposes the ventral premental processes of *Anopheles* (Fig. 6) and *Chagasia* (Fig. 7). In *Bironella* (Fig. 5) it has a distinct bilobed form and is similar in appearance to the ventral premental processes of *Uranotaenia* (Fig. 8), *Aedeomyia* (Fig. 14), *Hodgesia* (Fig. 15) and Mansoniini species (Figs. 18,19) with which it could be homologous.

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- Fig. 2. *Anopheles (Anopheles) quadrimaculatus* Say. Same as Fig. 1 except mandibles and maxillary palpi intact with maxillary bodies omitted. (Redrawn from Laffoon and Knight 1973)

The labiohypopharynges of

- Fig. 3. *Nothodixa campbelli* (Alexander).
- Fig. 4. *Paradixa neozelandica* (Tonnoir). (Redrawn from Harbach and Knight 1977b)
- Fig. 5. *Bironella (Brugella) hollandi* Taylor.
- Fig. 6. *Anopheles (Nyssorhynchus) albimanus* Wiedemann. (Redrawn from Harbach and Knight 1977b)
- Fig. 7. *Chagasia bathana* (Dyar).
- Fig. 8. *Uranotaenia (Uranotaenia) barnesi* Belkin.
- Fig. 9. *Uranotaenia (Pseudoficalbia) lagunensis* Baisas.
- Fig. 10. *Culex (Lutzia) halifaxii* Theobald.
- Fig. 11. *Culex (Culex) nigripalpus* Theobald.
- Fig. 12. *Galindomyia leei* Stone and Barreto. (Drawn as seen through venter of cranium; from slide GML:03848 on loan courtesy of J.N. Belkin)
- Fig. 13. *Deinocerites cancer* Theobald.
- Fig. 14. *Aedeomyia (Aedeomyia) squamipennis* (Lynch Arribalzaga).
- Fig. 15. *Hodgesia solomonis* Belkin.
- Fig. 16. *Culiseta (Culiseta) inornata* (Williston).
- Fig. 17. *Mimomyia (Etorleptiomyia) solomonis* (Belkin).
- Fig. 18. *Mansonia* sp.
- Fig. 19. *Coquillettidia (Coquillettidia) perturbans* (Walker).
- Fig. 20. *Orthopodomyia fascipes* (Coquillet).
- Fig. 21. *Opifex fuscus* Hutton. (Redrawn from Harbach and Knight 1977b)
- Fig. 22. *Eretmapodites (Eretmapodites) chrysogaster* Graham.
- Fig. 23. *Zeugomyia* sp.
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- Fig. 26. *Heizmannia* sp. (Slightly dorsal; drawn from poor specimen)
- Fig. 27. *Aedes (Ochlerotatus) canadensis* (Theobald). Redrawn from Harbach and Knight 1977b)
- Fig. 28. *Haemagogus (Haemagogus) equinus* Theobald.
- Fig. 29. *Psorophora (Janthinosoma) ferox* (von Humboldt).
- Fig. 30. *Malaya genurostris* Leicester.
- Fig. 31. *Topomyia (Topomyia) vijayae* Ramalingam.
- Fig. 32. *Tripteroides (Tripteroides) nepenthis* (Edwards).
- Fig. 33. *Maorigoeldia argyropus* (Walker).
- Fig. 34. *Phoniomyia* sp.
- Fig. 35. *Trichoprosopon (Shannoniana) moralesi* (Dyar and Knab).
- Fig. 36. *Wyeomyia (Wyeomyia) smithii* (Coquillet).
- Fig. 37. *Limatus durhamii* Theobald.

- Fig. 38. *Sabethes (Sabethinus) undosus* (Coquillett).
 Fig. 39. *Toxorhynchites (Toxorhynchites) brevipalpis* Theobald. (Redrawn from Harbach and Knight 1977b)
 Fig. 40. *Toxorhynchites (Lynchiella) rutilus* (Coquillett). (Anteroventral aspect)
 Fig. 41. *Eucorethra underwoodi* Underwood.

ABBREVIATIONS USED IN FIGURES

CB	= cibarial bar	LPT ₁	= lateral premental teeth 1
Dm	= dorsomentum	LPT ₂	= lateral premental teeth 2
Hy	= hypopharynx	LPT ₃	= lateral premental teeth 3
HyB	= hypopharyngeal bar	PAP	= premental apodeme
HyM	= hypopharyngeal mala	PCP	= premental chordate process
L	= lingua	PCu	= premental cusps
LbHy	= labiohypopharynx	PDA	= premental dental arch
Lg	= ligula	PLT	= prementoligular teeth
LP	= labial palpus	PM	= premental mala
LPP	= lateral premental processes	PRT	= premental ridge teeth
LPS ₁	= labial palpal sensorium 1	PS	= premental sensorium
LPS ₂	= labial palpal sensorium 2	Sl	= superlingua
LPS ₃	= labial palpal sensorium 3	SM	= salivary meatus
LPS ₄	= labial palpal sensorium 4	Vm	= ventromentum
LPS ₅	= labial palpal sensorium 5	VPP	= ventral premental processes
LPT	= lateral premental teeth		

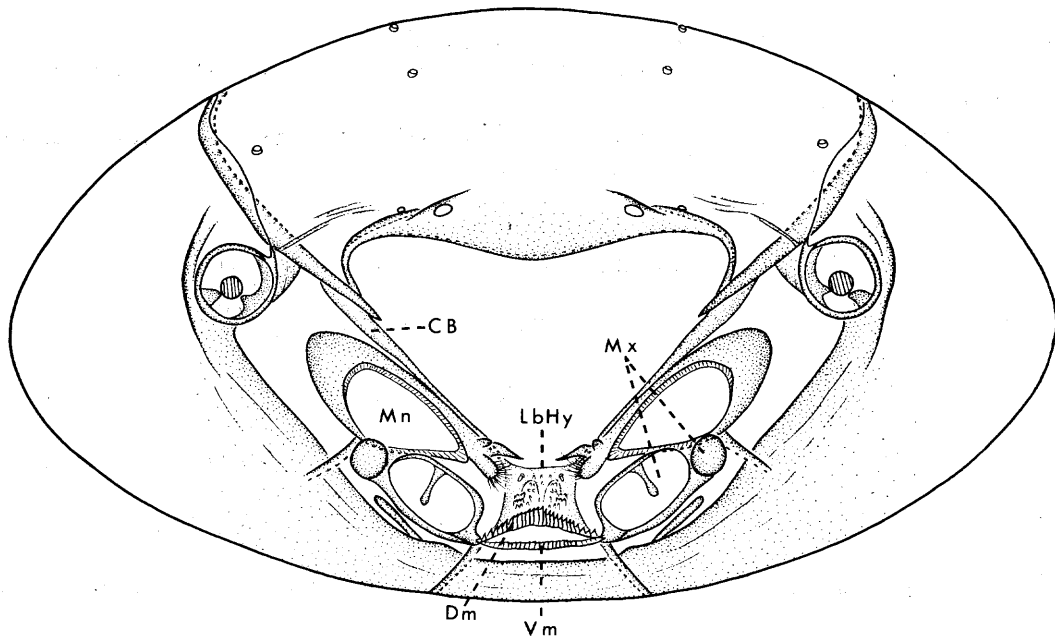


Fig. 1

Aedes (Ochlerotatus)

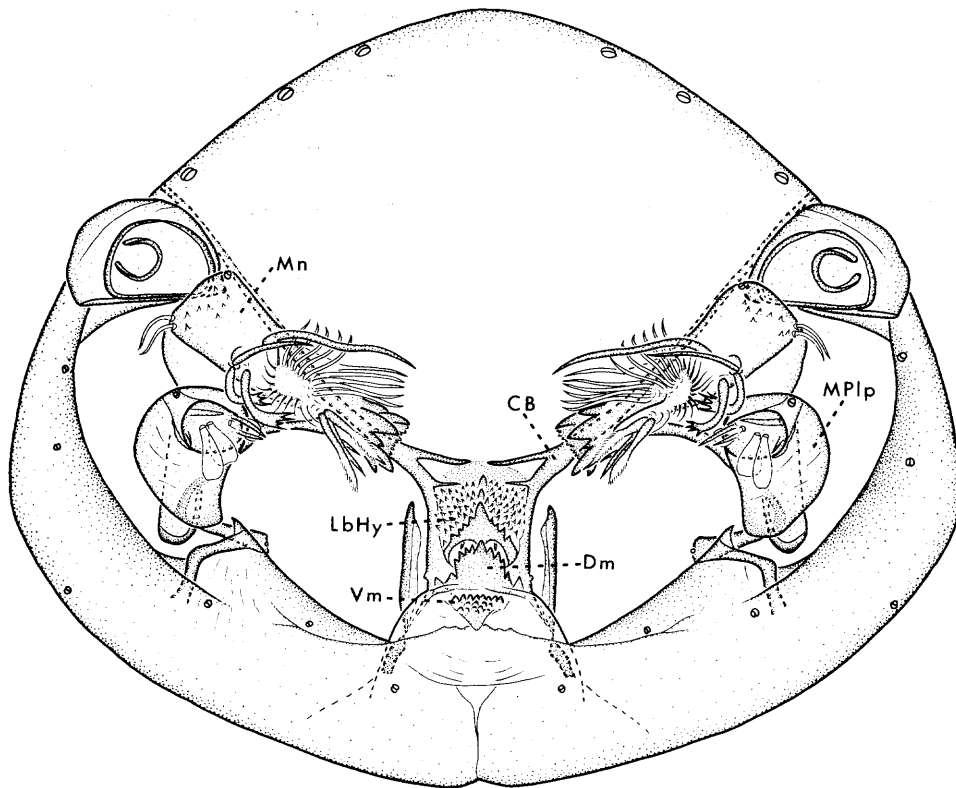


Fig. 2

Anopheles (Anopheles)

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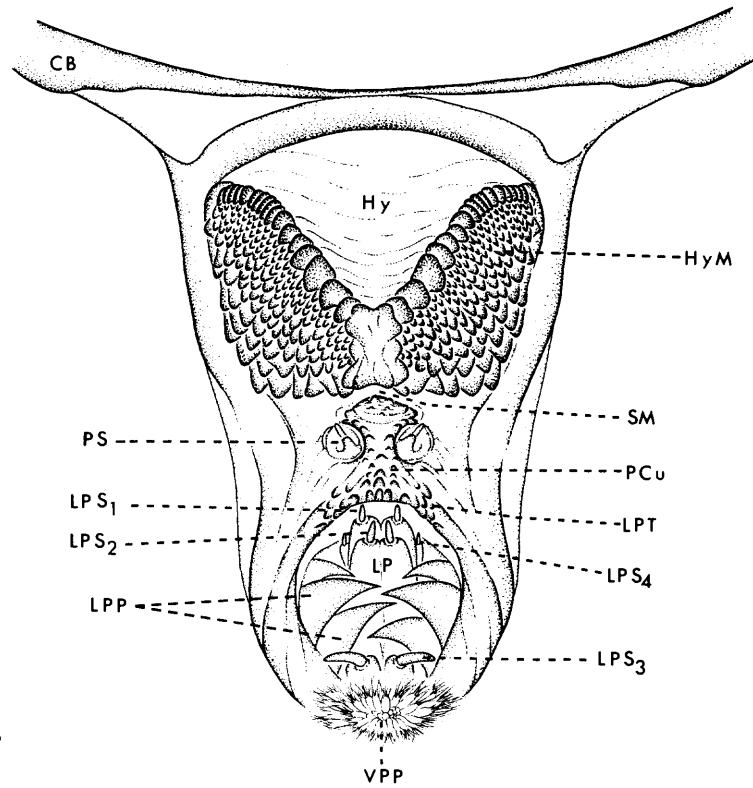


Fig. 3
Nothodixa

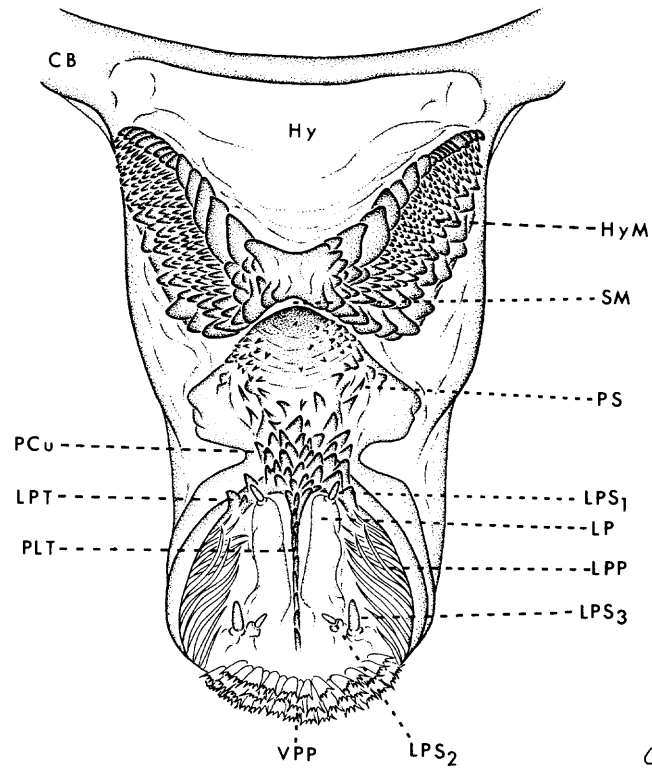


Fig. 4
Paradixa

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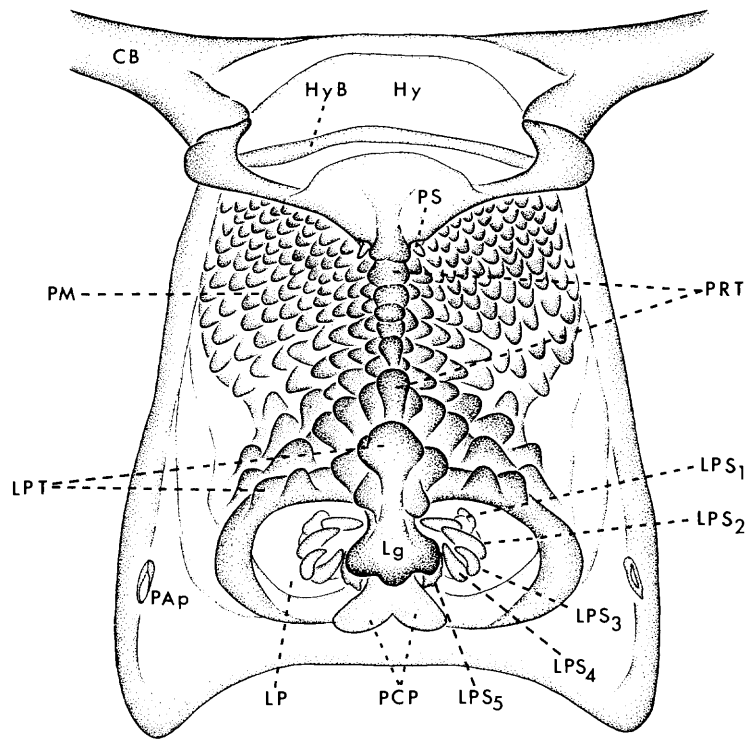


Fig. 5
Bironella
(*Brugella*)

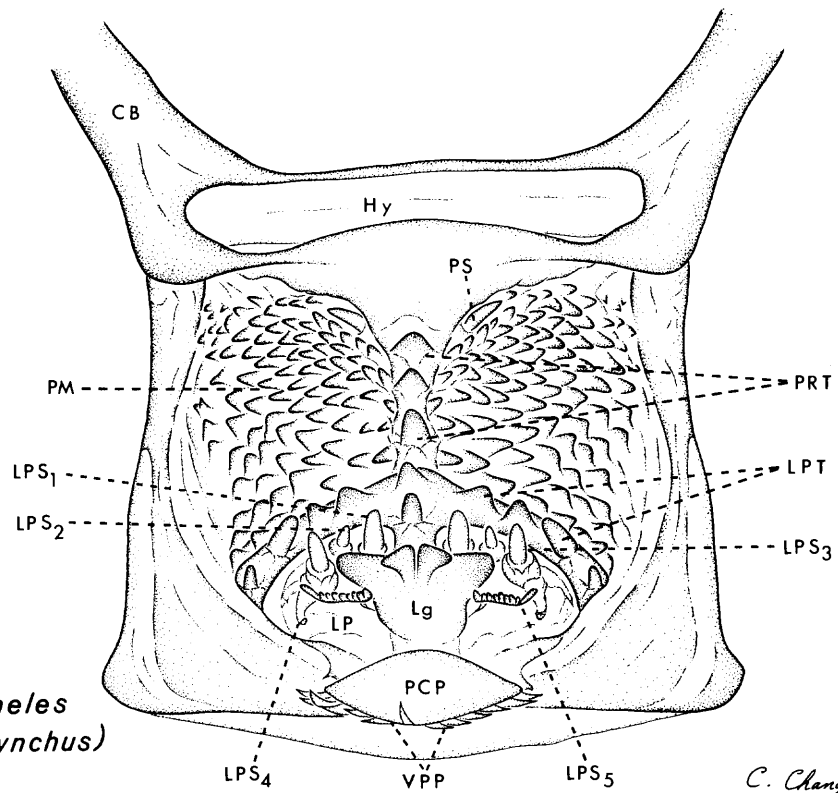


Fig. 6
Anopheles
(*Nyssorhynchus*)

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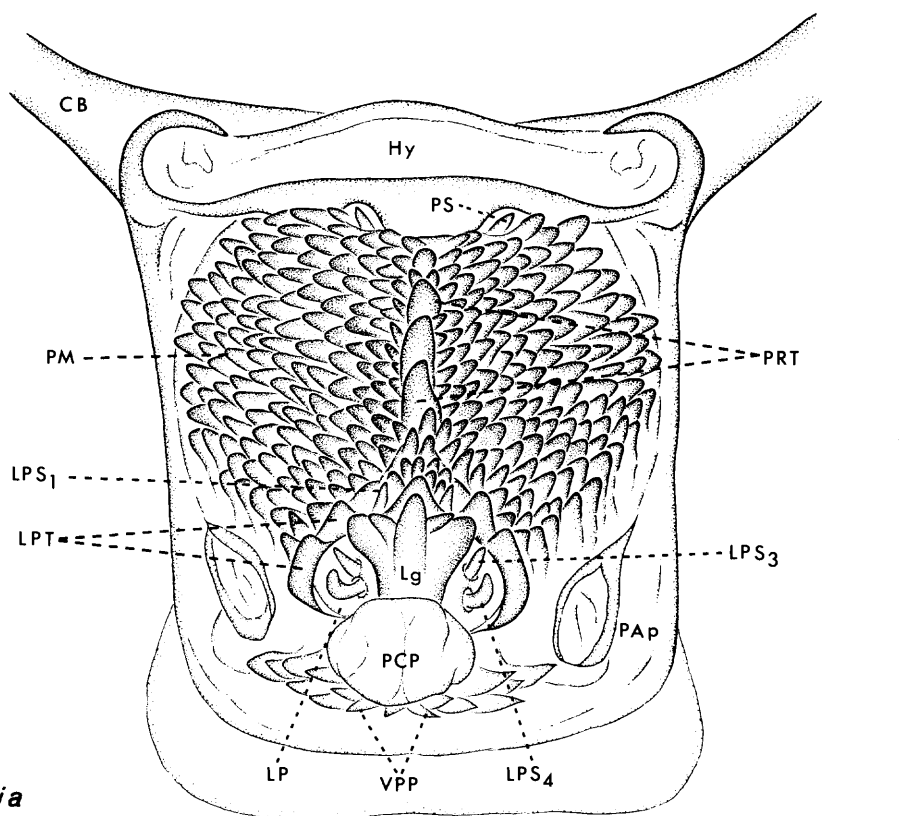


Fig. 7
Chagasia

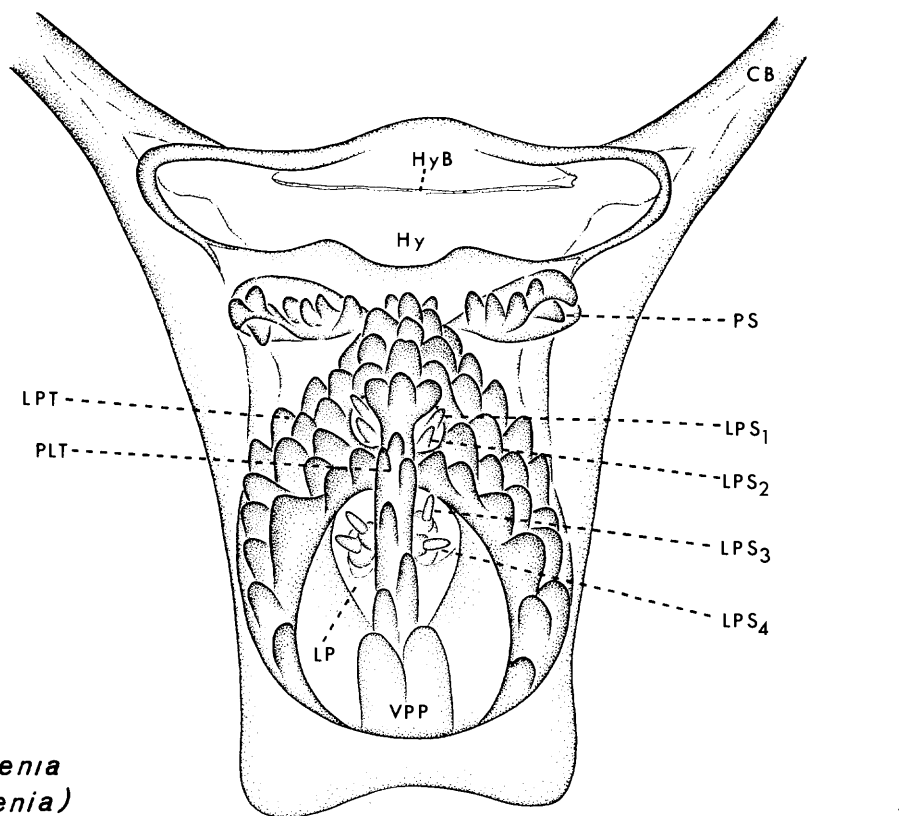


Fig. 8
Uranotaenia
(Uranotaenia)

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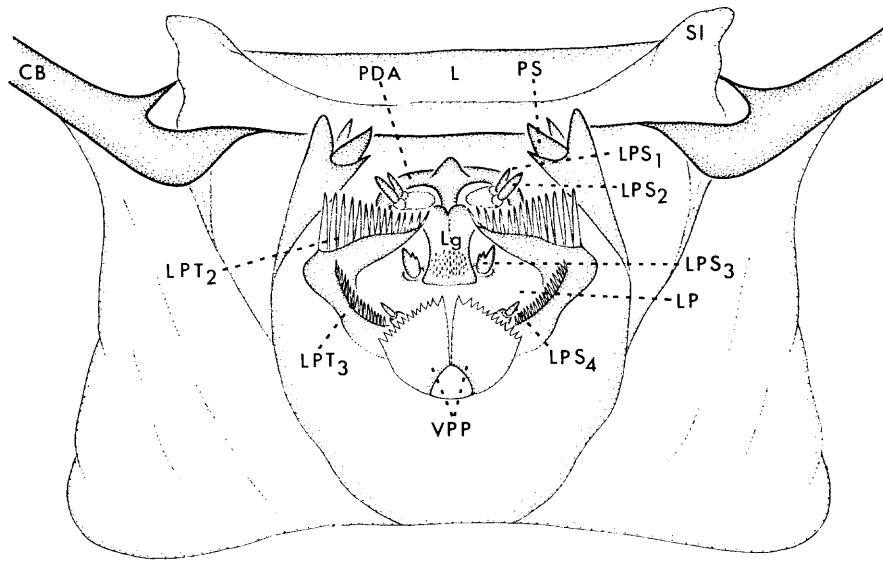


Fig. 9

Uranotaenia (Pseudoficalbia)

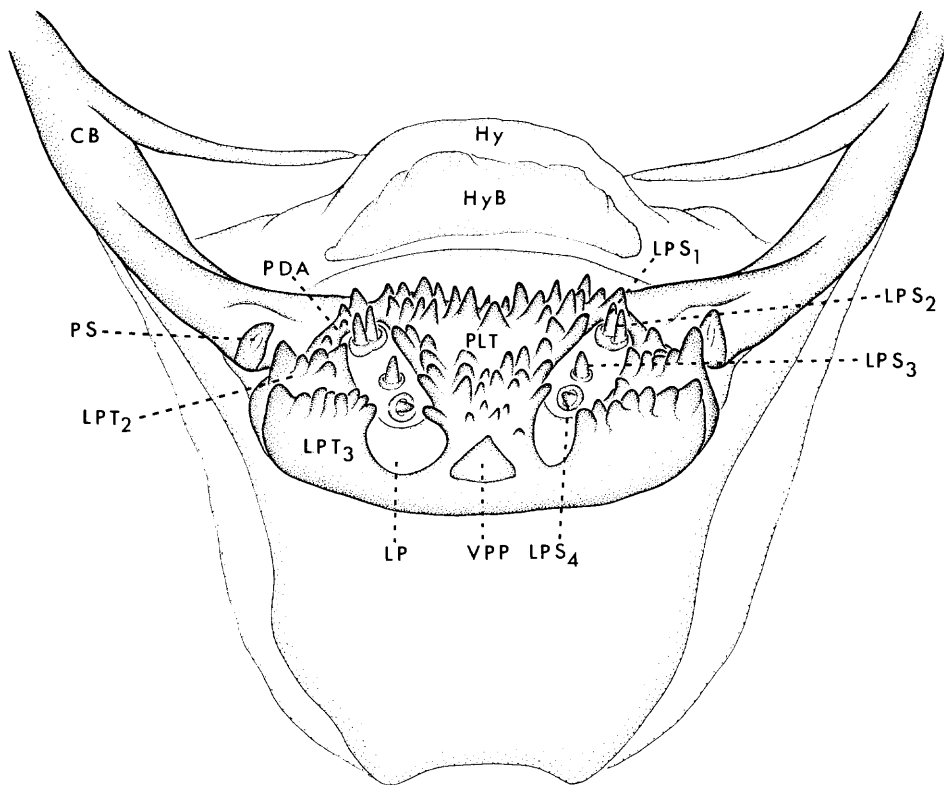


Fig. 10

Culex (Lutzia)

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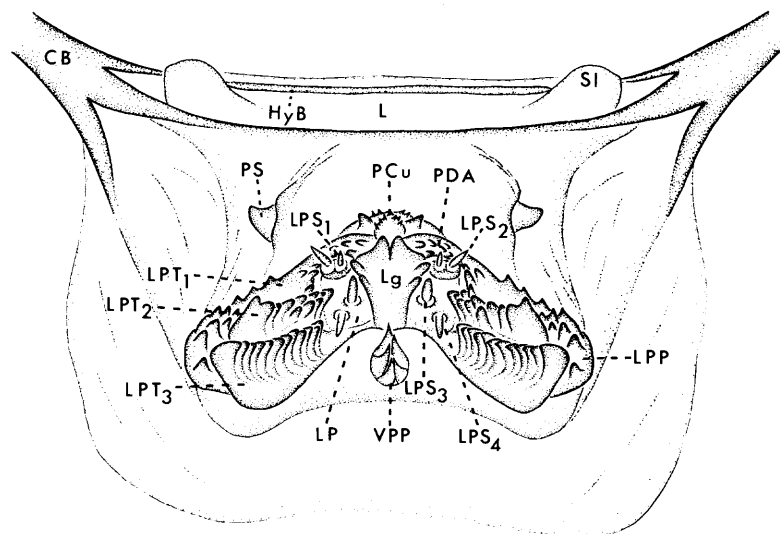


Fig. 11

Culex (Culex)

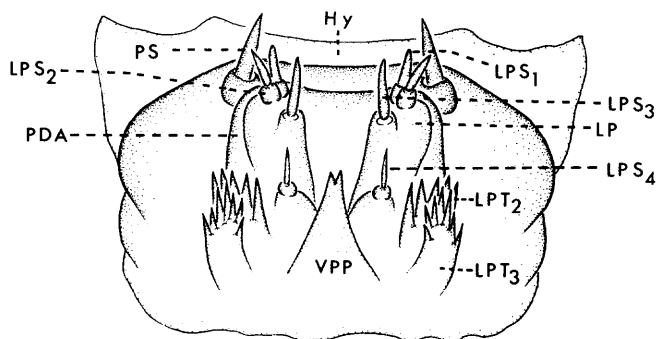


Fig. 12

Galindomyia

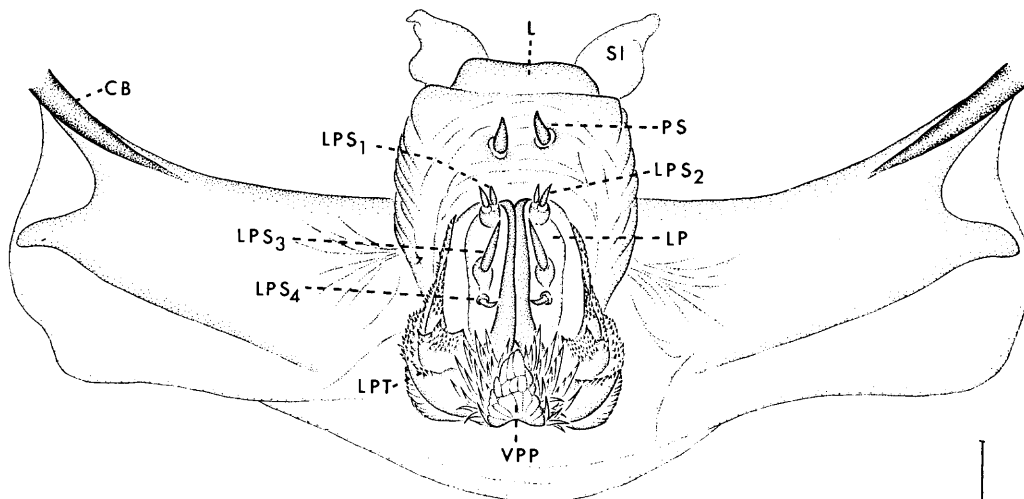


Fig. 13

Deinocerites

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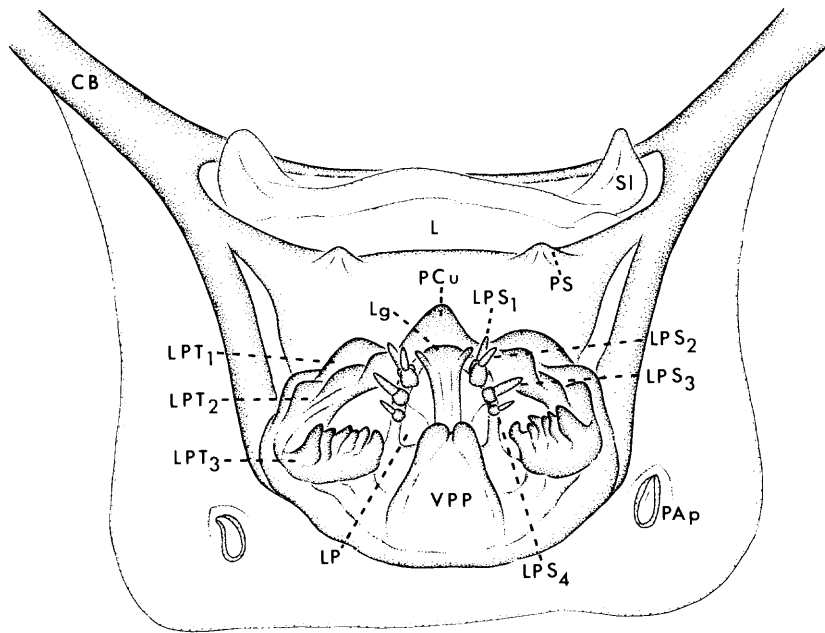


Fig. 14

Aedeomyia (Aedeomyia)

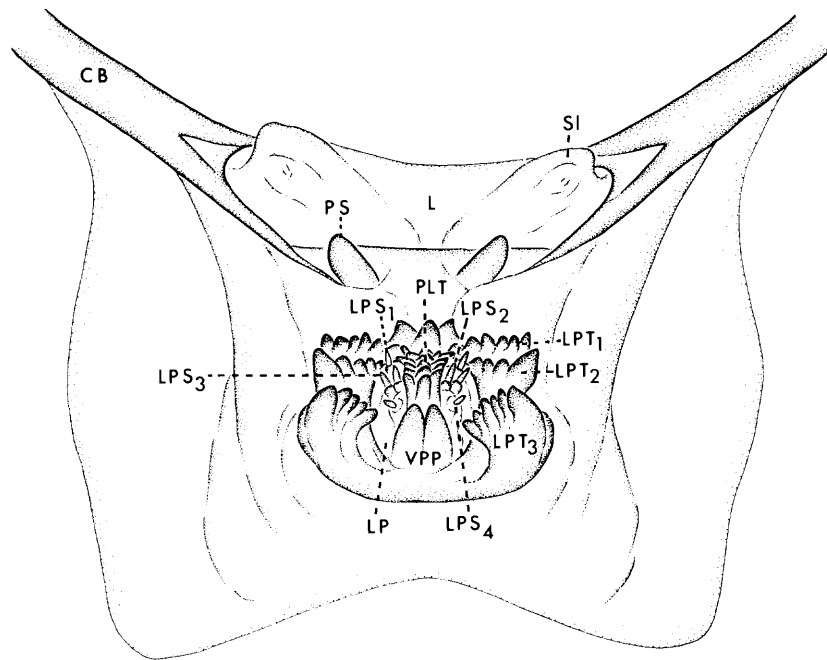


Fig. 15

Hodgesia

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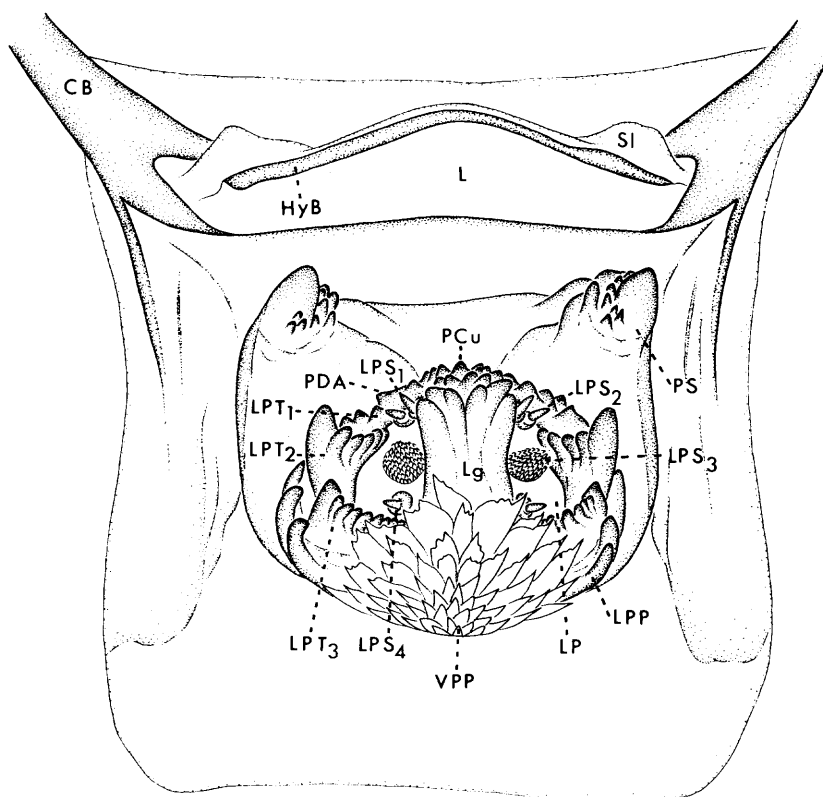


Fig. 16

Culiseta (Culiseta)

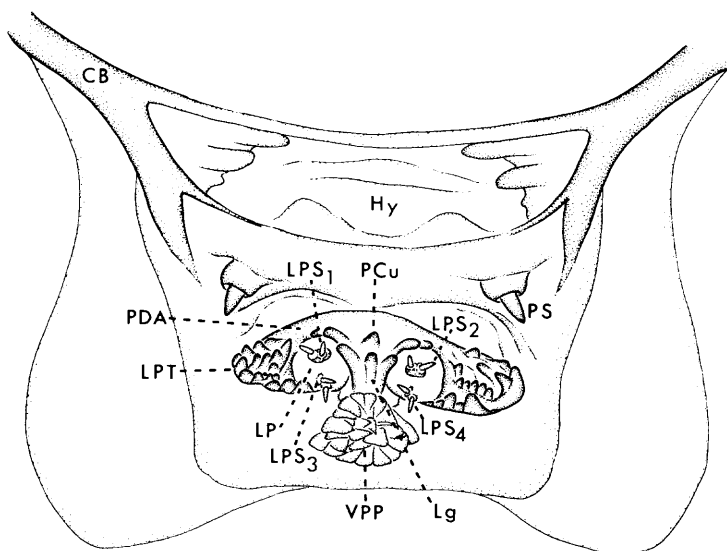


Fig. 17

Mimomyia (Etorleptomyia)



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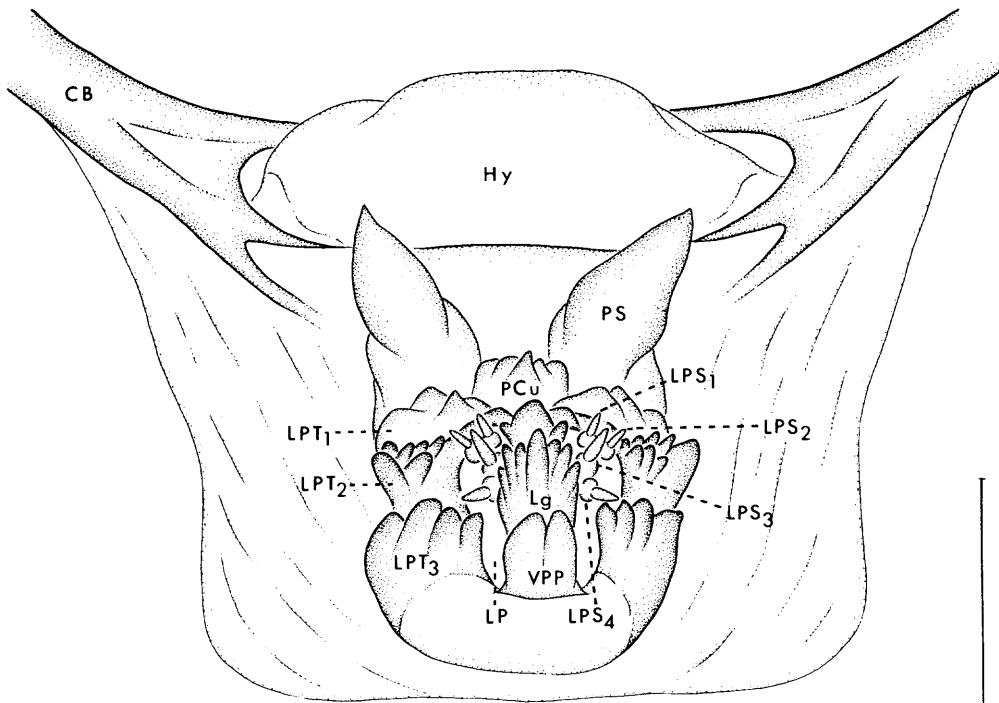


Fig. 18

Mansonia

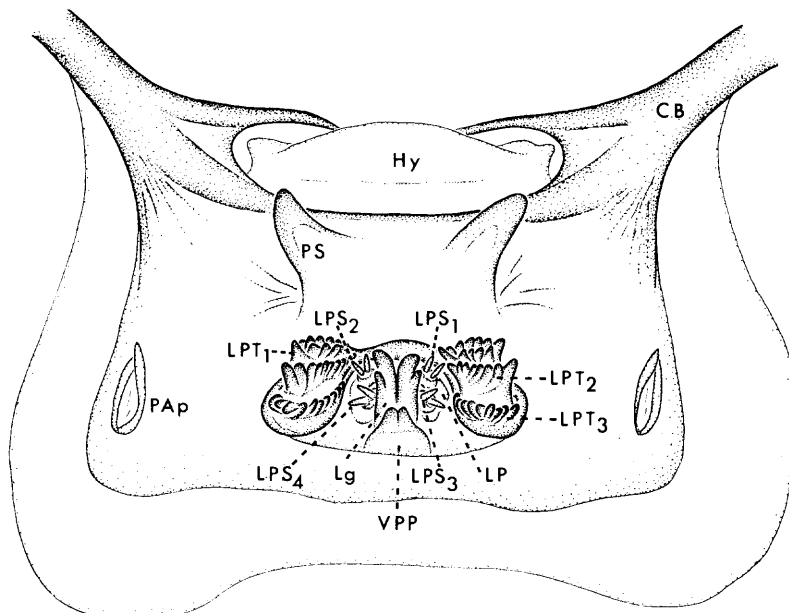


Fig. 19

Coquillettidia (Coquillettidia)

C. Chang

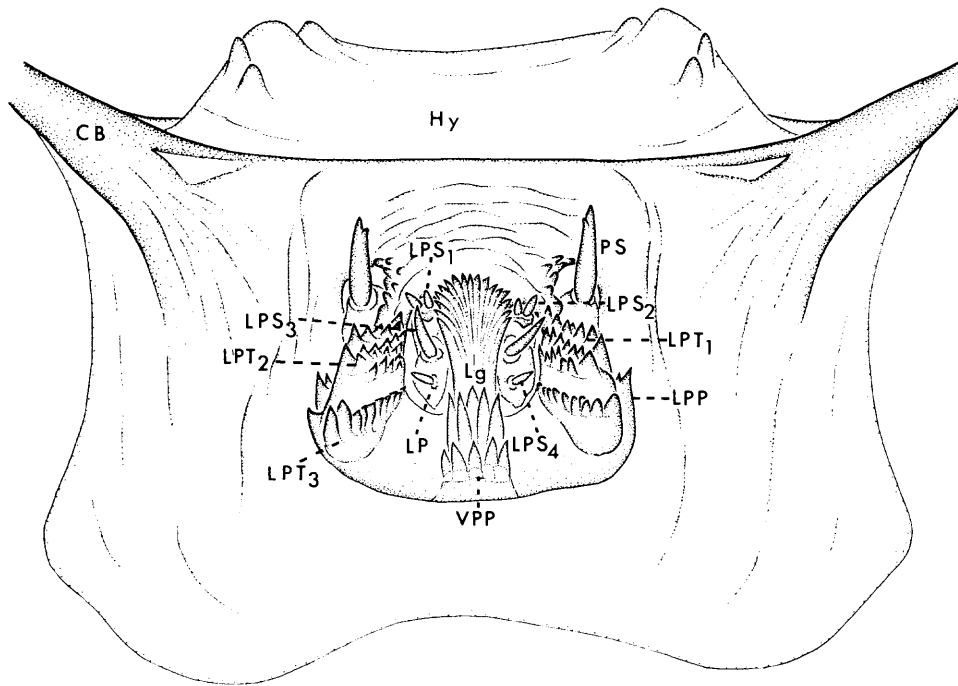


Fig. 20

Orthopodomyia

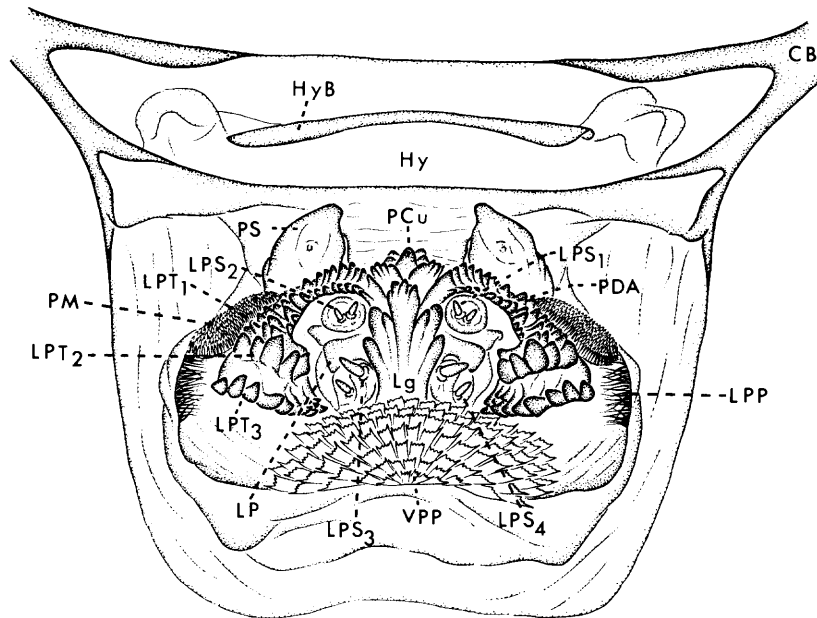


Fig. 21

Opifex

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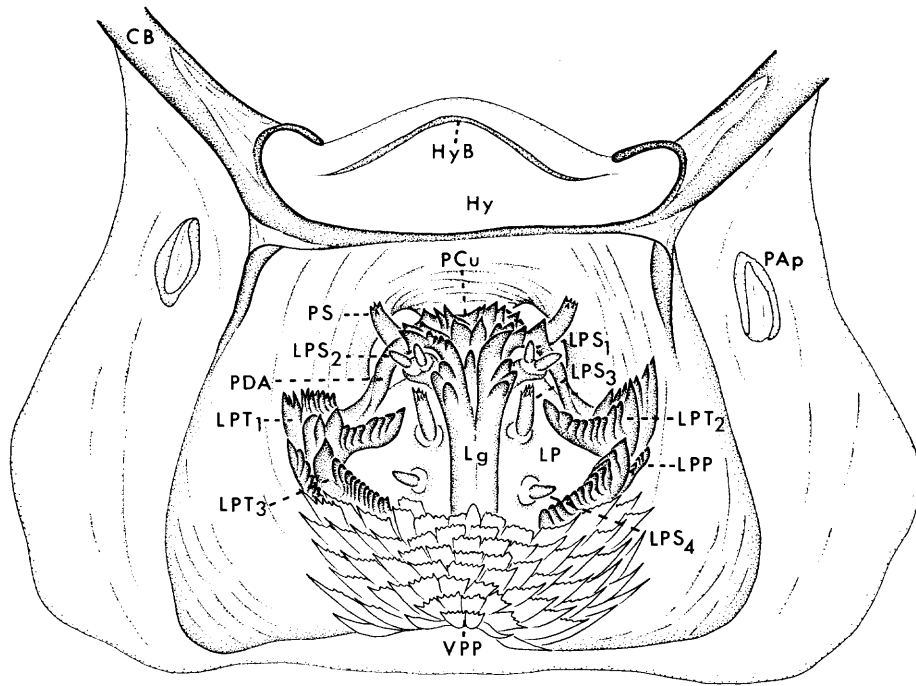


Fig. 22 *Eretmapodites (Eretmapodites)*

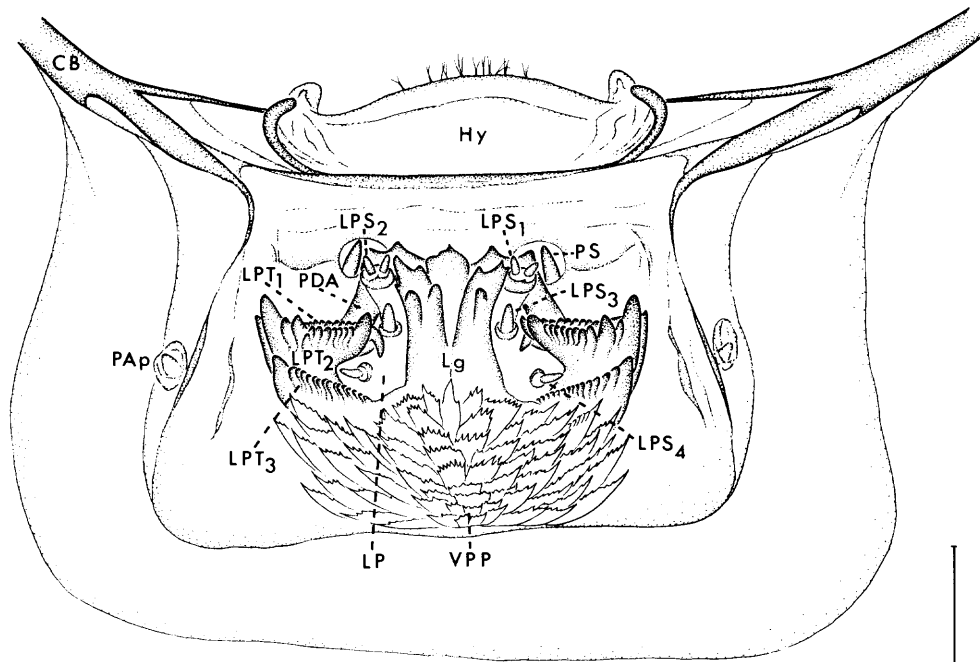


Fig. 23 *Zeugomyia*

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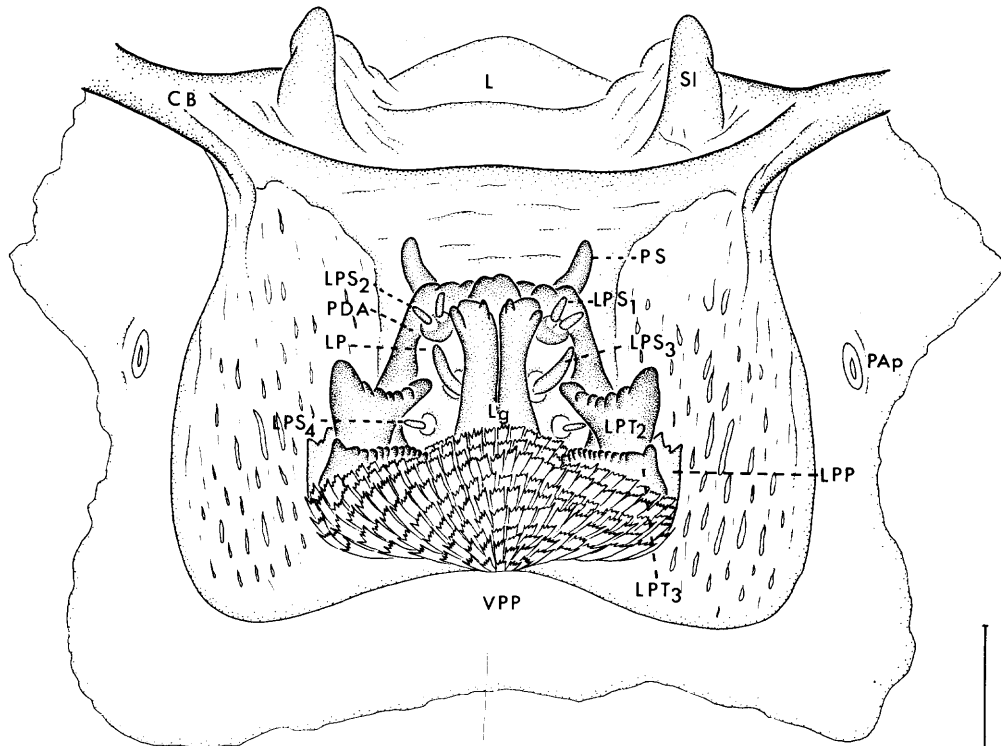


Fig. 24

Udaya

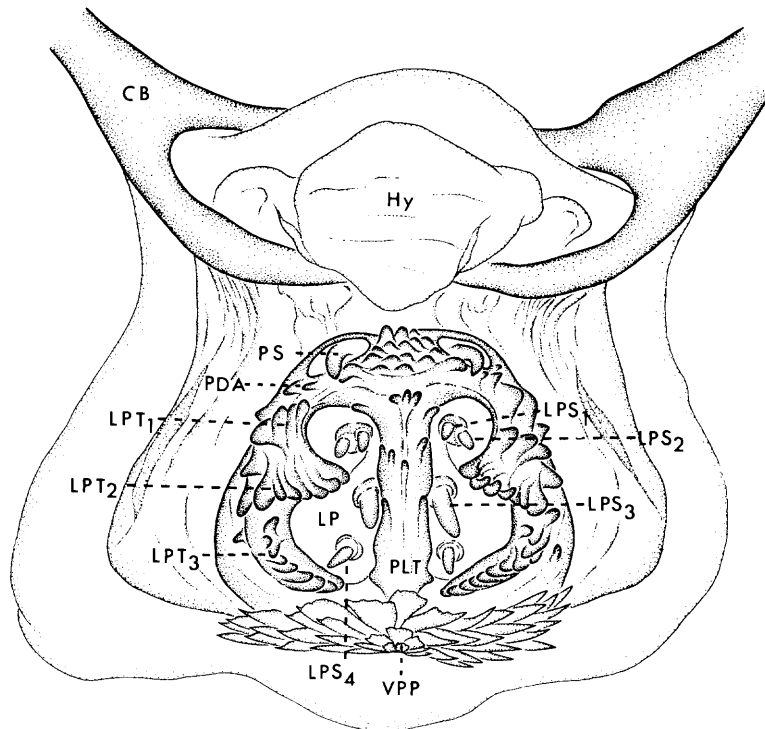


Fig. 25

Armigeres (Armigeres)

c. Chang

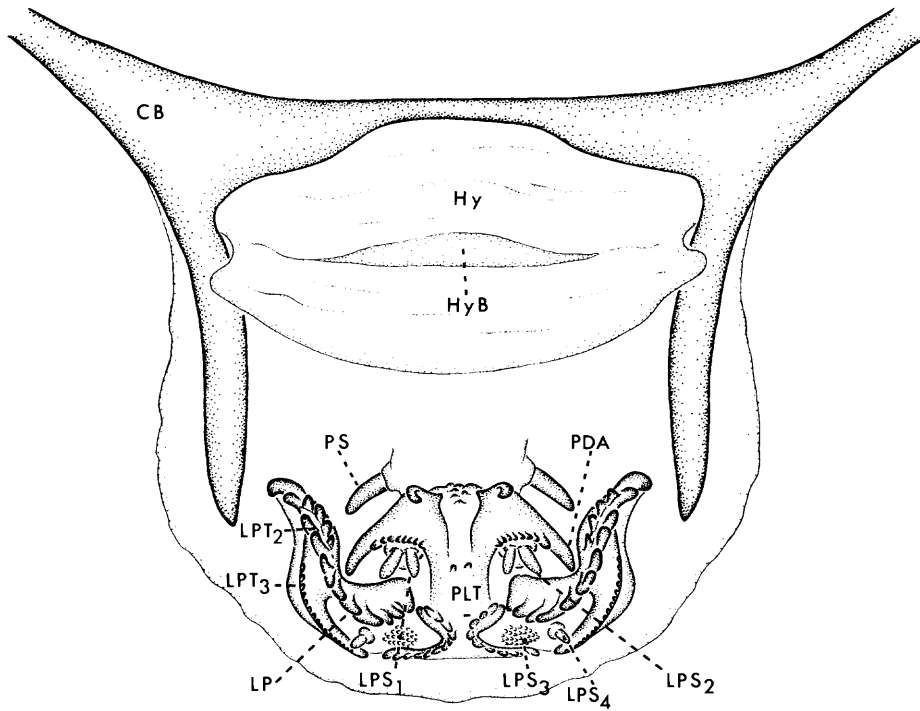


Fig. 26

Heizmannia

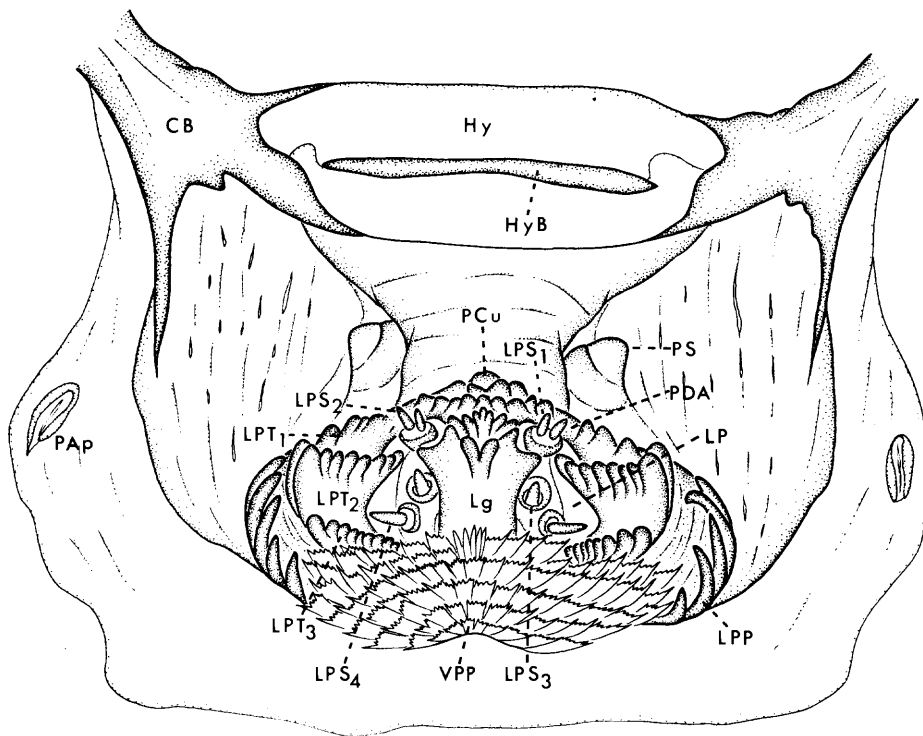


Fig. 27

Aedes (Ochlerotatus)

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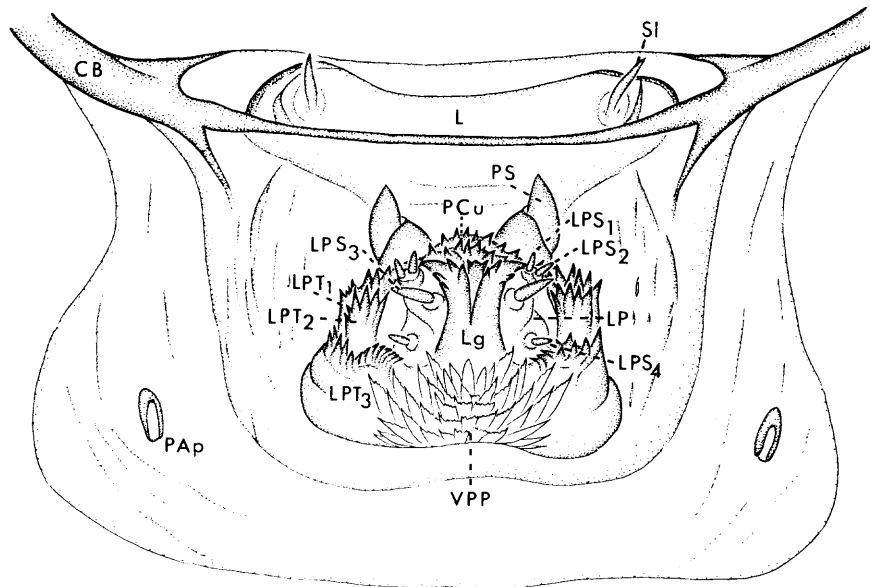


Fig. 28

Haemagogus (Haemagogus)

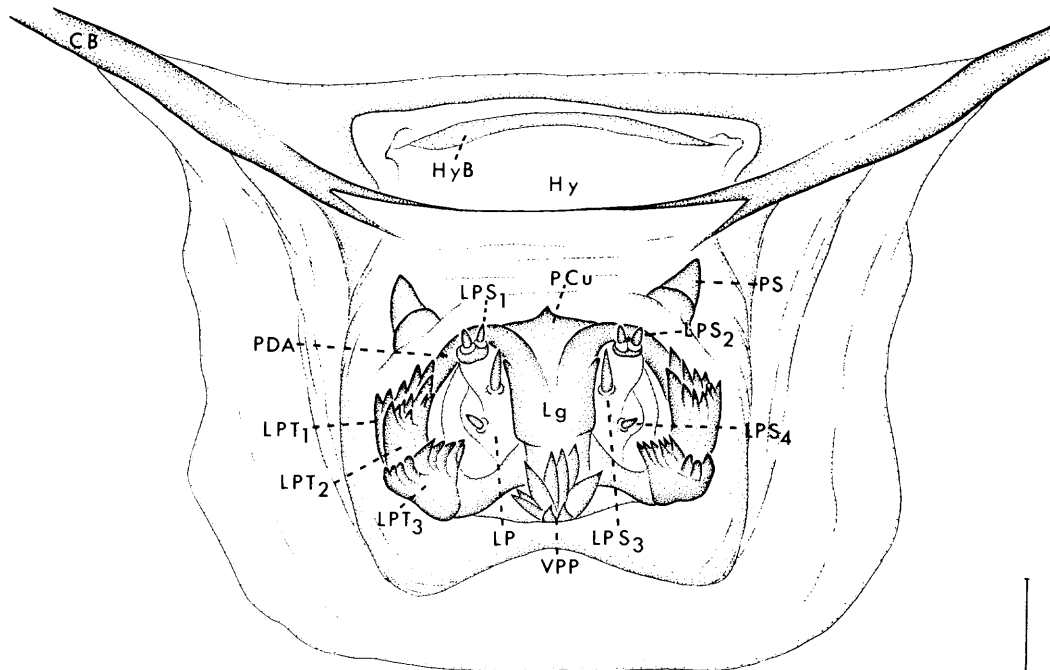


Fig. 29

Psorophora (Janthinosoma)

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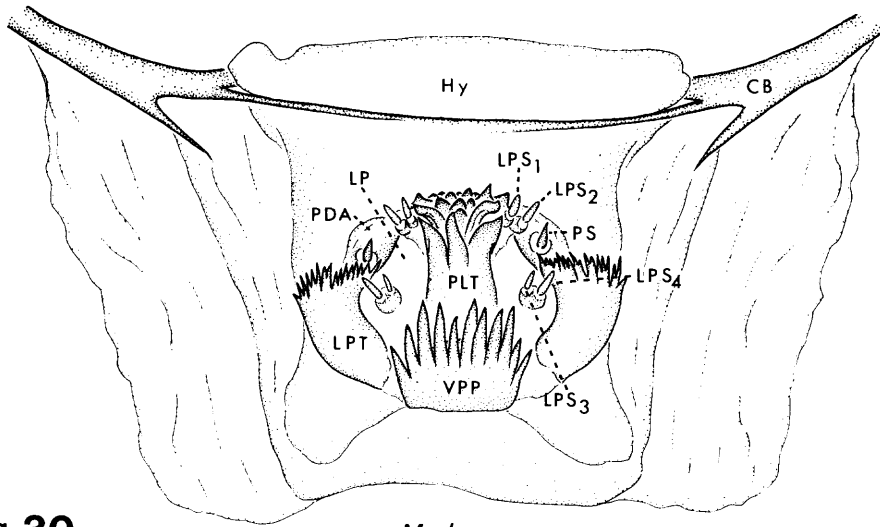


Fig. 30

Malaya

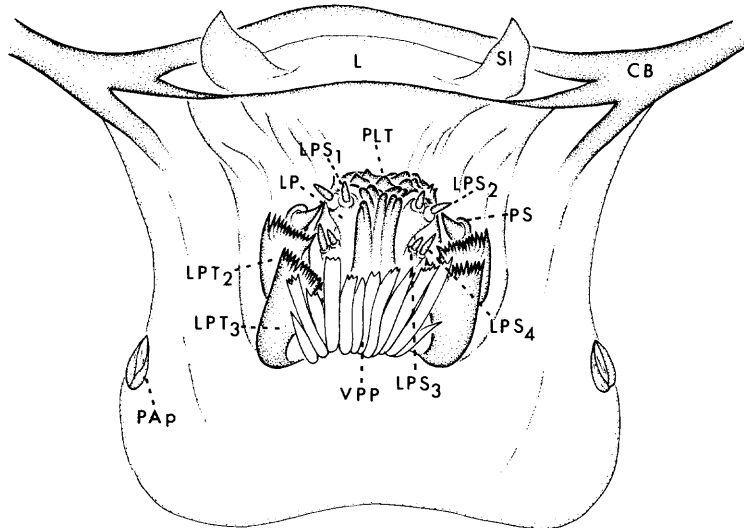


Fig. 31

Topomyia

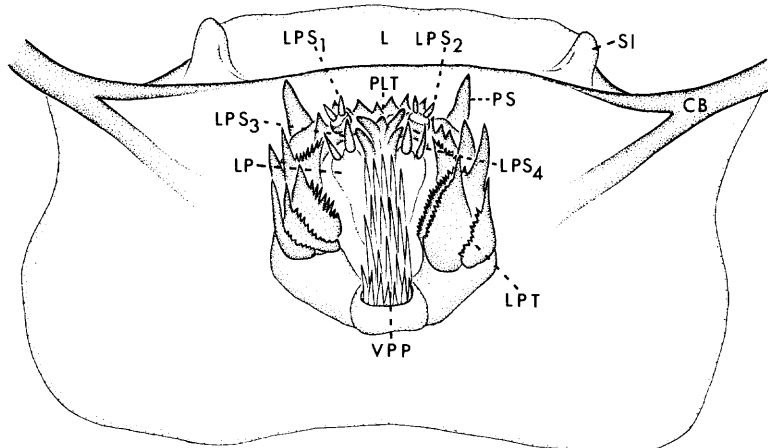


Fig. 32

Tripteroides (Tripteroides)

C. Chang

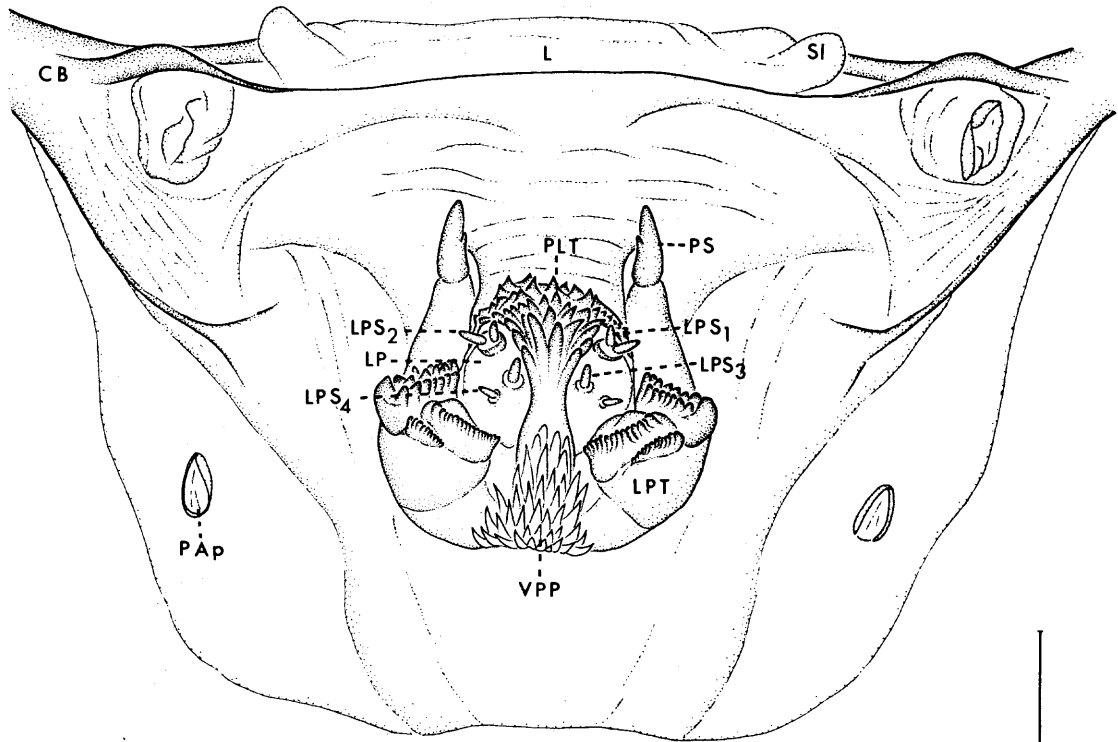


Fig. 33

Maorigoeldia

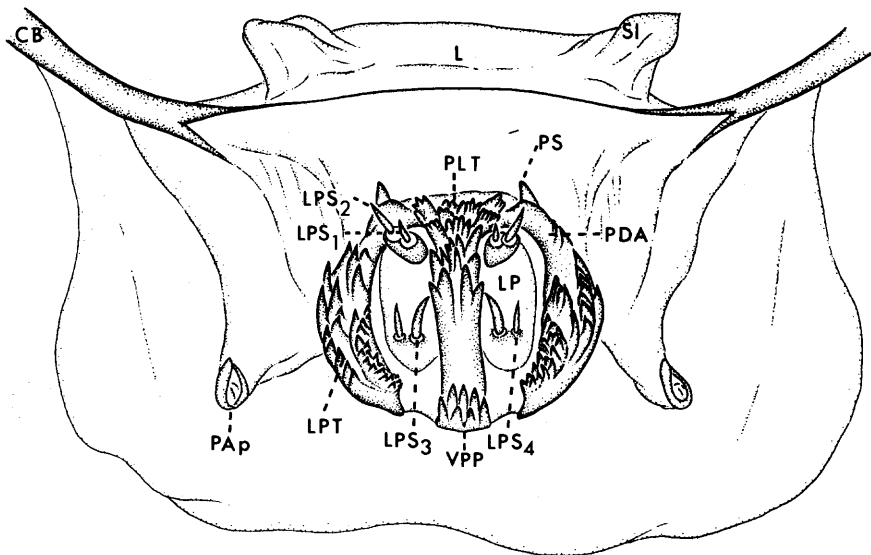


Fig. 34

Phoniomyia

C. Chang

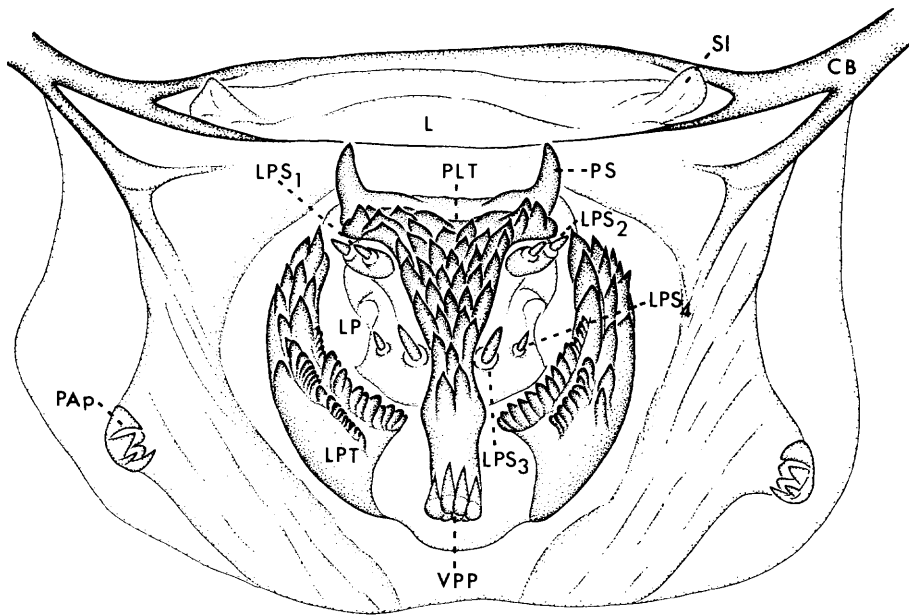


Fig. 37

Limatus

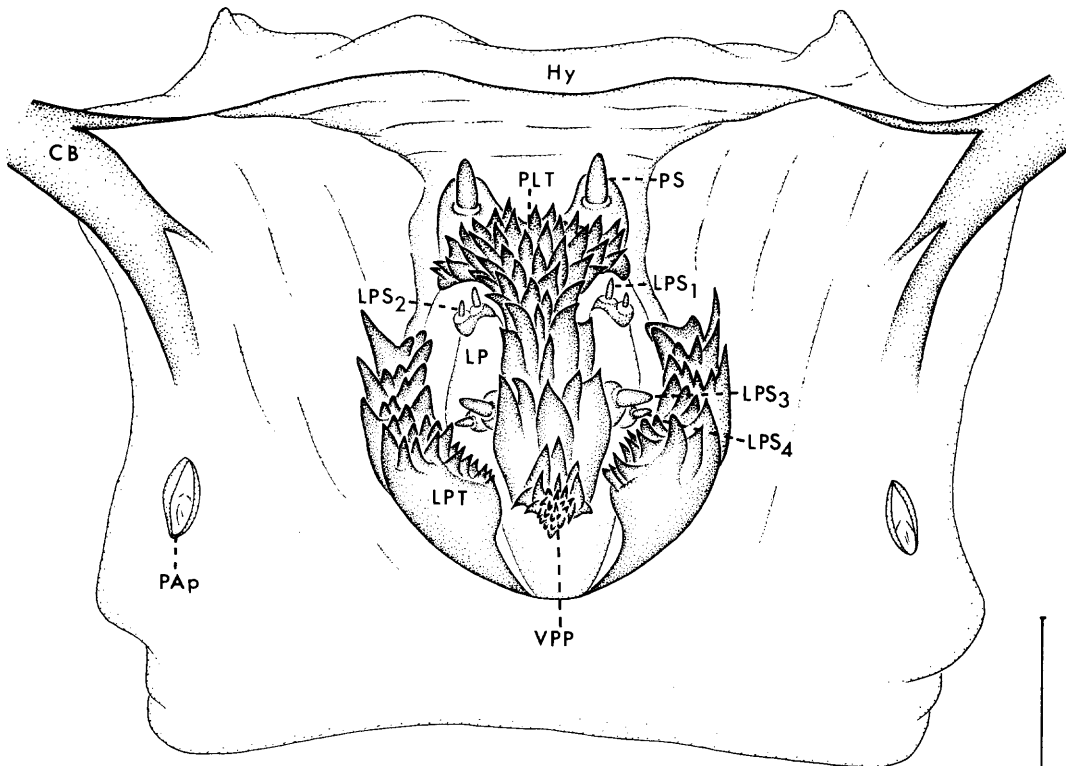


Fig. 38

Sabethes (Sabethinus)

C. Chang

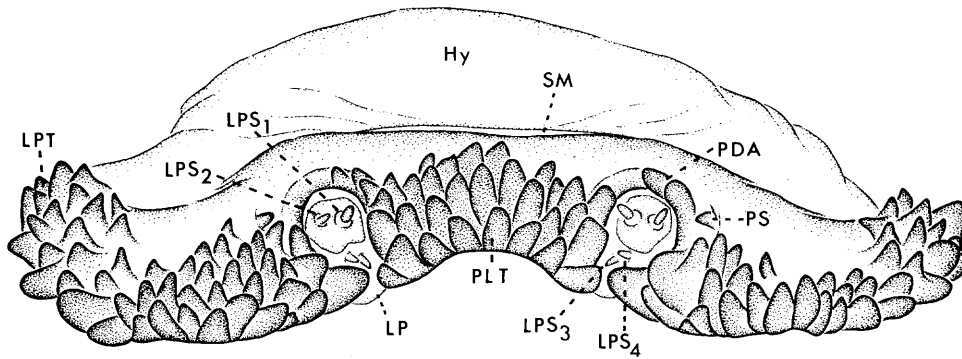


Fig. 39 *Toxorhynchites (Toxorhynchites)*

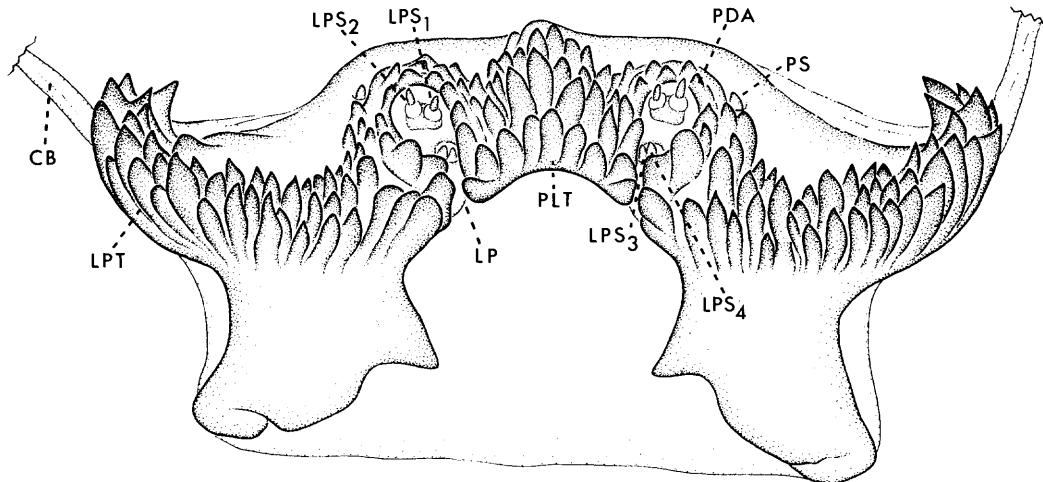


Fig. 40 *Toxorhynchites (Lynchiella)*

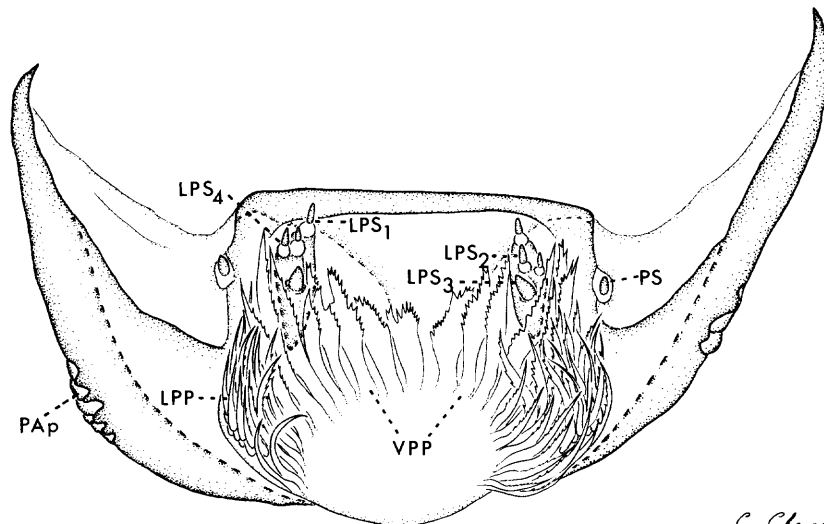


Fig. 41 *Eucorethra*

C. Chang

DISCUSSION

Although capable of being retracted, the larval labiohypopharynx is only a passive participant in the feeding process. In non-predatory species the organ is said to serve as an "anvil" upon which food matter is comminuted by the mandibular teeth. In predatory species the labiohypopharynx is evidently not acted upon by the mandibles and plays an unknown role during feeding.

An examination of the "anvil" in non-predatory species reveals the presence of two basic structural forms. The first occurs in the Dixinae and Anophelinae (surface feeders); the second in the Culicinae (primarily suspension and sediment feeders). In the former, the dixine hypopharyngeal malae and the anopheline premental malae are the primary areas of the labiohypopharynx used for the breakdown of food. These areas occupy the dorsal portion of the "anvil" and occlude with the numerous peglike accessory teeth (molar areas) borne on the mesodorsal margins of the mandibles (Schremmer 1950; Félix 1962). In the culicines, the ventrally-located ligula and premental teeth are the principal structures used for the comminution of large food particles. These typically occlude with the ventral teeth (incisors) of the mandibles (Gardner and Nielsen 1973).

Forms intermediate between the above types are virtually unknown. Besides dixine and anopheline larvae, mandibular accessory teeth are presently known to occur only in *Uranotaenia barnesi* (pers. obs.), *Opifex fuscus* and certain *Aedes* species (Knight 1971). Corresponding premental malae occur only in *Opifex* indicating that these structures are a primitive feature of the labiohypopharynx. The malalike structures of *Uranotaenia barnesi* (see Fig. 8) and the anopheline premental malae are homomorphic, the former being chiefly modified premental teeth.

The premental teeth and the ventral mandibular teeth which occlude with them in most culicine larvae are poorly developed in surface feeders. Since as a general rule the mandibles of nematoceros larvae have strongly developed incisors and weakly developed or no molar regions, I am convinced that the reduced incisors and the expanded molar areas of dixines and anophelines are specializations associated with the surface-feeding habit. In culicines the main ventral tooth of each mandible (ventral tooth 0 of Gardner *et al.* 1973 and Harbach and Knight 1977a) normally occludes with the ligula (Gardner and Nielsen 1973) or the prementoligular teeth. This tooth and the ligula are both well developed in anophelines indicating that the anopheline ligula is a plesiomorphic structure and that the weakly developed incisors represent a derived condition.

The numerous scalelike ventral premental processes which occur principally in the Dixinae, Aedini and Culisetini appear to be more primitive than the smaller collection of variously modified but homologous structures found in other tribes of the Culicinae. Although the premental cordate process appears to be unique to anopheline larvae, a corresponding structure may actually occur in certain culicines. It seems to be homologous with the similarly located "premental spine" of *Aedes vexans* (Pao and Knight 1970) and its possible homology with the bilobed ventral premental processes of members of the tribes Uranotaeniini, Aedeomyiini, Hodgesiini and Mansoniini was noted previously. It is possible therefore that the premental cordate process is a primitive structure which has been retained in certain taxa while the ventral premental processes have been reduced or lost.

I envision an ancestral culicid larva with (1) a somewhat hypognathously-carried prognathous head with mandibles which occluded with the prelabium and (2) a body similar to that of living dixine larvae but with prolegs and/or ambulacral combs on all abdominal segments. From this hypothetical larva, I surmise that the first steps toward the evolution of modern culicid larvae included (1) the lateral movement of the ambulacral combs of abdominal segment IX to give rise to the pectens (this may have accompanied the formation of the spiracular apparatus) and (2) the differentiation of mandibular and premental dentitions similar to those of *Opifex* but with better developed molar and malar areas, respectively. Since the spiracular lobes of extant dixine and *Chagasia* larvae bear a fringe of filaments, and since vestiges of these are present on the posterior spiracular lobes of various chaoborine, toxorhynchitine, culicine and other anopheline larvae¹, it is likely that they were a characteristic of the prototypal culicid larva. Likewise, since many dixine and *Chagasia* larvae rest with the body bent into a U and culicines assume the same attitude when they occasionally feed on the surface film (Horsfall 1955), the prototypal larva probably had the ability to assume this posture as well. The larva was probably an unspecialized feeder which obtained fragments of food from the surfaces of submerged objects, flocculent masses and the surface film. It can be assumed that food matter was reduced to fine particles between the mandibular molar areas and the premental malae before entering the pharynx.

I believe that an ancestral stock with the above characteristics gave rise to two lines, one being the progenitor of extant dixines and the other the stem group from which the other subfamilies arose. Along the dixine line the body retained many ancestral characters while the head acquired a complete prognathous condition and the mandibles and labiohypopharynx derived the specializations necessary for feeding entirely (?) on the surface film. I suspect that the dixine hypopharyngeal malae are strictly homologous with the premental malae of *Opifex* and have migrated to their present location in response to a shortening of the mandibles. Since the Dixinae acquired the surface-feeding habit early, enough time has elapsed for the malae to have moved to the hypopharynx and for the ligula, premental teeth and mandibular incisors to atrophy. Surface feeding as a primary means of obtaining food may have evolved in response to a lack of suitable nutriment as is indicated by the culicine habit of feeding at the surface under starvation conditions (Christophers 1960).

I conjecture that the aforesaid stem group (1) retained the *Opifex*-like mandibles and labiohypopharynx; (2)² developed the ability to extract suspended particulate matter out of the water; (3) lost all abdominal prolegs and ambulacral combs except those of segment VIII which moved laterally to form the

¹The vestiges occur at the outer margins of the lobes and are visible in the scanning electron microscope as corrugated or undulated membranes. Montschadsky (1930) figured these as striae in species of *Anopheles*, *Aedes*, *Uranotaenia*, *Culex* and *Culiseta*. In addition to these genera, I have observed the structures in *Bironella*, *Armigeres* and *Toxorhynchites* larvae. The margin of each lobe is set with a row of minute filaments in *Eucoethra*.

²Although living Anophelinae feed substantially on the surface film, they also remove particulate matter from suspension (Horsfall 1955). This and the recent discovery of a unique suspension-feeding chaoborine larva, *Australomochlonyx nitidus* Freeman (Colless 1977), leads me to believe that the ability to feed on suspended matter was established along this line.

combs; and (4) underwent a shortening of the abdomen and a fusion of the thoracic segments. I feel that this ancient stock gave rise to the Anophelinae and a siphon-bearing ancestor. Once formed, the siphon-bearing progenitor diverged along two lines, one comprising the subfamily Culicinae and the other the subfamily Chaoborinae.

As with the Dixinae, the Anophelinae may have become specialized for feeding largely on the surface film under stress conditions, perhaps coincident with the disappearance of large swampy areas. In addition to well developed mandibular and premental triturative surfaces, anopheline larvae developed a number of other specializations associated with surface feeding. These include the unique structures which hold the feeding larva to the water's surface, i.e., the scalelike structures on the apexes of the maxillary palpi and antennae, Nuttall and Shipley's organs on the prothorax and palmate setae on abdominal segments. The combs of abdominal segment VIII have been retained in the first stage larva only.

The evolution of a siphon in the culicine-chaoborine ancestor probably accompanied the consummation of suspension and sediment feeding.³ Concomitant with these developments, (1) the premental malae and mandibular molar areas atrophied and were eventually lost in most taxa; and (2) the elements of the mandibular brushes acquired rows of villiform processes for removing food particles from the mouthbrushes (Colless 1977; Harbach 1977). The abdominal pectens were incorporated into the siphon while the combs remained on lateral areas of segment VIII.

The subfamily Chaoborinae was probably established early as a group divergent from the Culicinae. With the one exception noted above, all Chaoborinae larvae are predatory and have lost many of the ancestral characters. These include the structures associated with suspension feeding, i.e., the mouthbrushes, combs, pectens and even the siphon in larvae of the genus *Chaoborus*. Consequently, the labiohypopharynx has been highly modified and/or reduced while the mandibles and the mandibular incisors have become strongly developed for catching and holding prey.

The subfamily Toxorhynchitinae appears to have been derived from a culicine ancestor, specifically a sabethine, for they share some characters with this tribe. Affinities between these groups are evident in the structure of the labiohypopharynx. Both have an aggregate of prementoligular teeth and similar complexes of lateral premental teeth. It should be noted that the Toxorhynchitinae are rapacious and like the Chaoborinae have lost the combs and pectens. Although reduced in number, the mouthbrush elements have been strengthened to help secure prey (Surtees 1959).

Taxonomy

The structural characteristics of the labiohypopharynx appear to be useful for separating genera but probably offer little assistance at the specific level except for the genera *Uranotaenia* and *Psorophora*. The three species examined from each of these genera are quite distinct and easily separated from

³Sediment feeding is a specialized form of suspension feeding where settled particles are stirred up by the action of the mouthbrushes and then collected from the water.

one another. The labiohypopharynges of larvae representing such genera as *Anopheles*, *Mansonia*, *Wyeomyia* and especially *Toxorhynchites* are very difficult if not impossible to distinguish even when examined with the scanning electron microscope. The morphology of the labiohypopharynx might be used for the recognition of the subgenera of *Aedes*, and perhaps those of other aedine genera.

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APPENDIX

The species examined in addition to those illustrated are listed below by subfamily and in alphabetical order.

Anophelinae

Anopheles (Anopheles) crucians Wiedemann

Chaoborinae

Corethrella laneana Vargas

Culicinae

Aedeomyia (Aedeomyia) catasticta Knab
Aedes (Ochlerotatus) taeniorhynchus (Wiedemann)
Aedes (Mucidus) painei Knight
Culex (Lutzia) bigoti Bellardi
Culex (Melanoconion) opisthopus Komp
Culex (Melanoconion) pilosus (Dyar and Knab)
Culiseta (Climacura) melanura (Coquillett)
Deinocerites pseudus Dyar and Knab
Haemagogus (Haemagogus) panarchys Dyar
Malaya sp.
Mansonia (Mansonioides) uniformis (Theobald)
Mimomyia (Mimomyia) chamberlaini Ludlow
Orthopodomyia phyllozoa (Dyar and Knab)
Phoniomyia splendida (Bonne-Wepster and Bonne)
Psorophora (Grabhamia) pygmaea (Theobald)
Psorophora (Psorophora) ciliata (Fabricius)
Sabethes (Sabethes) cyaneus (Fabricius)
Trichoprosopon (Trichoprosopon) digitatum (Rondani)
Uranotaenia (Uranotaenia) geometrica Theobald
Wyeomyia (Wyeomyia) grayii Theobald

Dixinae

Dixa sp.

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