

## HOMOLOGIES IN ELEMENTS OF THE LARVAL LABRUM IN CHAOBORIDAE AND CULICIDAE (DIPTERA)

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### Abstract

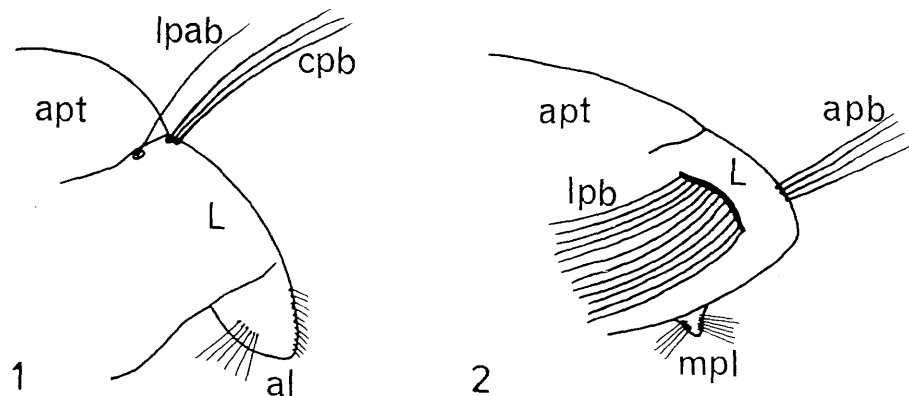
A scheme of homology is proposed under which the so-called "labrum" of *Chaoborus* larvae becomes an apical lobe of the labrum proper and homologous with the midpalatal lobe of Culicidae. Some phylogenetic implications are noted.

### Evidence and discussion

During a study of Australian Chaoboridae (in preparation), I have found that current interpretations of structures in the area of the larval labrum (e.g., Cook 1956; Saether 1970; McGowan 1976) are difficult to reconcile with those accepted for the Culicidae (e.g., Laffoon and Knight 1973); [despite some recent vacillation (Colless 1977), I now accept family status for the Chaoboridae]. As shown below, certain changes are required if a uniform terminology is to be used, reflecting homologies across these related families.

As in most Nematocera, the main dorsal plate of the chaoborid larval head is the dorsal (or cephalic) apotome, delineated laterally by the ecdysial lines (Snodgrass 1960; Hinton 1963) and including unidentifiable parts of the primitive frons and/or clypeus. In passing, I would suggest that the older term 'frontoclypeus' has been discarded rather too hastily. The functional homology remains good, since the relevant muscles still arise from the sclerite in question; and I cannot regard it as terminologically fatal that the lateral boundaries of the frontoclypeus have been variously redrawn in the endopterygote grade and that none of its boundaries is now reflected in the underlying epidermis.

In Culicoidea the apotome is usually delimited anteriorly by a ridge or sulcus, e.g. the clypeolabral suture of Culicidae [unless otherwise implied, I am following the terminology of Laffoon and Knight (1973)]. In *Chaoborus* Lichtenstein the anterior boundary seems to lie on what I shall call the *clypeal apodeme*, which lies between the antenna bases and the "postantennal filaments" and is rather weakly developed in most species. Schremmer (1950) seems to interpret it as the ventral wall of the antennal socket (cf. his Fig. 16a, *vFr*). Anterior to the apotome is a protruding area (the "labrum" of Culicidae), that is for the most part lightly sclerotised or membranous. For the present, I shall call it the *preapotomal lobe* (Fig. 1, *L + al*). In Chaoboridae it is more or less clearly differentiated into a broad, somewhat tapering basal section (Fig. 1, *L*), and a flap-, or tongue-, or finger-like apical section (Fig. 1, *al*).



FIGS 1, 2—Diagrammatic representation of structure of the labrum (lateral view) in: (1) Chaoboridae; (2) Culicidae. (Fig. 1 is based largely on *Mochlonyx*). *al* = anterior lobe; *apb* = anteromedian palatal bristles; *apt* = dorsal apotome; *cpb* = central preapotomal bristles; *L* = labrum; *lpab* = lateral preapotomal bristle; *lpb* = lateral palatal bristles; *mpl* = midpalatal lobe.

In *Australomochlonyx* Freeman (Colless 1977) and (weakly) in *Promochlonyx*\* Edwards and *Corethrella* Coquillett (Cook 1956), the basal section is sclerotised laterally (homologous perhaps with the intertorma or torma of Culicidae). In all but *Eucorethra* Underwood and *Corethrella* it bears, near the junction with the apotome, a characteristic set of what I shall call *preapotomal bristles* (Fig. 1, *lpab*, *cpb*; the "postantennal filaments", or "Labrumborsten", of *Chaoborus*, and "clypeal setae" of *Mochlonyx* Loew). In all but *Chaoborus*, these are differentiated into a central group and a pair of lateral groups; and, in all but *Australomochlonyx*, are strongly developed and flattened, and in some cases barbed. *Eucorethra* (Cook 1956) has weak setae that may be homologous with the preapotomals, but the anterior pair of strong spines seems to arise on the apotome and represent head hair l-C of the Culicidae. *Corethrella*, too, has paired, relatively strong setae, placed in a fashion that suggests homology with the preapotomals.

The apical section of the chaoborid preapotomal lobe is invested dorsally with hairs or scales that may be concentrated in sublateral tufts (e.g., *Chaoborus*); ventrally, it bears paired tufts, fans, or brushes of setae or scale-like processes, and often one or two pairs of spines (see figures in Schremmer 1950, and Cook 1956). In *Chaoborus*, this section alone is traditionally interpreted as the labrum (e.g., Cook 1956; Sæther 1970; McGowan 1976), in which case the basal section must be interpreted as an extension of the apotome, continuing across the clypeal apodeme. On the other hand, Cook (1956) explicitly refers to the whole preapotomal lobe of *Mochlonyx* and *Eucorethra* as the homologue of the "labrum" of *Chaoborus*.

This is unacceptable, principally because of the preapotomal bristles. There is no reason to doubt their homology in *Chaoborus* and *Mochlonyx*, a conclusion strongly reinforced by their rather intermediate nature in *Promochlonyx* (to be described elsewhere). Cook (1956) himself regarded the homology as 'probable', and any other interpretation would be distinctly unparsimonious. It would be quite inconsistent, then, to place those bristles on the labrum of *Mochlonyx*, etc., but on the dorsal apotome of *Chaoborus*. In addition, it seems more likely that the clypeal apodeme represents an invagination of the anterior margin of the apotome rather than some intermediate part of that sclerite; and in any case the differentiation of the preapotomal lobe into basal and apical sections seems convincingly homologous across all chaoborines.

The problem that remains is to interpret that differentiation in general terms and establish a uniform terminology for Chaoboridae and Culicidae. In this regard, the detailed study by Schremmer (1950), and the relationships that he inferred, seem to me very convincing. The main points that emerge are: (a) on the basis of external structure, chaetotaxy, musculature, and function, the "labrum" of *Chaoborus* is homologous with only the midpalatal lobe of the culicid "labrum" (Fig. 2, *mpl*; called 'epipharynx' by Schremmer); (b) the entire preapotomal lobe in Chaoboridae thus remains as the homologue of the "labrum" in Culicidae (Fig. 2, *L*). My own studies confirm that (a) applies to the apical section of the preapotomal lobe in other chaoborids; and as regards *Australomochlonyx*, I had independently arrived at this conclusion (Colless 1977) before reading Schremmer.

I also see no reasons for rejecting (b) above, and some points that confirm it. For instance, Schremmer (1950) demonstrates a close correspondence between the preapotomal bristles of *Chaoborus* and the anteromedian palatal brush of *Anopheles* Meigen (see his Fig. 8). The correspondence is even more striking in the case of the central group of preapotomals in *Mochlonyx*, *Promochlonyx*, and also *Cryophila* Edwards (Edwards, 1932, Plate 4, fig. 13), all of which are barbed as in *Anopheles*. One might speculate that the lateral palatal brushes of Culicidae are represented by the lateral preapotomals in *Mochlonyx*, etc., the tormal sclerites and muscles being now lost (or perhaps never developed; see below).

Schremmer (1950), for reasons that are not clear, restricted the term 'labrum' in *Chaoborus* to denote only the preapotomal bristles and the plaque on which they stand.

\*The larva of *Promochlonyx* will be described in a forthcoming publication.

Accepting that the labrum is a *lobe*, not just a dorsal sclerite, I see no reason to follow him in that regard. But there do seem good reasons for regarding the basal and apical sections of the chaoborid preapotal lobe as homologues of the culicid "labrum" and its midpalatal lobe. The question now remains: what are the homologies of these parts to those of the generalised insect?

There seem just two possibilities: (a) the apical section of the chaoborid preapotal lobe, and consequently the culicid midpalatal lobe also, represent the "true" labrum, the basal section (and the culicid "labrum") representing a preclypeal or clypeal structure; or (b) the basal section (etc.) represents the labrum and the apical section a ventral palatal lobe, as currently seen in Culicidae. The first suggestion, although somewhat revolutionary, is not to be dismissed too lightly. In its musculature, with extensor and retractor muscles, and its position as the (morphologically) anterior, dorsal lobe of the head capsule, the apical section of the preapotal lobe is remarkably like the labrum of, say, Orthoptera (compare Schremmer, 1950, fig. 6, with Snodgrass, 1935, fig. 60a and 1960, fig. 20). This could be fortuitous; but it is not hard to envisage a course of evolution in the culicid larva, whereby a clypeal region became greatly enlarged to accommodate the massive development of the "mouth-brushes", with concurrent, ventral migration of the labrum to provide a more effective feeding organ (its function is discussed by Schremmer 1950).

It is generally agreed that homology, no matter how "operational" (Sneath and Sokal 1973), should be consistent with accepted phylogeny (Simpson 1961). In that regard both the foregoing alternatives have problems. The close correspondence between labral (and especially palatal) structure in the Culicidae and the related Chironomidae (Cook 1944) argues strongly for possession of similar structure in their common ancestor. If we accept that the Chaoboridae are phyletically closer to the Culicidae than are the Chironomidae, we should also accept that the chaoborid-type labrum is derived from the culicid-type, rather than vice versa (the apparently "primitive" structure being a secondary development). Nonetheless, this raises the awkward problem of just how well-based is that phylogeny, and whether the resemblance between Culicidae and Chaoboridae may not be "primitive" (symplesiomorphous; Hennig 1966); i.e., Chaoboridae + Culicidae represents a paraphyletic group (Hennig 1966). It is notable that Chironomidae differ from Chaoboridae and Culicidae mainly in the *absence* of structures such as wing veins, biting mouthparts, larval siphon, etc.; and when we recall the "primitive" chironomid *Archaeochlus* Brundin with, inter alia, its mandibulate proboscis (Colless and McAlpine 1974) and functional larval spiracles (Brundin 1966), it becomes quite credible that the common ancestor of the Culicomorpha had many of the distinctive features of today's Chaoboridae; i.e., that the latter (or parts thereof) represent a separate, conservative, "primitive" stock.

However, we do not at present have a firm enough picture of culicoid phylogeny to support either of the above alternative schemes of homology. The second alternative (of labrum plus palatal lobe) represents an interpretation now so well-entrenched in the much-studied Culicidae that nothing short of impeccable evidence is likely to upset it. So, on pragmatic grounds, I propose to follow it. However, it would seem rather absurd to call the apical section of the chaoborid-preapotal lobe the 'midpalatal lobe', as in Culicidae; so I propose that it be called the *apical lobe* of the labrum. When relevant, the points discussed above could be borne in mind.

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