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Autor: Marzo, L. de / Nilsson, A. N.
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Morphological Variation and Fine Structure of Some Head Structures in Larvae of Dytiscidae (Coleoptera)

by L. De Marzo & A.N. Nilsson

Abstract: A survey, including unpublished data, is presented of the comparative morphology and fine structure of the following head structures of dytiscid larvae: fronto-clypeal region, clypeal marginal setae, glandular organs of epipharynx, premaxillary lobes, cibarial pubescent area, mandibular grooves, and frontal closure of the cibarium. The evolutionary trends found in these structures are discussed.

Key words: Coleoptera Dytiscidae – larvae – comparative morphology – head – feeding apparatus – evolutionary trends.

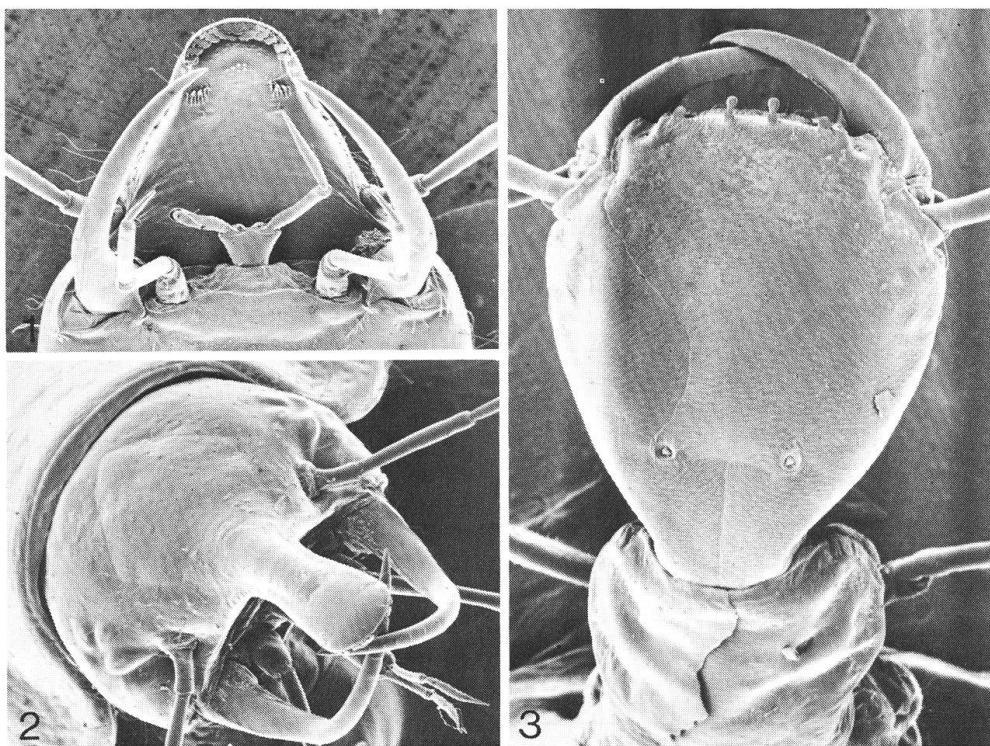
1. Introduction

In dytiscid larvae, the feeding apparatus evolves towards the piercing-sucking form and becomes much improved. The external digestion of the prey is generally carried out in a very specialized way. The mandibles, because of the very different specialization of their grooves, provide more direct evidence of the evolution of the feeding apparatus in this family. Other structures, directly or indirectly involved in the feeding function, also have evolved. The aim of this paper is to document the variability of the organs and to draw attention to some enigmatic points.

2. Observations and discussion

2.1. Fronto-clypeal region

Two main evolutionary trends, related to different evolution of the mandibles, affect the head shape of dytiscid larvae. The primitive shape in the family can be thought to be that of *Copelatus* (DE MARZO, 1976a, Fig. 2): subsquare, with a moderately broad clypeal margin and a large occipital orifice.



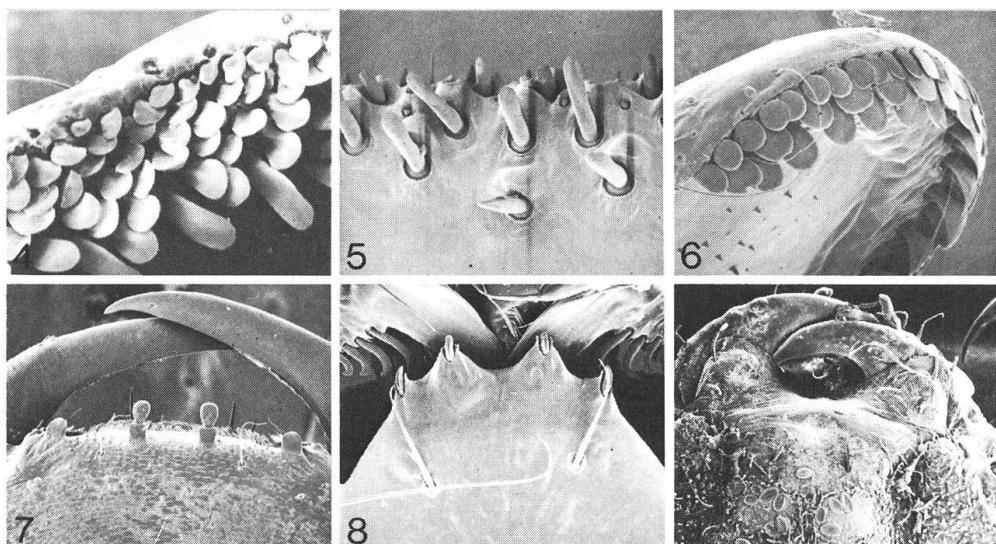
Figs 1–3: Head of larva: 1, *Hydroporus limbatus*, third instar, ventral view. 2, *Hyphydrus aubei*, third instar, dorso-anterior view. 3, *Laccophilus minutus*, first instar, dorsal view.

The first trend is oriented towards the broadening of the clypeal margin, and occurs in both the Colymbetinae (DE MARZO, 1974, Fig. 2) and the Dytiscinae (BERTRAND, 1928, Tab. 23, Figs 4–6). In this case the mandibles are moved in a horizontal plane. The second trend, which has been active in the Hydroporinae, has resulted in the development of the “clypeal horn” (Figs 1–2). In this subfamily the mandibles are moved in two oblique planes, and the prey items are very efficiently held with the help of the horn.

At the origin of these divergent trends we may hypothesize a particularly large plasticity, from a genetic point of view, of the fronto-clypeal region, so that the evolution was promoted. We can get an intraspecific example of such a plasticity from the larvae of *Laccophilus*. In this genus, the fronto-clypeal region is subtriangular in the second and third instars (DE MARZO, 1979b, Figs 2, 10), as it is in Colymbetinae and Dytiscinae, but it exhibits in the first instar (Fig. 3) a markedly different shape, with a posterior prolongation where the frontal tubercles are located. Such an arrangement of this region is closely suggestive of that of the Hydroporinae (DE MARZO, 1977b, Figs 2, 7, 10, 15).

2.2. Clypeal setae

The clypeal margin in dytiscid larvae is usually provided with a characteristic row of setae (BERTRAND, 1928, Figs 13–31). In most cases they are flattened, oar-like (Figs 4–6), sometimes they are bristle-like (*Cybister*). A preliminary study of their fine structure in *Agabus bipustulatus* (L.) and *Dytiscus marginalis* L. shows both the compact structure (without cavity inside) of their free part and the presence of nervous material at their base. As already suggested from their flattened shape, they are most probably mechanoreceptors, and possibly they sense water movements, such as those produced by prey.



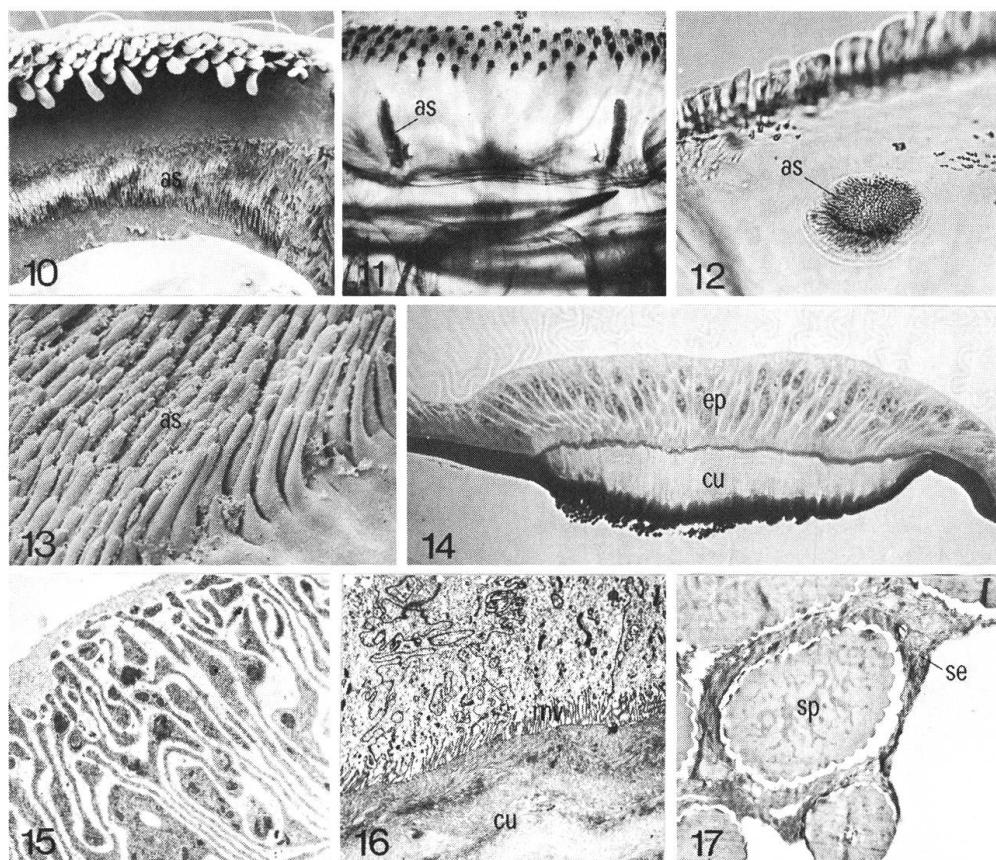
Figs 4–9: Clypeal marginal setae of larva: 4, *Colymbetes fuscus*. 5, *Dytiscus marginalis*. 6, *Hyphydrus aubei*. 7, *Laccophilus minutus*, first instar. 8, *Aulonogyrus* sp. 9, *Haliplus* sp.

As general rule, their number is lower in the first-instar larva of each species and increases (two or three times) in the second and third instars, because more setae are added in between. Usually, the number is not lower than 10, and the basic number in the family seems to be 12, as in the first instar of *Copelatus* (DE MARZO, 1976a, Fig. 7). However, an abrupt reduction in the number of the clypeal setae occurs in the first-instar larva of *Laccophilus* (Fig. 7), which has only two oar-like setae and two bristle-like ones along the clypeal margin. In the second and third instars of *Laccophilus* the setae are, on the contrary, numerous, in accordance with the general rule (DE MARZO, 1976b, Figs 2, 10). We think that the first-instar larva of *Laccophilus* exhibits the primitive low number of clypeal setae within the Hydradephaga, as in some Gyrinidae (Fig. 8) and Haliplidae (Fig. 9). It is very interesting to note

that the primitive pattern of *Laccophilus* also can be seen in the genus *Lancetes* (BRINCK, 1978, Figs 1–2).

2.3. Glandular organs of epipharynx

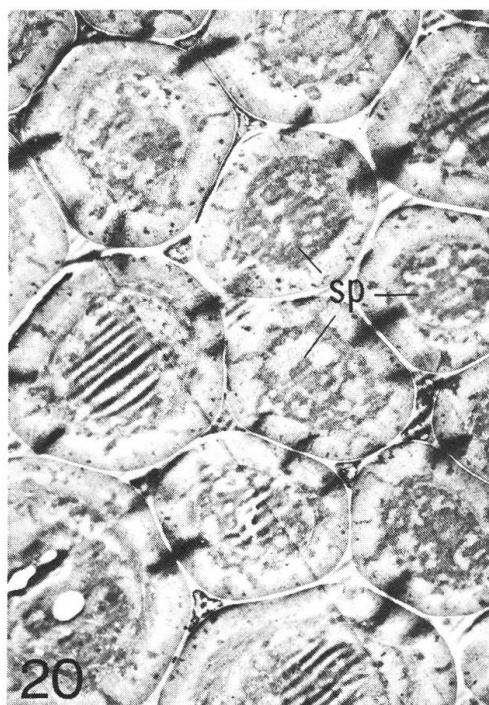
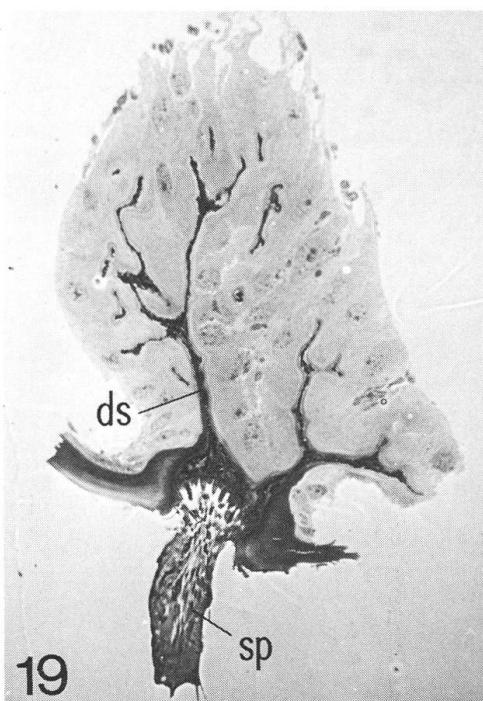
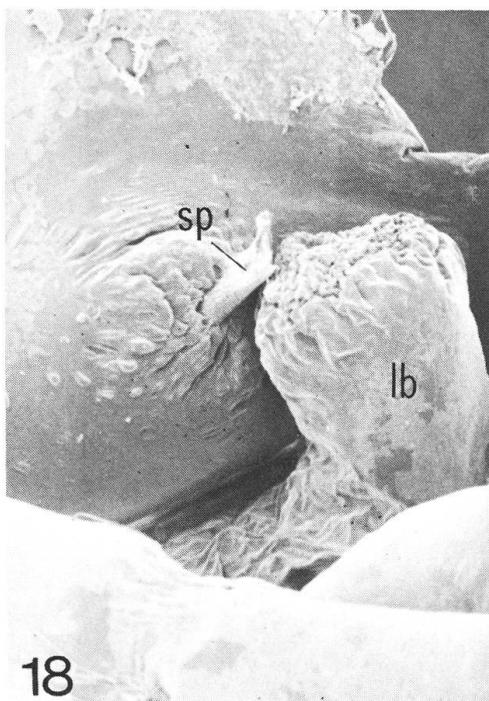
In dytiscid larvae the ventral surface of the head, between the clypeal margin and the frontal closure of the cibarium, is usually adorned with numerous minute spinulae (BERTRAND, 1928, Figs 35–43). In some cases the spinulae are arranged in a single transverse band (Fig. 10). Otherwise there are two distinct spinulose areas with more or less defined borders (Figs 11–12), located just where the tip of the opposite mandible touches the head surface.



Figs 10–17: Spinulose areas (as) of epipharynx and corresponding epithelium (ep) in larva: 10, *Colymbetes fuscus*. 11, *Hydaticus exclamationis*. 12, *H. transversalis*. 13–17: *Dytiscus marginalis*: 13, Detail of spinulae. 14, Cross-section of epithelium (ep) and cuticle (cu). 15, Detail of epithelium. 16, Microvilli (mv). 17, Cross-section of spinulae (sp).

In certain taxa (*Acilius*, *Colymbetinae*, *Hydroporinae* and *Laccophilus*) the corresponding epithelium does not show evident peculiarities compared to that of other head regions, and the spinulose layer

could merely be a reinforcing structure that protects against mechanical and chemical wear to the cuticle caused by eating. But in most



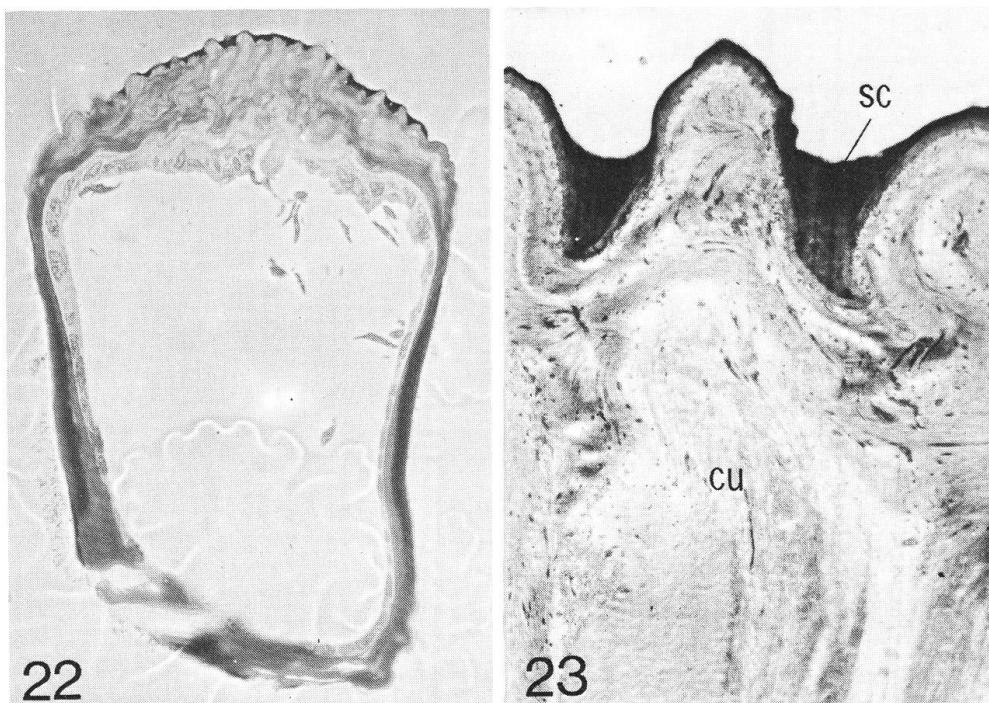
Figs 18–21: Epipharyngeal bristle-brush and corresponding epithelium in larva of *Cybister lateralimarginalis*: 18, Bristle-brush with spinulae (sp) and premaxillary lobe (lb). 19, Longitudinal section with spinulae (sp) and secretory ducts (ds). 20, Cross-section of spinulae. 21, Microvilli (mv) of the glandular cells.

Dytiscinae (*Cybister*, *Dytiscus*, *Eretes* and *Hydaticus*) it is evident that the two areas constitute specialized organs (DE MARZO, 1979, Figs 5, 11, 14). For example, in *Dytiscus marginalis*, both a thick layer of soft cuticle and a cap of large epithelial cells correspond to the spinulose region (Figs 13, 14). The cuticular layer increases 3–4 times in thickness during each instar. A secretion is produced by the cellular cap and is discharged through the cuticle. The cells have large nuclei, are strongly digitated towards the basal membrane and show a very rich system of microvilli (Figs 15–17).

In *Cybister* the glandular function of the homologous organs is also evident, based on morphological considerations. The spinulae form a bristle-brush (Figs 18, 20) at which level the cuticle is deeply invaginated and gives rise to branched secretory ducts (Figs 19, 21). At present we can only provide tentative hypotheses on the functional significance of the secretion: (1) it is a detergent substance for the mandible tips, (2) it is poisonous to prey, and (3) it attracts prey.

2.4. Premaxillary lobes of *Cybister*

In all the known larvae of *Cybister* the head has a pair of characteristic protuberances, located just anterior to the insertion of the maxillae



Figs 22–23: Longitudinal section of premaxillary lobe in larva of *Cybister laterimarginalis*. 23, Detail with soft cuticle (cu) and secretion (sc).

(BERTRAND, 1928, Fig. 47; DE MARZO, 1979, Fig. 13). The protuberances are positioned so that the tip of the opposite mandible can touch their apex, and the latter nearly touches the glandular bristle-brush of the epipharynx (Fig. 18). From a morphological point of view these protuberances are unarticulated productions of that part of the head that gives rise to the floor of the cibarial meatuses.

We have carried out a study of the fine structure of these protuberances. Their lateral walls are made up of stratified cuticle and ordinary epithelial cells, but the distal wall is made up of a thick layer of soft cuticle, and a hypertrophic epithelium corresponds to it (Figs 22–23). The apical surface is strongly irregular and an unidentified substance, it may be secretion, fills the depressions.

In our view, these lobes could, in addition to the glandular brushes, represent further glandular organs of the head, equally related to the mandibles with regard to their (unknown) function. Otherwise, they could represent collectors for the secretion of the glandular brushes.

2.5. Cibarial pubescent area of the Agabini

In most larvae of the Agabini the sucking chamber of the head is equipped with: (1) a transverse comb of the floor, and (2) a pubescent area on the ceiling (DE MARZO, 1983). A direct relationship has been observed between the number of the comb spinulae and the density of the pubescence. Within dytiscid larvae, such an arrangement of the sucking chamber is only found in the tribe Agabini, but a somewhat similar one is present in larvae of Gyrinidae (DE MARZO, 1983, Fig. 4A).

The histology and fine structure of the pubescent area, examined in *Agabus bipustulatus* (Fig. 24), suggest that it could be a glandular one. Both a thick layer of soft cuticle (which can be easily crossed by substances) and large epithelial cells correspond to it. Anyhow, from a mechanical point of view, comb and pubescence together appear to be a filtering apparatus, variably improved in the tribe.

Now let us postulate a hypothesis: because agabine larvae mainly feed on larvae of Culicidae and Chironomidae, which are sometimes infested by Nematodes, such a filter may be useful to prevent these parasites from entering the alimentary canal. The same consideration can be applied to gyrinid larvae. The entry of parasites into the sucking chamber is possible in Agabini because their mandibular grooves are entirely open. In other dytiscid larvae the barrier to Nematodes is provided by the narrow anterior orifice, obviating the need of a cibarial filter.

2.6. Mandibular grooves

Obviously, in dytiscid larvae the evolution of the mandibles is first of all linked to an improvement of the external digestion. In the recent larvae we can observe several evolutionary steps of the mandibles with-

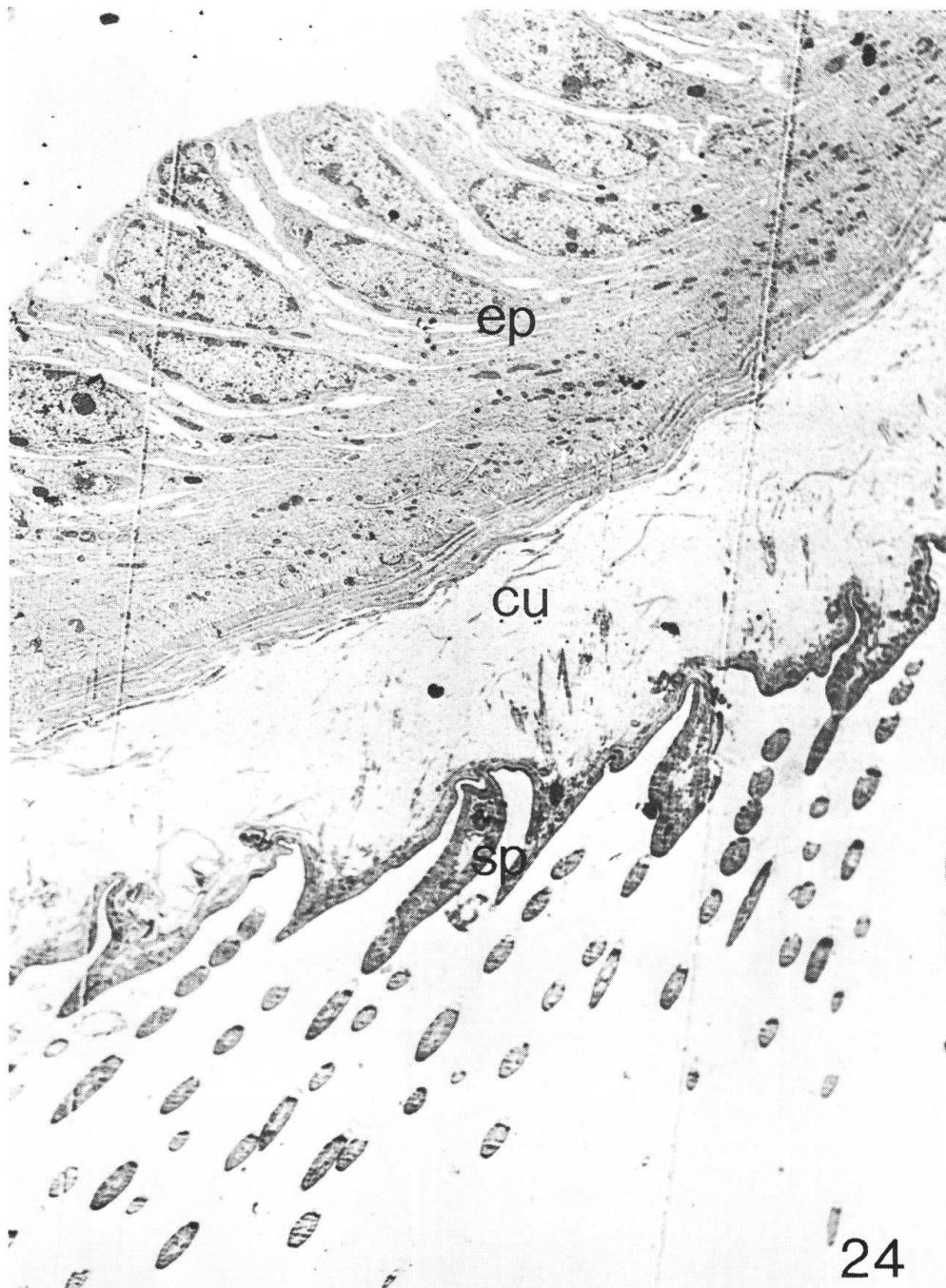


Fig. 24: Longitudinal section of cibarial pubescent area in third-instar larva of *Agabus bipustulatus*; note soft cuticle (cu), epithelium (ep) and spinulae (sp).

in the family, including an early stage of the development of the grooves: –*Copelatus* exhibits a very primitive form of mandibles (DE MARZO, 1976c, Fig. 2), without grooves and strongly serrated; –*Agabetes* has primitive, widely open mandibular grooves (1.c., Fig. 10); –in most Agabini and *Colymbetes* the groove lips are close to each other in their median part, but they are not in touch (l.c., Figs 3–5), so that the grooves are still open along their whole length; –in *Rhantus* the lips are in touch along their median part, but there is not fit between them (1.c., Fig. 6).

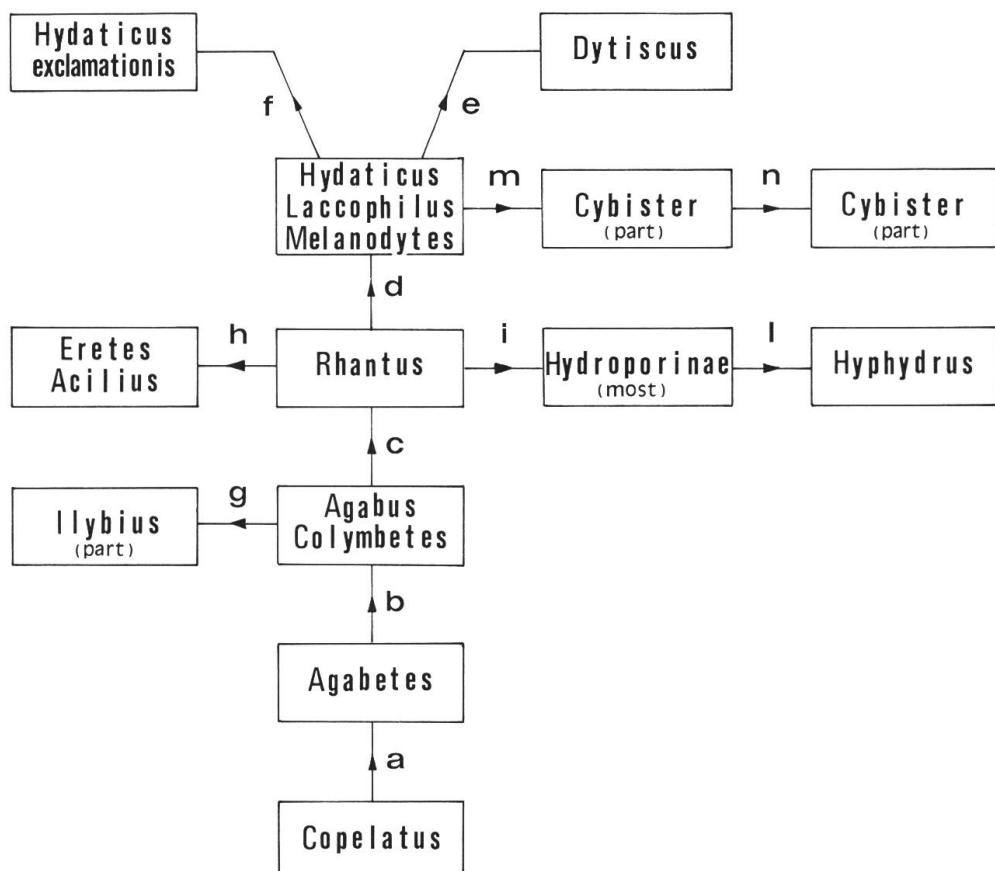
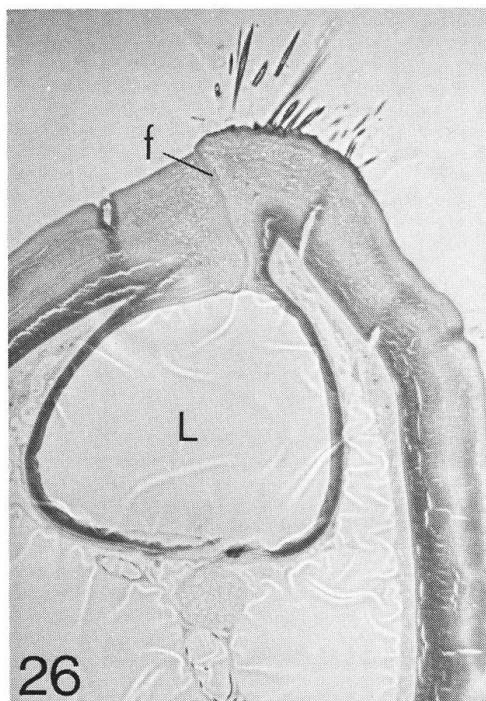


Fig. 25: Supposed evolutionary table of the mandibles in dytiscid larvae. Description of the steps: (a) the groove is sketched, a pubescence appears on the ventral lip of the groove; (b) the groove lips draw nearer to each other; (c) the lips touch each other, the pubescence moves forwards; (d) the mandibles become more and more slender, the mutual fit of the lips improves; (e) a comb of spinulae appears along the ventral lip; (f) the mandibles become strongly curved; (g) the mandibles become more slender, the pubescence disappears, the fit between the groove lips does not improve; (h) the mandibles tend to recover biting power; (i) the mandibles bend out of the horizontal plane; (j) the pubescence of the ventral lip disappears, a valve-like structure of the anterior orifice appears; (k) a pubescence appears on the dorsal lip, the lips fuse with each other; (l) a subapical crown of setae appears, the mandibles tend to lose the slender shape.

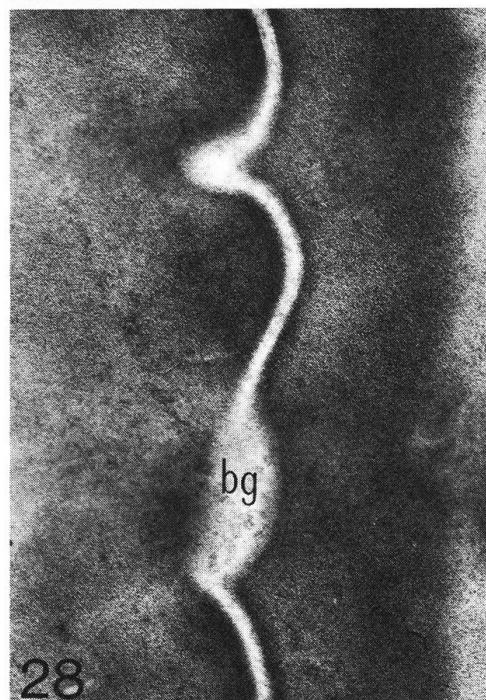
Subsequent evolutionary steps have fundamentally resulted in a lenghtening of the mandibles, and an improvement of the fit between



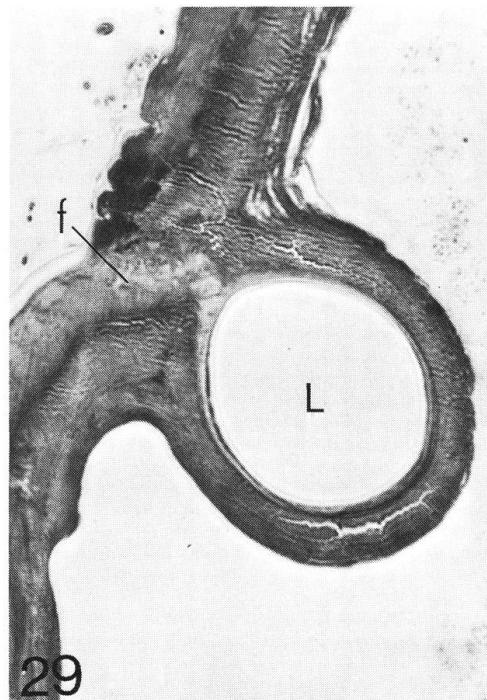
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Figs 26–29: Fused area (f) between lips of mandibular groove (L) of larva: 26–28: *Cybister lateralimarginalis*: 27, Detail of fused area. 28, Close-up of bridge (bg) of cuticular substance between the groove lips. 29, *Lampyris noctiluca*.

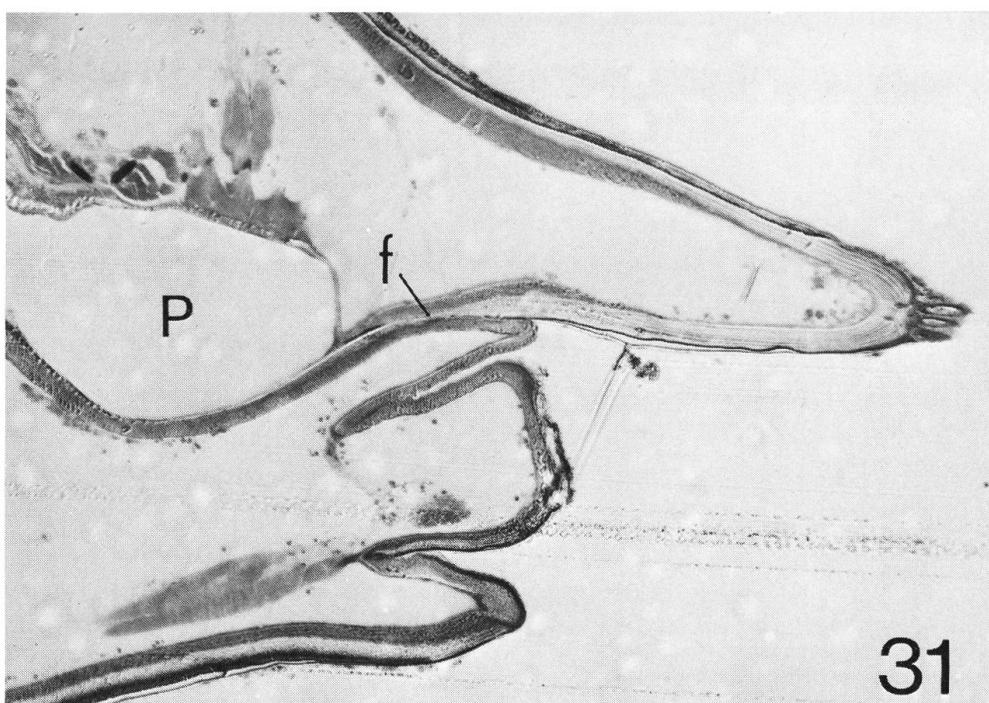
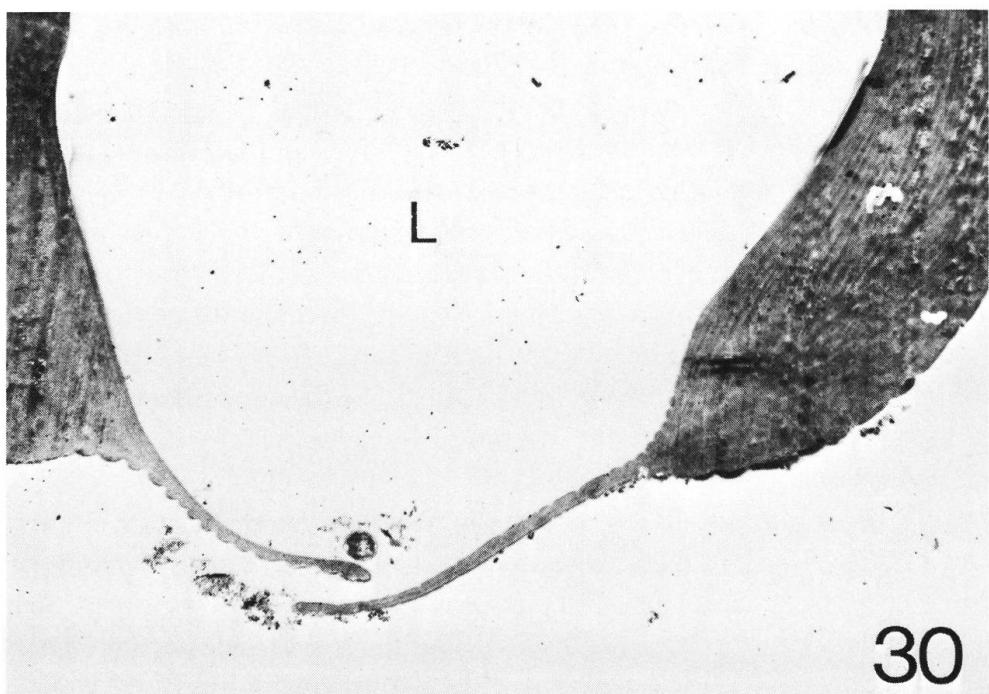
the groove lips. In spite of this, a recovery of a chewing function seems to occur in *Acilius* and *Eretes* (DE MARZO, 1977a, Figs 4–5), and a secondary loss of slender shape seems to occur in some *Cybister* species.

Considering the improvement of the grooves and looking at smaller morphological details (e.g. the pubescence of the ventral lip), we have in figure 25 sketched a simplified evolutionary table of the different forms of mandibles. We could discuss this table in detail, but will concentrate our attention to two branches, where particular evolutionary events take place: (m-n) in *Cybister* the fit of the groove lips is apparently simple (Fig. 26) because the two surfaces are flat; but a very high stability of the closure is in reality assured by a structural fusing by means of bridges of cuticular substances (Figs 27–28); such a fusion is clearly analogous to that which we find in the grooved mandibles of *Lampyris* larvae (Fig. 29); (l) in *Hyphydrus aubei* Ganglb., both the dorsal and the ventral lips of the anterior orifice bear a thin and flexible plate (Fig. 30); undoubtedly these plates bend when liquids cross the anterior orifice and possibly they act together as a filtering apparatus to prevent large food particles from entering and obstructing their very thin canals.

2.7. Frontal closure of cibarium

It is common knowledge that most dytiscid larvae have a powerful cibarial-pharyngeal sucking chamber, which is open at the sides towards the mandibular grooves but anteriorly closed. This frontal closure is variously arranged, and it improves stepwise as do the mandibular grooves. It is absent in *Copelatus*, a genus that lacks grooves (DE MARZO, 1979, Fig. 33). It is primitive in *Agabus* and *Ilybius*, where a simple approach between the dorsal and ventral surfaces of the cibarium is present (1.c., Figs 29–30), and the larvae prevent the frontal loss of digestive fluids by pressing the prey against their head during the meals.

In subsequent evolutionary steps a morphological adaptation between the two surfaces occurs and is highly improved upon. The evolutionary parallelism between the frontal closure of the sucking chamber and the closing of the mandibular grooves is highly evident in *Cybister*. The frontal closure is apparently simplified, but, in reality, it shows the same cuticular fusion that we found between the lips of the mandibular grooves (Fig. 31).



Figs 30–31: Larva: 30, Anterior orifice of mandibular groove (L) with flexible plates in *Hyphydrus aubei*. 31, Frontal closure of cibarium (P) in *Cybister lateralimarginalis*; note fused area (f) between cibarial lips.

3. Conclusive remarks

The radiation of the Dytiscidae has most probably included evolutionary shifts to the utilization of different prey organisms and different habitats. The feeding habits of most taxa are poorly known (see BALDUF, 1935; GALEWSKI, 1971), especially so in the tropical region. It seems that most larvae are capable of handling a broad range of prey items and size might prove to be the strongest limitation. A lot of the literature data on larval diets are from studies in aquariums, and under these unnatural conditions the resulting diets might actually be wider than in nature. To include important factors, such as competition, field studies should be pursued.

Within the Dytiscidae it is evident that the different subfamilies differ markedly in size, though the overlap cannot always be disregarded. This would suggest that there are important differences in food choice, and this is also sustained by the different structure and function of the larval feeding apparatus. Put in another way: the adaptations of the larval feeding apparatus are very important in determining the optimal size of the included species in relation to their prey items. Within the Hydroporinae the evolution of the clypeal horn might have been connected with the exploitation of microcrustaceans as a larval food base. This would allow for the relatively small size of the members of this subfamily. Microcrustaceans are also eaten by some larger dytiscid larvae (ARTS et al., 1981), but this seems to be exceptional and is reflected in special adaptations of the feeding apparatus. Though primarily designed for catching microcrustaceans, the clypeal horn together with the slender mandibles of the Hydroporinae work also for other prey, especially chironomid larvae as shown by PAJUNEN (1983) for *Potamonectes griseostriatus* (DeG.).

The larval diet of the colymbetine genera includes as its major part various Diptera larvae, especially Chironomidae and Culicidae. The feeding apparatus of the colymbetine larvae shows no striking examples of structural adaptations to this kind of food, but the preoral comb of the Agabini might be at least one example. The wide gap of the mandibles in many larvae of the Dytiscinae, such as *Dytiscus*, has also made larger prey, such as amphibian larvae and small fish, available.

Nevertheless, there are details of the feeding apparatus which escape analysis from an adaptive point of view. For example, we think that the improvement of both the closure of the cibarium and that of the mandibular grooves are neither functionally necessary nor dependent

upon specialization to certain prey. Moreover, the presence of glandular organs in Dytiscinae – highly complex in *Cybister* – suggests that important details of the feeding behaviour in these larvae have still to be discovered.

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Authors' addresses:

Dr Luigi De Marzo
Istituto Entomologia Agraria
Università, Via Amendola 165/A
I-70126 Bari

Dr Anders N. Nilsson
Department of Ecological Zoology
University of Umeå
S-901 87 Umeå