

INVITED REVIEW

THE BRANCHIAL BASKET IN TELEOST FEEDING

by

Pierre VANDEWALLE (1), Éric PARMENTIER (1) & Michel CHARDON (1)

ABSTRACT. In teleosts, feeding is effected principally by suction and food is handled by the branchial basket. Preys are carried to the oesophagus by the pharyngeal jaws (PJs). The pharyngobranchial bones constitute the upper pharyngeal jaws (UPJs) and the 5th ceratobranchial bones, the lower pharyngeal jaws (LPJs). In lower teleosts, these jaws have well-separated spindly parts attached to the neurocranium, pectoral girdle, and hyoid bar; they only transport food and LPJ activity predominates. In acanthopterygians, the PJs become stronger, the left and right ceratobranchials fuse into one LPJ, and the pharyngobranchials join together to form two big UPJs articulating with the neurocranium. In labrids and scarids, the LPJ is also joined to the pectoral girdle. In acanthopterygians, a new retractor dorsalis muscle gives the UPJs the major role in food chewing and transport. Cypriniforms have developed original PJs with strong 5th ceratobranchials opposed to a postero-ventral neurocranial plate. Small-sized preys and food particles are seized by the gill rakers, small skeletal pieces supported by the branchial arches.

RÉSUMÉ. Le rôle de la corbeille branchiale dans l'alimentation des téléostéens.

La prise de nourriture des téléostéens est surtout réalisée par aspiration et le traitement des aliments est assuré par la corbeille branchiale. Les grosses proies sont amenées à l'oesophage par les mâchoires pharyngiennes. Les pharyngobranchiaux constituent les mâchoires supérieures et les cinquièmes cératobranchiaux les inférieures. Chez les téléostéens primitifs, ces mâchoires sont grêles et formées d'éléments osseux bien séparés, suspendus entre le neurocrâne, la ceinture scapulaire et la barre hyoïdienne; elles n'assurent que le transport de la nourriture et le rôle des mâchoires inférieures est prédominant. Chez les Acanthoptérygiens, les mâchoires pharyngiennes deviennent plus fortes, les cératobranchiaux gauche et droit fusionnent en une mâchoire pharyngienne inférieure unique tandis que les pharyngobranchiaux se solidarisent pour constituer des mâchoires supérieures puissantes articulées au neurocrâne. Enfin chez les Labridae et les Scaridae, la mâchoire pharyngienne inférieure est en plus articulée sur la ceinture scapulaire. Chez les Acanthoptérygiens, l'apparition d'un muscle rétracteur dorsal donne aux mâchoires supérieures le rôle principal dans le traitement et le transport de la nourriture. Les Cypriniformes ont développé des mâchoires pharyngiennes originales constituées des cinquièmes cératobranchiaux très puissants opposés à une plaque ventro-postérieure du neurocrâne. Les aliments de très petites tailles sont saisis par les branchiospines, petits éléments squelettiques portés par les arcs branchiaux.

Keywords. Teleosts - Branchial basket - Pharyngeal jaws - Gill rakers - Feeding.

In teleosts, suction feeding is the mechanism most commonly used to bring food into the buccal cavity (Lauder, 1983a). Suction involves a succession of movements of the different head components, creating a backward-moving water stream (Osse, 1969; Vandewalle and Chardon, 1981; Lauder, 1983a).

All fishes can perform suction, which is necessary to breathing (see for example Ballintijn, 1969). Breathing movements are small, however, and prey capture requires fast, ample movements. In many cases, the buccal jaws have no contact with the food.

(1) Université de Liège, Institut de Chimie, Laboratoire de Morphologie fonctionnelle et évolutive, Bâtiment B6, Sart Tilman, B-4000 Liège, BELGIUM. [P.Vandewalle@ulg.ac.be]

Between the buccal cavity and the oesophagus, the branchial basket is believed to play an important role in food chewing, processing, and transport.

The aim of the present simplified synthesis is to present the morphology, movements, and biological roles of the elements of the branchial basket during feeding, with emphasis on the pharyngeal jaws and gill rakers.

OSTEOLOGY

Pharyngeal jaws

In teleosts, the skeleton of the branchial basket consists of five branchial arches (Fig. □). The first three arches are complete, with a median basibranchial and, on each side, a series of bones: a hypobranchial, a ceratobranchial, an epibranchial and a pharyngobranchial. The fourth arch consists at least of paired ceratobranchials and epibranchials, and sometimes additionally of pharyngobranchials and a basibranchial (Nelson, 1969; Rosen, 1974). Hypobranchials are seldom present (Holstvoogd, 1965). The 5th ceratobranchials form the base of the lower pharyngeal jaws (LPJs), and the 2nd, 3rd and 4th pharyngobranchials (according to the case), that of the upper pharyngeal jaws (UPJs). All endochondral elements may be covered by or connected to toothed dermal plates. The inner concave faces of the epibranchials and ceratobranchials, and often those of the hypobranchials, bear two rows of small interlocking skeletal pieces, the gill rakers.

Lower teleosts

In elopomorphs, which are primitive teleosts, the branchial basket hangs from the neurocranium by levatores muscles. The pharyngeal jaws (PJs) are small (Forey, 1973; Taverne, 1974). The independent lower pharyngeal jaws (LPJs) each bear a series of small, independent toothed plates. The latter are continued by toothed plates borne by the basibranchials and basihyal. The ceratobranchials, hypobranchials, and ceratohyals also bear toothed plates. To this ventral toothed-plate array is opposed a dorsal one. Posteriorly, the almost independent pharyngobranchials associated with toothed plates constitute the upper pharyngeal jaws (UPJs). In front of them, the parasphenoid and vomers bear toothed plates (opposite those of the basibranchials and basihyal). Laterally there are also teeth on the palatines, ectopterygoids, and entopterygoids. This means that in elopomorphs, the whole buccopharyngeal cavity from the mouth to the oesophagus is a large toothed system in which the PJs are not prominent. All teeth are simple and sharp.

In the course of evolution, the number of toothed bones appears to have decreased while the PJs became increasingly important. In osteoglossomorphs (Nelson, 1968; Greenwood, 1973; Taverne, 1977, 1978), the organisation of the branchial skeleton is much like that of elopomorphs (Fig. □). The fifth ceratobranchials associated with the ventral toothed plates of the LPJs are opposed to the dorsal toothed plates, the first of which constitutes with the pharyngobranchials the UPJs. The teeth are pointed and still numerous, despite their absence on the ceratohyals, epihyals, ceratobranchials, and epibranchials; the median dorsal and ventral dentition is particularly developed (Taverne, 1977; Lauder and Liem, 1983). Samford and Lauder (1989) even view osteoglossomorphs as possessing three successive jaws: the buccal jaws, the parasphenoid-basihyal toothed apparatus, and the PJs.

The protacanthopterygians or lower Euteleostei include families such as the salmonids and esocids (Greenwood *et al.*, 1966). Their PJs are much like those of the osteoglossomorphs or elopomorphs, but their dentition is reduced in the buccal cavity and on the branchial arches (especially on the basibranchials) (Norden, 1961; Rosen, 1974; Weitzman, 1974). The

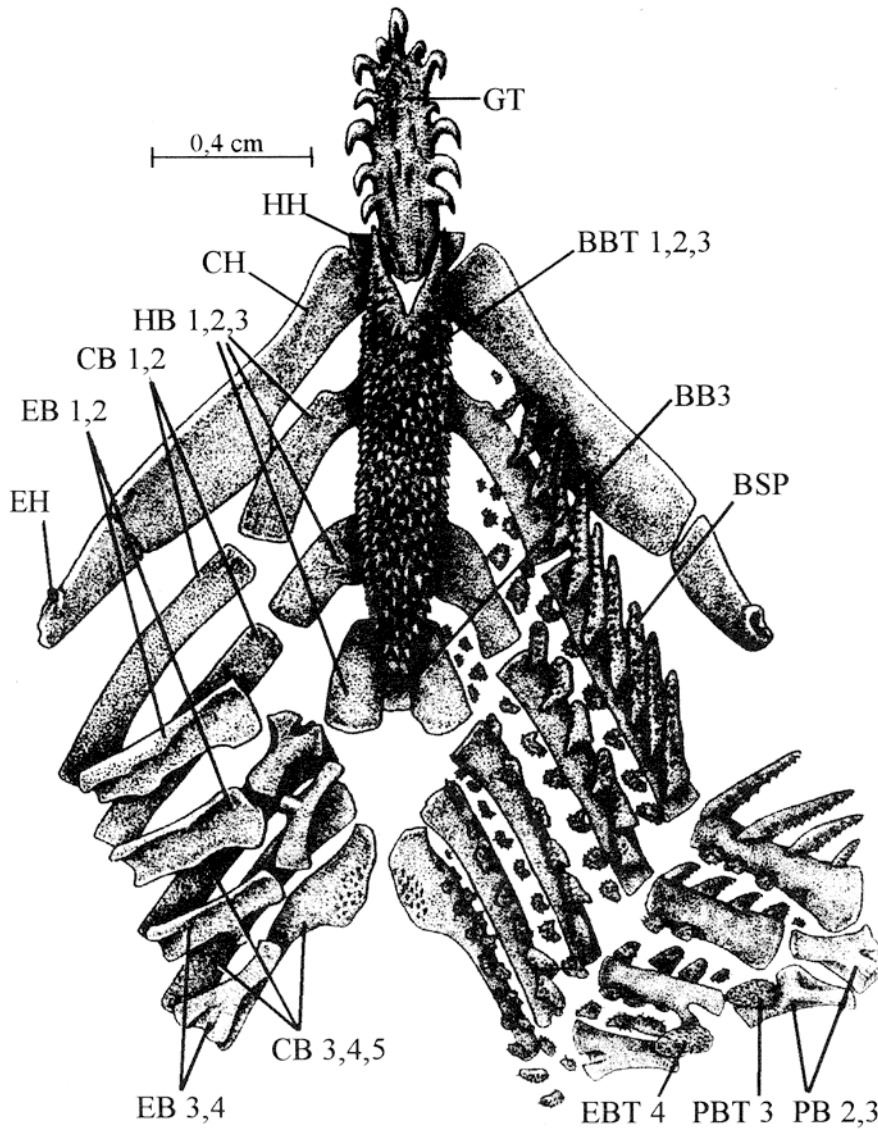


Fig. 1. Dorsal view of the hyoid and branchial skeleton of *Notopterus notopterus* (adapted from Taverne, 1978). The left branchiospines and tooth plates are removed. BB: basibranchial; BBT: basibranchial tooth plate; BH: basihyal; CB: ceratobranchial; CH: ceratohyal; EB: epibranchial; EBT: epibranchial tooth plate; EH: epihyal; GR: gill rakers; GT: gular teeth; HB: hypobranchial; HH: hypohyal; PB: pharyngobranchial; PBT: tooth plate of the pharyngobranchial; TBB: tooth plate of the basibranchials; TCB: tooth plates of the ceratobranchial elements; TPB: tooth plates of the pharyngobranchial elements.

pharyngeal dermal toothed plates are often fused with the endochondral branchial elements (Rosen, 1974; Weitzman, 1974; Lauder and Liem, 1983). This reinforces the cohesion of the PJs, although the pharyngobranchials are but loosely bound together.

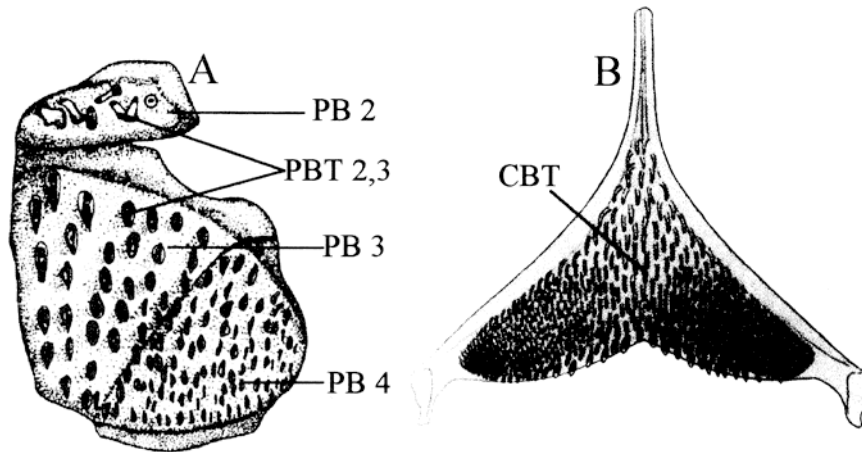


Fig. 1. A: Ventral view of the upper pharyngeal jaw of *Tilapia tholloni* (adapted from Goedel, 1974); B: Dorsal view of the lower pharyngeal jaw of *Tilapia louka* (adapted from Thys Van den Audenaerde, 1970). CBT: ceratobranchial tooth plate; PB: pharyngobranchial; PBT: pharyngobranchial tooth plate.

Higher teleosts

In acanthopterygians, which possess a protrusive mouth (Greenwood *et al.*, 1966), we observe greater development of the PJs and the disappearance of teeth in the buccal cavity.

Primitive acanthopterygians such as the centrarchids, haemulids, and serranids show few to no teeth on the parasphenoid, vomer, entoglossal, and basihyal, and above all there remain only a few teeth on the pterygoid bones (Benmouna *et al.*, 1984a; Comes *et al.*, 1988; Johnson and Fritzsche, 1989). The left and right LPJs are fused with their toothed plates, but remain free with respect to each other; they are attached to the rest of the branchial basket by their anterior ends. The UPJs consist of the second and third pharyngobranchials, each bearing a toothed plate, and of one posterior toothed plate (Liem, 1970; Rosen, 1973; Vandewalle *et al.*, 1992). The three latter bones can be associated with toothed plates borne by the second and/or third pharyngobranchials (Dineen and Stokely, 1956; Rosen, 1973; Wainwright, 1989a). The discrete elements of this functional ensemble are but loosely bound together and hang from the skull by the first pharyngobranchial and the levatores muscles. The teeth are sharp and uni- or bicuspid. They differ in size according to the skeletal element, being much smaller on the posterior toothed plate than on the pharyngobranchials (Lauder and Liem, 1983; Vandewalle *et al.*, 1992).

In more specialised acanthopterygians such as the cichlids and embiotocids, there are no longer any teeth in the buccal cavity (Vandewalle, 1972; Liem and Osse, 1975; Liem, 1978). The left and right LPJs are fused into a large triangular toothed plate (Nelson, 1967; Thys van den Audenaerde, 1970; Liem, 1973; Barel *et al.*, 1977; Witte and Van Oijen, 1990) (Fig. 2). This single LPJ is opposed to paired UPJs. In cichlids, each UPJ consists of a small, toothed second pharyngobranchial and a large ensemble formed by the third and fourth pharyngobranchials. [Note that Liem (1978) describes a fourth pharyngobranchial in cichlids, while Lauder and Liem (1983) describe a posterior toothed plate in its place]. In embiotocids, the UPJs consist of only the third and fourth pharyngobranchials (Nelson, 1967a; Liem, 1986).

The UPJs of cichlids and embiotocids articulate with a posterior ventral apophysis of the parasphenoid through their third pharyngobranchials. Their teeth are often specialised

(unicuspid, bicuspid, tricuspid, molar-like, and so on) and adapted to the diet: microphagous and planctivorous species generally have small, crowded teeth while molluscivorous species have large, rounded teeth for crushing shells (Witte and Van Oijen, 1990). The size of the PJ bones is also related to the diet. They are more slender in piscivorous than in molluscivorous cichlids (Hoogerhoud and Barel, 1978).

In labrids and scarids, the fifth ceratobranchials are fused into an often-large single LPJ articulating posteriorly with the cleithra via a synovial joint (Quignard, 1962; Liem and Greenwood, 1981; Gobalet, 1989; Monod *et al.*, 1994; Bullock and Monod, 1997). The UPJs consist of large pharyngobranchials (Monod, 1951; Nelson, 1967a). They articulate through a diarthrosis with the pharyngeal process of the parasphenoid (Kaufman and Liem, 1982; Liem and Sanderson, 1986). The teeth can be specialised as in cichlids (Yamakoa, 1978).

Hemiramphids (Aterinomorpha) have also developed strong PJs, and notably a single toothed LPJ articulating with the pectoral girdle opposite the distinct 2nd and large 3rd pharyngobranchials (Rosen and Parenti, 1981; Vandewalle, in prep.).

Ostariophysii

A parallel evolution is observed in the Ostariophysii. In characiforms, the mouth, usually not protrusive, bears many teeth, including palatal teeth (Bertin, 1958a; Roberts, 1969). The PJs are constituted by independent fifth ceratobranchials bearing toothed plates, facing toothed pharyngobranchials loosely bound to one another (Weitzman, 1962; Roberts, 1969; Miquelarena and Aramburu, 1983). The branchial basket hangs under the neurocranium (Weitzman, 1962; Roberts, 1966). The teeth are conical and differ in size and number.

In catfishes, all the pharyngobranchials present contribute to the UPJs, except for the first ones. As in characiforms, they are loosely bound to one another (Mahy, 1974; Arratia, 1987; Adriaens and Verraes, 1998).

Cyprinids have evolved a special protrusion mechanism (Ballintijn *et al.*, 1972; Vandewalle, 1978), different from that of the acanthopterygians. The buccal jaws are completely toothless (Ramaswami, 1955a, 1955b; Vandewalle, 1975). Teeth are borne only by the well-developed fifth pharyngobranchials (PJs), which alone constitute the left and right PJs (Fig. 3). These PJs are associated with a chewing pad borne by the basioccipital (Ramaswami, 1955a, 1955b; Sibbing, 1982) and acting as a UPJ (Fig. 3). The pharyngobranchials are thus excluded from the PJs. Teeth are rare, often sharp and strong, but sometimes molariform (Ramaswami, 1955a, 1955b; Vandewalle, 1975; Sibbing, 1982).

Gill rakers

Gill raker (branchiospine) morphology (Fig. 4) is related to diet and can vary not only from one species to another but even from one branchial arch to another within a species (Bertin, 1958b; Roberts, 1969; Whitehead and Teugels, 1985).

The hypo-, cerato- and epibranchials of elopomorphs bear rows of branchiospines, decreasing in size from the outside to the inside. Most of them are denticulate.

In osteoglossomorphs, the branchiospines are very similar in morphology and disposition to those of elopomorphs. There are just two rows of branchiospines per arch, except on the fifth arch, where there is only one row (Fig. 4) (Taverne, 1977, 1978).

In clupeomorphs, gill raker organisation is very complicated (Kirchoff, 1958; Monod, 1961). The gill rakers are often long and crowded, particularly on the ceratobranchials. On the epibranchials they may be transformed, forming part of a suprabranchial organ (Monod, 1961). In *Sierrathrissa leonensis* for example, no ceratobranchial or epibranchial bears more than 9 of them (Whitehead and Teugels, 1985).

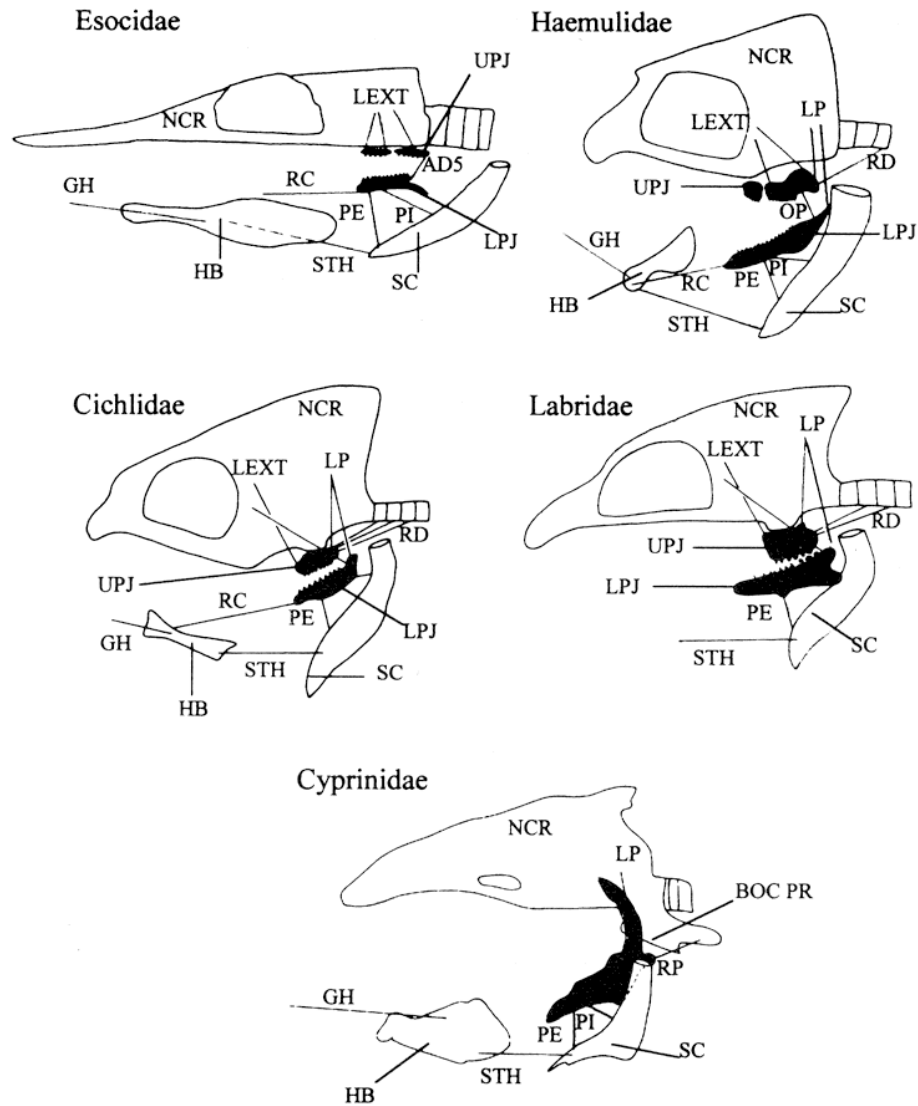


Fig. 3.15 Schematic lateral views of the neurocranium and pharyngeal jaws of Esocidae (modified from Lauder, 1983b), Haemulidae (modified from Wainwright, 1989a), Cichlidae and Labridae (modified from Liem and Greenwood, 1981), and Cyprinidae (modified from Sibbing, 1982). AD5: adductor 5 muscle; GH: geniohyoideus muscle; HB: hyoid bar; LEXT: elevator externus muscle; LP: levator posterior muscle; LPJ: lower pharyngeal jaw; NCR: neurocranium; OP: obliquus posterior muscle; PE: pharyngohyoideus externus muscle; PI: pharyngohyoideus internus muscle; RC: rectus communis muscle; RD: retractor dorsalis muscle; RP: retractor posterior muscle; SC: scapular girdle; STH: sternohyoideus muscle; UPJ: upper pharyngeal jaw.

In salmonids, the branchiospines show considerable variation (Berg, 1948; Scott and Crossman, 1973). They are more numerous and longer in planktivorous species (e.g., *Coregonus alba*) than in euryphagous ones (e.g., *Salmo trutta*). They generally bear denticles, the number and size of which are related to the diet (Hessen *et al.*, 1988).

In acanthopterygians the gill rakers also vary considerably. Only some examples are presented here. In some serranid species, the gill rakers are denticulate; their length decreases from the first to the fourth arch and they are larger on the outer than on the inner side (Benmouna *et al.*, 1984a).

In mugilids, the general organisation of the gill rakers is quite constant, but original. The angle between the inner and outer gill raker rows varies from 45° to 180°. Each gill raker bears two rows of secondary gill raker processes, which are conical, cylindrical, or flattened. On certain arches, the secondary processes in turn bear tertiary expansions constituted by projections of epithelial cells (Guinea and Fernandez, 1992).

In cichlids, the branchiospines are simple or bear a single toothed plate (Vandewalle, 1971, 1972). Moreover, there is a serrated row of microbranchiospines on the lateral (external) sides of the 2nd, 3rd, and 4th branchial arches (Greenwood, 1953; Gosse, 1956; Beveridge *et al.*, 1988).

Microbranchiospine-like structures have also been found in several other percoids (Greenwood, 1976; Stiassny, 1981).

The generally simple branchiospines of the ostariophysans vary only in size and number (Weitzman, 1962; Gauba, 1969; Lammens and Hoogenboezem, 1991). In characins, however, they are sometimes shaped like small, toothed balls (Roberts, 1969), and in some species there is only one row per arch (Roberts, 1966; Miquelarena and Aramburu, 1983).

In gonorynchiforms, considered to be closely akin to the Ostariophysi (Rosen and Greenwood, 1970; Nelson, 1994), the branchiospines are simple, but those of the last two arches contribute to supporting a suprabranchial organ quite similar to that of clupeids (Monod, 1949, 1963; Thys van den Audenaerde, 1961).

MUSCULATURE

Pharyngeal jaws

Generally speaking, the muscles related to the PJs vary little among teleosts. Some differences, however, have a major functional impact, making it necessary to consider two types of branchial musculature: that of lower teleosts and that of acanthopterygians. The list of branchial muscles presented below for the lower teleosts is based on a survey of the literature (Vetter, 1878; Dietz, 1912; Holstvoogd, 1965; Bishai, 1967; Nelson, 1967b; Greenwood, 1971; Winterbottom, 1974; Lauder and Liem, 1980; Lauder, 1983b).

Lower teleosts

There are four levatores externi inserting at one end on an epibranchial and at the other end on the neurocranium. There are two to three levatores interni extending from the second and third pharyngobranchials to the neurocranium. In most cases, these muscles lift the UPJs and shift them forward at the same time. In esocids, however, at least the first two levatores muscles draw the UPJs backward (Holstvoogd, 1965; Lauder, 1983b). Generally the levatores externi, the upper insertion of which is more external than the lower one, adduct the left and right UPJs. Two transversi dorsales, binding two left epibranchials to their right symmetricals, draw them together.

There can be an adductor between the ceratobranchial and the epibranchial of a same arch. The fifth adductor, always present, binds the fourth epibranchial to the fifth ceratobranchial. It lifts the posterior part of one LPJ (left or right).

The LPJs are adducted by two transversi ventrales extending between the left and right fourth and fifth ceratobranchials. Usually, the rectus communis joins the fifth ceratobranchial to the third hypobranchial, but interspecies variation is observed (Dietz, 1912; Nelson, 1969; Greenwood, 1971; Winterbottom, 1974). The main role of the rectus communis is to lower the LPJ. Sometimes recti ventrales join one ceratobranchial to the preceding hypobranchial.

The pharyngocleithrales interni and externi extend from the pectoral girdle to the LPJs. The pharyngocleithrales interni draw the PJs backward and the pharyngocleithrales externi draw them downward. At the same time these muscles pull the PJs apart.

It seems that the obliqui ventrales joining the first hypobranchials and ceratobranchials exert little influence on the PJs.

The sternohyoideus extending from the urohyal to the pectoral girdle may pull the hypobranchial system backward, while the geniohyoidei joining the lower jaw with the hyoid bars may pull this system forward.

In summary, the PJs are lifted by the levatores muscles, lowered by the pharyngocleithralis externus and rectus communis, pulled forward by the geniohyoideus and levatores, and pulled backward by some levatores, the pharyngocleithralis internus, and the sternohyoideus. They are brought together by the adductores and pulled apart by the simultaneous activity of the levatores and the pharyngocleithralis externus. The observed complex movements of the PJs depend on the ordered contraction of many branchial muscles.

Higher teleosts

The branchial musculature of acanthopterygians differs from that of the lower teleosts by the following features (Liem, 1970, 1973, 1978, 1986; Vandewalle, 1972; Yamaoka, 1978, 1980; Lauder, 1983a, 1983b; Benmouna *et al.*, 1984b; Vandewalle *et al.*, 1992) (Fig. 3). All the levatores externi and interni are turned forward; they lift, protract, and pull apart the UPJs. The fourth levator externus is more developed than the others. Part of it may be fused with part of the obliquus posterior (which joins the fifth ceratobranchial with the fourth epibranchial and thus works as a levator of the fifth ceratobranchial (Aerts, 1982; Liem, 1986; Gallis, 1993, 1994).

A levator posterior extends from the back of the skull to the fourth epibranchial and, thanks to this nearly vertical orientation, works as a perfect levator (Fig. 3). Like the fourth levator externus, it is sometimes fused with part of the obliquus posterior and thus also becomes a levator of the fifth ceratobranchial (Claeys and Aerts, 1984; Liem, 1986). Such is notably the case in labrids, where this muscle is often so highly developed that it inserts at the top of the skull (Yamaoka, 1978).

A big retractor posterior extends from at least the third pharyngobranchial to the ventral surface of the first vertebrae. It lifts and pulls each UPJ backward (Fig. 3). The existence of this muscle seems related to the forward orientation of all the levatores externi.

Last of all, the pharyngohyoideus (homologous to the rectus communis, according to Lauder (1983b), extends from the fifth ceratobranchial to the urohyal; the length of its fibres and the mobility of the urohyal increase the possibilities of movement of the LPJs (lowering, pulling apart the left and right parts, and even forward displacement).

Wainwright (1989b) reports that in some acanthopterygians such as the haemulids, the protractopectoralis muscle inserts on the neurocranium and on the fifth ceratobranchial, not on the pectoral girdle; it thus occupies the place of a levator posterior.

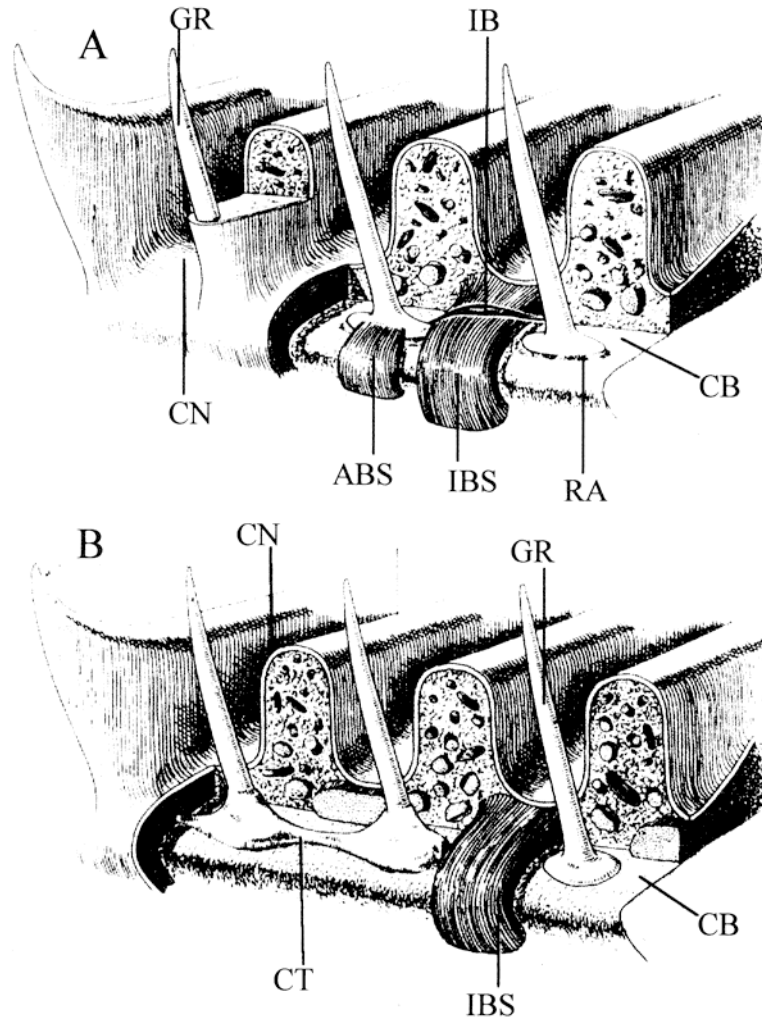


Fig. 4.11 **A**: Lateral side of the gill arch; **B**: Medial side of the gill arch (adapted from Hoogenboezem *et al.*, 1991). ABS: abductor branchiospinalis muscle; CB: ceratobranchial bone; CN: canal; CT: compact connective tissue; CU: raker cushion; GR: gill raker; IB: interbranchiospinalis muscle; IBS: constrictor canalis interbranchiospinalis muscle; LR: lateral gill raker; RA: raker articulation.

Despite a general plan common to all teleosts, the acanthopterygians possess some special muscles, the size of which suggests a more important role of the PJs in food handling. Among the upper teleosts, furthermore, the development of the pharyngeal muscles is related to diet. A fish-eating cichlid, for example, has far less bulky branchial muscles than a molluscivorous one (Hoogerhoud and Barel, 1978).

In hemiramphids, the branchial musculature differs from that of the acanthopterygians only by a retractor dorsalis of the 2nd pharyngobranchials, inserting at the back of the neurocranium (Vandewalle *et al.*, in prep.).

Ostariophysii

In Ostariophysii, the particularities of the branchial skeleton are associated with an original musculature. The branchial muscles of characiforms are much like those of the lower teleosts (Gijssen and Chardon, 1976). Cypriniforms, on the contrary, with their powerful PJ constituted only by the fifth ceratobranchials, have evolved an original musculature (Takahasi, 1925; Holstvoogd, 1965; Winterbottom, 1974; Vandewalle, 1975; Sibbing, 1982) (Fig. 3). There is an enormous retractor posterior ensemble between the PJs and the posterior process of the basioccipital, and a bulky levator branchialis 5 between the PJ and the neurocranium. Ventrally, there is a large transversus muscle, the contraction of which brings the PJs toward each other and at the same time rotates them axially so that the teeth are properly turned toward the skull (Sibbing, 1982).

Gill rakers

There are muscles associated with the gill rakers, despite past partial confusion with the branchial filament muscles (Bijtel, 1949; Hoogenboezem *et al.*, 1991). Descriptions are rare and the most thorough studies concern cyprinids (Hoogenboezem *et al.*, 1991; Van den Berg *et al.*, 1994a). Despite discrepancies between the two cited papers, we may consider for each gill raker the following muscles (Fig. 4):

-The adductor branchiospinalis is a thin sheet of fibres inserting on the side of each external gill raker (Hoogenboezem *et al.*, 1991) and, at the other end, on the base of the corresponding branchial filament (Van den Berg *et al.*, 1994a). There is no such muscle on the internal branchiospines; it would seem to be only partly distinct from the abductor filament. The abductor branchialis lowers the gill raker.

-The interbranchiospinalis, inserting via tendons on two successive external gill rakers, is described by Hoogenboezem *et al.* (1991) in 30-cm *Abramis brama* specimens, but Van den Berg *et al.* (1994a) failed to find it in two 14.9-cm (SL) *Blicca bjoerkna* specimens, *Rutilus rutilus*, and *Abramis brama*. This muscle may control the distance between successive external gill rakers.

-The constrictor canalis interbranchiospinalis is very complex morphologically (Hoogenboezem *et al.*, 1991; Van den Berg *et al.*, 1994a). It extends from the ventral side of the ceratobranchial to the bottom of a channel and up inside the walls of the same channel (Hoogenboezem *et al.*, 1991). According to Van den Berg *et al.* (1994a), its functions might be (a) to act as an abductor branchiospinalis, (b) to contract the soft tissues of the branchiospines so as to squeeze out the mucus from the caliciform cells, and (c) to straighten the channels.

MOVEMENTS AND FUNCTIONS

Among the branchial basket structures, the PJs are particularly related to a macrophagous diet, while the branchiospines are essential to a microphagous diet. In a same species the diet usually changes during growth and a same food item may be macroscopic for the fry and microscopic for the adult fish. Monophagous teleosts are few, and the diet often changes according to the season and to food availability (Boikova, 1986).

Cineradiographic and electromyographic techniques are required to observe PJ movements. Such observations are extremely difficult because of the deep positions of the very thin muscles embedded in the very delicate and highly vascularised branchial lamellae.

As it is generally assumed that the PJs play a greater role in food handling in higher

than in lower teleosts, this role has been studied more frequently in the former, and neglected in the latter.

Pharyngeal jaws

Lower teleosts

Lauder (1982, 1983b) divides food capture in *Esox niger* into four distinct phases: initial strike, buccal manipulation, pharyngeal manipulation, pharyngeal transport (including deglutition). During the initial strike, some muscles (third and fourth levatores, fifth adductor, □.) work variably, in a manner suggestive of a preparatory phase and a positioning of the PJs. During the two manipulation phases, the third and fourth levatores and the pharyngocleithrales externi and interni are active, while the fifth adductor is no longer working. As a result, the lower and upper pharyngeal jaws move apart, especially in front, as for a forward-oriented gape. These movements probably allow a good orientation of the prey relative to the PJs, ready to seize it, before pharyngeal transport.

The three periods just described are brief and devoid of cyclic events. Pharyngeal transport, on the contrary, lasts long (several minutes) and comprises repeated and rather similar cycles of muscle activity; it is the most important phase in food capture in *Esox*.

During transport, the sternohyoideus does not work, and the geniohyoideus and pharyngocleithralis are but occasionally active. The first and second levatores externi work simultaneously with the pharyngocleithralis externus, so that the upper and lower pharyngeal jaws are pulled backward at the same time (or nearly so). The third and fourth levatores externi are the antagonists of the former muscles, and protract the UPJ. However, taking into account the orientation of the levatores externi, these longitudinal movements of the UPJ seem limited. In *Elops saurus*, only the first levator is not inclined forward (Winterbottom, 1974), while in *Salvelinus fontinalis*, all the levatores are inclined backward (Lauder and Liem, 1980). It thus seems that the backward displacements of the PJs are passive (Lauder, 1983b).

The only variability observed in *Esox* muscle activity is a possible asymmetry in the activities of the third and fourth left and right levatores (Lauder, 1983b).

According to Lauder (1983b), the UPJs and LPJs of *Esox* move together backward and to the midline, then forward and sideward, but the longitudinal movements of the LPJs may be greater, as suggested by the muscles. The movements predominating in food transport seem to be those of the LPJs, and anatomical observations suggest the same for other lower teleosts (Lauder, 1983b). Prey progression results from the difference in amplitude of the longitudinal movements of the upper and lower pharyngeal jaws. The PJs simply transport the prey to the oesophagus, without crushing or otherwise transforming it.

In the osteoglossomorph *Notopterus chitala*, intermediate jaws (parasphenoid and basihyal) seem to initiate transport the prey to the oesophagus (Sanford and Lauder 1989, 1990); the PJs are probably associated with them. The parasphenoid, attached to the neurocranium, may merely hold the prey fast while the basihyals transport it by means of broad longitudinal displacements. It is thus probable that the LPJs, placed just behind the basihyals, play the main role in prey transport, as in *Esox*.

Higher teleosts

Lauder (1983b) considers the same four phases in food capture in primitive acanthopterygians as in *Esox*, but Wainwright (1989a) believes there is no pharyngeal manipulation in haemulids and that in 90% of cases only seizing and transport are present. Food would thus be brought directly to the PJs.

Pharyngeal muscle activities are recorded during the first phases of prey capture. They are probably needed to place the PJs in the right position for seizing the prey.

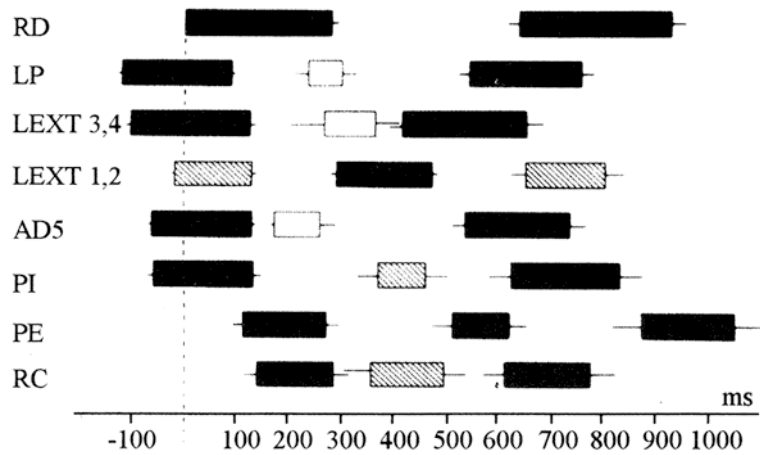


Fig. 3. Summary "block diagram" of muscle activity during pharyngeal transport in *Lepomis microchirus*. The left and right edges of the bars mark the mean time of onset and offset of muscle activity and the thin line indicates one standard error of this mean (adapted from Lauder, 1983c). Black bars indicate activity in 67-100% of all experiments, shaded bars indicate activity in 34-66% of them, and white bars indicate activity in 1-33% of them. AD5: adductor branchialis 5 muscle; LEXT 1,2: levatores externi muscles 1,2; LEXT 3,4: levatores externi muscles 3,4; LP: levator posterior muscle; PE: pharyngocleithralis externus muscle; PI: pharyngocleithralis internus muscle; RC: rectus communis muscle; RD: retractor dorsalis muscle.

During the transport phase, rather regular periodic activities of the branchial muscles are observed. The retractor dorsalis is particularly active (Fig. 3), while the sternohyoideus is often silent (Lauder, 1983b, 1983c; Wainwright, 1989a, 1989b).

A characteristic broad overlapping of the periods of activity of most muscles (Lauder, 1983b, 1983c; Wainwright, 1989a, 1989b) means that the movements of the upper and lower pharyngeal jaws are neither simultaneous nor in phase opposition, but simply asynchronous with the same frequency. The PJs thus do not move in opposite directions during part of the cycle. The UPJs are lifted (by the levator posterior and the third and fourth levatores externi), then pulled backward (by the retractor dorsalis), while the LPJs are retracted (by the pharyngocleithralis internus). Then the UPJs and LPJs are adducted (by the fifth adductor), but the LPJs are pulled forward (by the pharyngohyoideus and maybe by the geniohyoideus) while the UPJs are always shifted backward (by the retractor dorsalis). At the end of the cycle the LPJs are lowered (by the pharyngocleithralis externus) while the UPJs are protracted either by the first and second levatores externi or probably, in part, by inertia (Lauder, 1983b, 1983c). Before a new cycle begins, the PJs are actively repositioned (by the first and second levatores externi, the pharyngocleithralis externus and pharyngohyoideus) to their former anterior place, apart from each other (Lauder, 1983c). Contrary to observations on *Esox*, the UPJs play the predominant role in transporting food (Lauder, 1983b).

Lauder (1983b, 1983c) and Wainwright (1989b) think that, despite some asymmetries in the activities of the first and second levatores externi, the pattern of food transport is rather constant whatever the sort of prey (except in snail-crushing *Lepomis microlophus*). Vandewalle *et al.* (1992), on the contrary, observed major modulations of food transport movements in *Serranus scriba*. In this species, the movements of the PJs for transporting food into the oesophagus are either in phase opposition or asynchronous or simultaneous (Fig. 4).

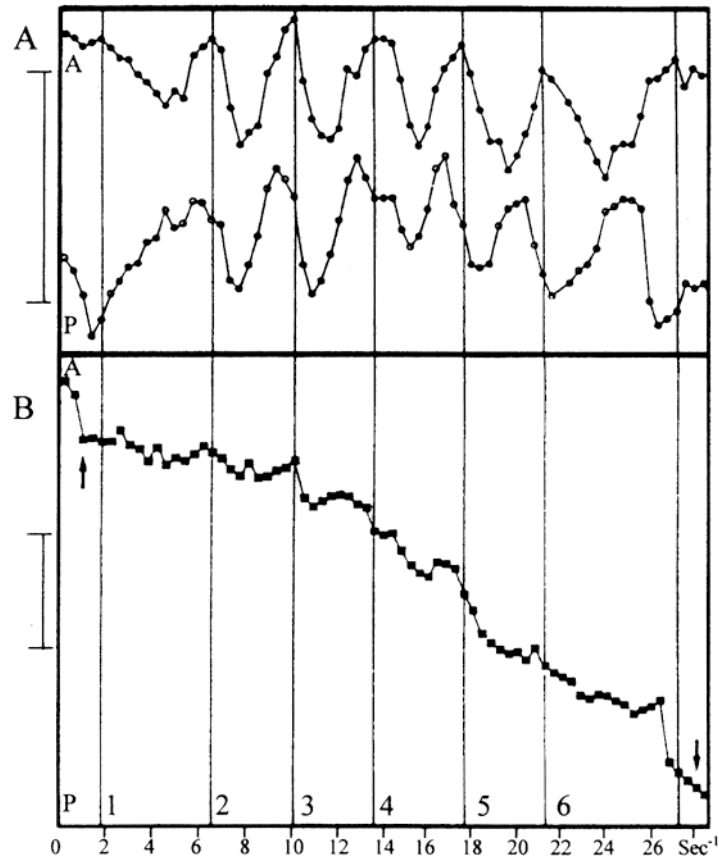


Fig. 10.11 **A**: Graphic representation of the antero-posterior movements of the left pharyngeal jaws of *Serranus scriba*; **B**: Displacement of a prey (a small fish, *Xiphophorus maculatus*) (adapted from Vandewalle *et al.*, 1992b). The maximum error on displacements is 0.4. The arrows indicate prey capture and swallowing. The vertical lines delimit the six successive anteroposterior movements of the left UPJ during prey transport. A: anterior; P: posterior.

In most cases, the cycles of the UPJs have a greater amplitude than those of the LPJs, a fact also observed by Lauder (1983b) in the centrarchid *Micropterus salmoides*. The efficiency of the transport movements is variable: transport is faster if the movements of the PJs are in phase opposition, especially if the prey is protected by hard teguments. Transport is also possible when the left and right UPJs move in opposite directions or with different amplitudes, or even when only one UPJ is working (Vandewalle *et al.*, 1992). Such different movement patterns imply equally different muscle activity patterns.

Vandewalle *et al.* (1992) further report that the three skeletal elements of the UPJs of *Serranus scriba* retain some reciprocal freedom, so that their displacements are not always identical and their reciprocal orientations are somewhat variable. The general shape of the UPJs is thus variable, showing an upward or a downward curvature, probably in response to

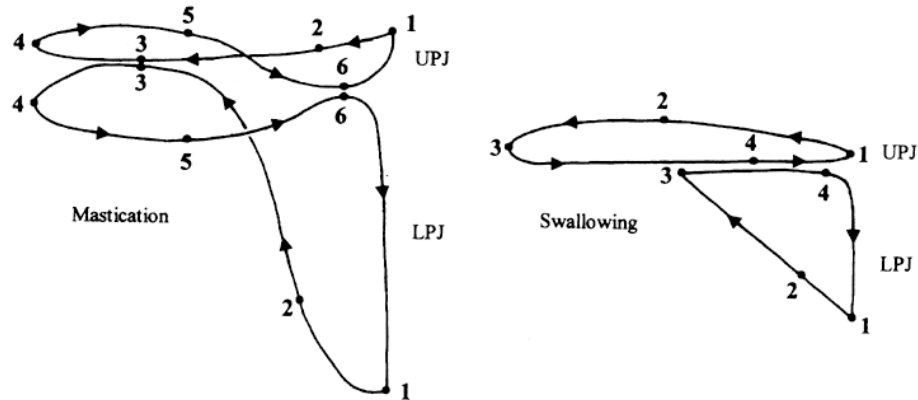


Fig. 1. Diagrammatic lateral view of pharyngeal jaw orbits derived from measurements obtained from cineradiographic film sequences of the labrid *Tautoga onitis* during mastication and swallowing. The anterior end is to the left. The orbits drawn indicate the motion of a point on the posteroventral corner of the upper pharyngeal jaw. During mastication: 1: resting positions; 1-4: shearing (activity period of the levator externus 4 and internus muscles); 4-5: transitional phase (activity period of the levator externus 4 and levator posterior muscles); 5-6: crushing (activity period of the levator externus 4, levator posterior and retractor dorsalis muscles); 6-1: recovery (activity period of the pharyngocleithrum externus muscle). During swallowing: 1-3: protraction; 3-4: retraction; 4-1: recovery. LPJ: lower pharyngeal jaw; UPJ: upper pharyngeal jaw (adapted from Liem and Sanderson, 1986).

prey particularities and behaviour. Such possibilities for deformation are likely to be shared by all teleosts provided with well-separated and loosely connected PJ elements.

The PJs of primitive acanthopterygians, protacanthopterygians, and osteoglossomorphs generally perform food transport only, through varied movements. All these possibilities of movement are related to the reciprocal freedom of the left and right, upper and lower pharyngeal jaws, and to their independence with respect to the skull and pectoral girdle. Preys are swallowed whole, without traces of injury or mechanical trituration by the PJs. The centrarchid *Lepomis microlophus* seems to be an exception in this regard. Lauder (1983c) reports that this species can break the shells of certain snails between the PJs before bringing them into the oesophagus, but other types of prey are just transported.

In higher acanthopterygians, the LPJs are fused together and the UPJs consist of very tightly bound elements articulating on the ventral surface of the skull. In cichlids, Liem (1978), Aerts *et al.* (1986), Claes and De Vree (1989, 1991), and Claes *et al.* (1991) describe cyclic movements of the PJs during feeding, but these movements follow very different patterns according to the type of food. In *Oreochromis niloticus*, an earthworm, for example, is transported to the oesophagus by regular movements of the PJs (Claes and De Vree, 1991; Claes *et al.*, 1991); the movements of the upper and lower pharyngeal jaws are in opposite directions or nearly so, and they barely alter the shape and structure of the prey (Claes and De Vree, 1991). When the same species is fed hard pellets, major masticating movements are observed. The pellets are crushed and sheared by opposite movements of the upper and lower PJs before being swallowed (Aerts *et al.*, 1986; Claes and De Vree, 1991). Gallis (1994), furthermore, shows flexible muscle activity patterns during crushing in response to changes in demand. *Haplochromis* (= *Dimidiochromis*) *compressiceps* chews small fish by in-phase movements of the PJs (Liem, 1978). This seems to be an exception. In both *Oreochromis*

niloticus and *Astatotilapia* (= *Haplochromis burtoni*), movements in phase opposition are involved in chewing the same sort of prey (Liem, 1986; Claes and De Vree, 1989). *Cichlasoma minckleyi* crushes mollusc shells by the same movements (Liem and Kaufman, 1984). Mastication may be performed preferentially by one UPJ and then by the opposite one (Claes and De Vree, 1989). Liem (1978) also reports activity periods of the pharyngeal muscles suggesting that the left and right UPJs are not always moved simultaneously. The amplitude of the handling cycles depends on the sort of prey, but the longitudinal movements of the UPJs are, as in lower acanthopterygians, more ample than those of the LPJs (Claes and De Vree, 1991).

Liem (1986) describes regular chewing cycles in embiotocids, with particularly constant muscular activity patterns whatever the food. The horizontal components of the movements of the upper and lower PJs are equal during chewing. Shearing and crushing result from in-phase movements, but during swallowing, the horizontal movements of the LPJs are clearly smaller than and somewhat in advance relative to those of the UPJs. This results in the backward displacement of the prey.

In cichlids and embiotocids there is thus pharyngeal reduction of food, distinct from food transport and swallowing. This is to be related to the partial fusion of at least the fourth levator and/or the levator posterior with the obliquus posterior (Aerts, 1982; Claeys and Aerts, 1984; Liem, 1986). These muscles transformed into levatores of the mandible, would allow more power for pressing the prey between the PJs and consequently crushing it (Liem, 1978, 1986; Liem and Kaufman, 1984).

In labrids and scarids, viewed as the most specialised teleosts (Liem and Greenwood, 1981; Lauder and Liem, 1983b; Monod *et al.*, 1994), the joint between the LPJ and the pectoral girdle causes stabilization of the LPJ, decreasing its freedom and causing its movements to be influenced by those of the girdle. The LPJ becomes a lever (Liem and Greenwood, 1981) and the muscles moving it (such as the levator posterior; Yamaoka, 1978) may be highly developed. The pharyngeal apparatus is a powerful crushing device, and movements of the neurocranium may contribute to crushing (Liem and Sanderson, 1986). Crushing cycles consist of "figure 8" movements with equal horizontal amplitudes for the lower and upper PJs (Fig. 1). The UPJ and LPJ are in phase when crushing or shearing. Characteristic large downward movements of the LPJ are observed (Liem, 1986). Swallowing movements are much like those of embiotocids (Liem, 1986; Liem and Sanderson, 1986).

The main feeding strategy of acanthopterygians is to suck in preys and handle them at the level of the PJs, but other feeding behaviours exist. For example, some cichlids crush molluscs with the buccal jaws (Witte and Van Oijen, 1990) and several sparids crush hard preys with their buccal jaws before transporting them to the oesophagus with the PJs (Vandewalle *et al.*, 1995).

Ostariophysii

In characiforms the branchial apparatus is much like that of lower teleosts, and it seems to function similarly in prey catching (Lauder, 1983a). In cyprinids, food is manipulated by the PJs with the help of the posterior floor of the neurocranium. Chewing sequences comprise trains of rhythmic cycles and end by swallowing movements. Sibbing (1982, 1991) divides each chewing cycle of *Cyprinus carpio* into three periods: a preparatory stroke, a feeding period called a power stroke, and a recovery stroke during which the skeletal elements are positioned as at the beginning of the cycle. During the preparatory stroke, the jaws are brought to a low position (principally by the pharyngocleithralis externus and rectus communis) convenient for seizing food; at this time, the gap between the floor of the skull and the jaws is wide. The period of food manipulation consists of a crushing phase and a grinding

phase. During the crushing phase, the PJs are lifted (by the levator posterior, retractor posterior, and transversus ventralis) and pressed against the basioccipital, closing the entry of the oesophagus and squashing the food. In the grinding phase the PJ are pulled backward (mainly and at least by the pharyngocleithralis internus, the retractor posterior, and the epaxial musculature), while the neurocranium rotates forward. In some chewing cycles crushing predominates, in others, grinding. At the end, the reset phase brings the PJs forward again and the skull downward (by relaxation of most muscles and contraction of the pharyngocleithralis externus). One or more chewing phases are followed by the swallowing stroke, during which the constrictor pharyngis and pharyngocleithralis externus show particular activity, while characteristic constrictions of the posterior pharynx and low-amplitude chewing-like movements are observed (Sibbing *et al.*, 1986).

In *Cyprinus carpio*, the PJ activity pattern varies according to the type of food. Not only the number and frequency of cycles may vary, but also the identity of the muscles at work. According to Sibbing (1982), the primary function of the pharyngeal apparatus is indeed chewing, but other roles are important in food mixing, lubrication, and transport.

Gill rakers

Filter feeding, (defined as feeding on prey of much smaller size than the predator (Weihs and Webb, 1983), relies on a backward water current in the buccal cavity. The current is induced by swimming while holding the mouth wide open and/or by active movements of the buccal and opercular pumps (Ballintijn, 1969; Vandewalle and Chardon, 1981) that modulate the filtration rate. In *Brevoortia tyrannus*, the swimming speed increases approximately hyperbolically with increasing prey density (Durbin *et al.*, 1981). When *Engraulis mordax* feeds on *Artemia* nauplii, it alternates two- to three-second active swimming periods during which the mouth is open with brief, passive glides during which the mouth is closed (Leong and O'Connell, 1969). Many filter-feeder cyprinids, on the contrary, swim slowly or not at all during filtration, which results from powerful ventilation-like movements (Sibbing, 1991).

The highly variable number and shape of gill rakers in teleosts are related to the diet (Zander, 1906; Bertin, 1958b; Kirchhoff, 1958; Mathes, 1963). Hyatt (1979) reports that the branchial sieve of benthic feeders is generally made of short gill rakers, while the gill rakers of zooplanktivorous fishes are long. For example, the branchiospines of *Crenicichla multispinosa* and *Abramis brama* (Vandewalle, 1971; Hoogenboezem *et al.*, 1991) are shorter than those of *Clupea harengus* (Kirchhoff, 1958). Lammens (1985), however, shows that the bream, *Abramis brama*, easily traps zooplankton.

It is generally believed that the size of the preys or particles trapped is related to the size of the sieve mesh. Fish with smaller interraker distances are expected to be able to trap smaller items (Gibson, 1988). Durbin and Durbin (1975) observed in *Brevoortia tyrannus* that the size of most preys caught was equal to or larger than the mean pore size of the sieve (80 μ m), but two percent of the preys were clearly smaller.

According to King and McLeod (1976), the branchial sieve mesh is the interval between gill rakers on each arch. This view is not in complete agreement with the two-dimensional interarch slit model (Zander, 1906), also called interdigitation model (Sibbing, 1991). In the latter, widely accepted model (for example Greenwood, 1953; Matthes, 1963), the measure of the mesh is the distance between a gill raker of the lateral row of one arch and the opposite one of the mesial row of the following arch. The interarch slit model rests functionally on the ability to modulate the breadth of the branchial slits according to the size of potential preys. In some species, the filtering efficiency is improved by microbranchiospines that can trap much smaller items (Greenwood, 1953; Gosse, 1956).

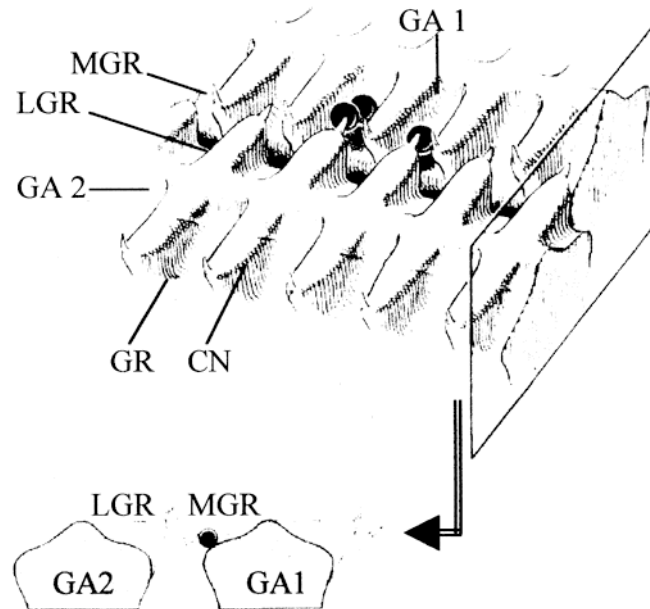


Fig. 3. The "channel model", food particles are presumably retained in a channel formed by two adjacent gill rakers. CN: channel; GA: gill arch; GR: gill raker; LGR: lateral gill raker; MGR: mesial gill raker (adapted from Hoogenboezem *et al.*, 1991).

The interdigitation model, however, does not explain satisfactorily why the bream captures preys smaller than the interarch slit. This is why Hoogenboezem *et al.* (1991) have proposed the "channel model" (Fig. 3). Each gill arch displays transverse ridges, each consisting of a cushion-like structure and a bony distal end. The space between two adjacent ridges forms a channel with a rounded bottom. The extremity of each lateral gill raker can move individually and can enter the mesial channel facing it on the next arch, and vice versa. With this structural ensemble are associated muscles (see above) that can straighten the channels and shift the lateral gill rakers down and laterally. The mobility of the gill rakers and the fact that the arches can be brought closer together might explain, notably, how the bream traps smaller particles, perhaps choosing food items individually. This interpretation gives no role to mucus in food retention.

According to Van den Berg *et al.* (1994b), the model would apply only to facultative filter-feeders that filter only small amounts of water, because it implies small-amplitude movements of the branchial arches to modulate the mesh size. It should not apply to true filter-feeding cyprinids possessing a very thin-meshed sieve, performing ample movements of the branchial arches, and filtering a large volume of water. For these, another model should be investigated. Van den Berg *et al.* (1994b) hypothesise that the particles trapped in the reduced channels stimulate the mucous cells of the walls of the channel and are encapsulated in a mucous layer, so that they stick to the wall and need no longer be retained by the lateral branchiospines. The mesh might also be reduced by the boundary layer created around the gill rakers as water is flowing through the sieve.

Sorting particles of food value is possible only if the gill rakers are particularly well equipped with taste buds and able to react individually. In the case of cyprinids, the vomero-palatine organ (on the buccal roof) can sort and aggregate in mucus strands very small

food particles, such as diatoms, so that the branchial sieve can trap them (Sibbing and Uribe, 1985).

To end this paragraph we will add more confusion to the debate by evoking the experiments of Drenner *et al.* (1987), showing that gill raker or microbranchiospine ablation does not modify at all the ability of cichlid *Tilapia galilea* (= *Arotherodon galileus*) to trap particles when filter feeding.

CONCLUDING REMARKS

1. Structural and functional comparisons of the branchial basket in teleosts reveal broad morphological diversity, albeit showing major evolutionary trends. From the Cretaceous period to the present, archaic teleosts such as the extant *Elops saurus*, whose bucco-pharyngeal dermal bones all bear teeth or toothed dermal plates, have coexisted with other teleost lineages showing various degrees of specialisation of the hyobranchial skeleton. The success of these taxa or lineages is very unequal, and one evolutionary trend has proved much more successful: the acanthopterygians, which became progressively dominant in marine waters during the cenozooid and now predominate in African rift lakes. In acanthopterygians, the PJs appear to have improved in various ways, particularly with new articulations of the PJs on the skull and scapular girdle and concomitant muscle specialisations. The most specialized orders or families (Cichlidae, Embiotocidae, Labridae) are particularly rich in species. Liem and Osse (1975) attribute the incredible adaptative radiation of cichlids in African lakes to the separation of functions in handling food between the buccal and pharyngeal jaws, allowing major adaptative transformations of both. The Ostariophysii are another group that has proven successful in fresh waters. Their main advantage could be the Weberian apparatus, more than any otherwise interesting but diverse transformations of the pharyngeal jaws, especially in cyprinids.

2. In lower teleosts, the main movements enabling the transport of food from the buccal cavity to the oesophagus are those of the ventral part of the hyobranchial apparatus. A new motor pattern appears in higher teleosts. A new muscle, the retractor dorsalis, gives the main role to the UPJs. In modern acanthopterygians, there are probably two motor patterns, one for food transport and a second for food manipulation. Cyprinid fishes show an original mechanism, supported by a new organisation of the branchial basket skeleton and musculature.

3. The notion "pharyngognathi" deserves discussion. The term was first used by Müller (1844) for a new taxonomic group including fishes whose pharyngeal bones are fused at the midline. More recently, Bertin and Arambourg (1958) used "pharyngognath" as an adjective, and Liem and Greenwood (1981) describe "pharyngognathy" in many families of higher teleosts, among which "the monophyletic assemblage" of the Pomacentridae, Cichlidae, Embiotocidae, and other Labroidei. These authors do not recognise pharyngognathy in the Nandidae, which possess hyal and parasphenoid teeth. But what about the Serranidae and Hemiramphidae? In fact, there is no morphological discontinuity in the food handling and transport apparatus from lower acanthopterygians such as serranids to modern perciforms such as scarids. This is why we propose to call "pharyngognathi", on a functional basis, all teleosts handling and transporting food with the PJs. Such a clearly polyphyletic assemblage would comprise the labrids, cichlids, serranids, maybe the lophiids... and also the cyprinids.

4. All teleosts have gill rakers that play a role in filtering water, to protect the thin secondary branchial lamellae and in some cases to catch small preys. Perhaps one should view all teleosts as facultative filter-feeders (*sensu* Van den Berg *et al.*, in press a). The branchiospine sieve is liable, in any teleost lineage, to transform into a more efficient filtering sieve, by

complexification, lengthening of the gill rakers, or reduction of the interraker distance. The very mechanism of filter-feeding remains poorly understood. It seems to be different in different species. In some cases, it seems to allow sorting of edible particles.

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