Particularities of the bucco-pharyngeal apparatus in *Zenarchopterus kampeni* (Pisces: Hemiramphidae) and their probable significance in feeding

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ABSTRACT. The present study shows several new anatomical particularities of the buccal and pharyngeal parts of the halfbeak *Zenarchopterus kampeni*. The upper buccal jaw consists of premaxillaries and maxillaries tightly joined by ligaments. A 10° lowering of the mandible leads to a 30° elevation of the upper jaw. The adductor mandibulae is reduced to bundles A^2 and $A\omega$. As in the Labridae, the lower pharyngeal jaw articulates with the scapular girdle. The upper pharyngeal jaw consists of distinct second pharyngobranchials followed by the third pharyngobranchials fused into a powerful posterior component. This part fits into and slides along a longitudinal ventral gutter of the neuroranium, thanks not only to the dorsal retractor muscles but also to specific retractors of the second pharyngobranchials. The power and dentition of the pharyngeal parts contrasts with the fragility of the buccal elements.

KEY WORDS: Pisces, Hemiramphidae, cephalic morphology, osteology, myology.

INTRODUCTION

"Halfbeak" is the common name for fish of the Hemiramphidae family containing approximately 80 species (ROSEN, 1964; COLETTE & SU, 1986; ALLEN, 1991; NELSON, 1994). It comes from the peculiar morphology of their buccal jaws: the upper jaw is short and the lower one is very long. Halfbeaks are long fish. Most species are marine and epipelagic, but some live in fresh or brackish water (ALLEN, 1991; NELSON, 1994).

Several authors have tried to establish a relationship, in fish, between the skeletal and muscular structures of the bucco-pharygeal apparatus on the one hand and feeding behaviour on the other (LAUDER, 1982; LIEM & OSSE, 1975; VANDEWALLE et al., 1995). From this point of view, the external morphology of the buccal parts of hemiramphids appears exceptional among teleosts. According to ALEXANDER (1967b), a slight lowering of the halfbeak mandible raises slightly the small upper jaw (almost) without changing the general shape of the body. This could represent an advantage for feeding at the water surface and as a means of misleading a predator by maintaining a "twig-like" appearance. The pharyngeal jaws are

also original: the 5th ceratobranchials can be fused together to form a single lower jaw with a large bony wing ventrally for insertion of fibres from the sternohyoid muscles (ROSEN, 1964), and the upper pharyngeal jaws consist of independent second pharyngobranchials and often fused third pharyngobranchials (ROSEN & PARENTI, 1981).

Data on the bucco-pharyngeal system, presented by ROSEN (1964), ALEXANDER (1967b), and ROSEN & PARENTI (1981), are not complete enough to explain several functional originalities. The aim of the present work was to complement the existing knowledge of bucco-pharyngeal morphology in hemiramphids with a study of this system in *Zenarchopterus kampeni* (Weber, 1913) (species determination according to ALLEN, 1991).

MATERIAL AND METHODS

The *Z. kampeni* specimens came from the little estuaries opening into Hansa Bay, north of Papua New Guinea.

Observation of the skeleton and musculature was done on 20 specimens (total length between 16 and 18 cm) that had either been preserved in 70% alcohol (15) or frozen (5). Seven specimens were trypsin-cleared and stained with alizarin according to TAYLOR & VAN DIJK (1985) in order to observe certain bony structures in greater detail.

The dentition was observed with a JEOL JSM 840A scanning electron microscope.

LIST OF ABBREVIATIONS

AA:	articulo-angular
Aω:	adductor mandibulae ω
$A_2\alpha$:	second adductor mandibulae α
$A_2\beta$:	second adductor mandibulae β
ADARC:	adductor arcus palatini
AD 1-5:	adductores branchiales 1 to 5
BOC:	basioccipital
DC:	dorsal crest
DE:	dentary
DIOP:	dilatator operculi
EBR1:	first epibranchial
EPOT:	epiotic
HM:	hyomandibular
IO:	interopercular
IGH:	insertion of the protractor hyoidei
IIM:	insertion of the intermandibular muscle
IRD:	insertion of the retractor dorsalis
IRPBR2:	insertion of the retractor muscle of the 2nd pharyngobranchial
K:	keel
LEAP:	levator arcus palatini
LEPO:	levator posterior
LETH:	lateral ethmoid
LEXT 1-4:	levatores externi 1 to 4
Li. 1-10:	ligaments 1 to 10
LINT 2-3:	levatores interni 2 and 3
LPJ:	lower pharyngeal jaw
MX:	maxillary
O:	opercular
PAL:	palatine
PASPH:	parasphenoid
PBR2-3:	pharyngobranchials 2 and 3
PCDE:	dentary coronoid process
PHCLE:	pharyngoclavicularis externus
PHCLI:	pharyngoclavicularis internus
PMX:	premaxillary
PO:	preopercular
PROT:	prootic
PTOT:	pterotic
Q:	quadrate
RA:	retro-articular
RD:	retractor dorsalis
RPBR2:	retractor of the second pharyngobranchial
SO:	subopercular
SOC:	supraoccipital
STH:	sternohyoideus
SUSP:	suspensorium
TAω:	tendon of the adductor mandibulae ω
$TA_2\alpha$:	tendon of the second adductor mandibulae α
$TA_2\beta$:	tendon of the second adductor mandibulae β
TRPBR2:	tendon of the retactor of the second pharyngobranchial
TRV:	transversus ventralis
UH:	urohyal

UPJ:	upper pharyngeal jaw
VO:	vomer
V2-3:	second and third vertebrae

RESULTS

Buccal apparatus

Skeleton

The left and right premaxillaries are flattened, bent, and tightly joined mesially over their entire length by very short fibres, thus constituting a triangular plate. They bear three to four rows of very small conical teeth. The maxillaries partly cover the premaxillaries ventrally and externally and are dorsally covered by the premaxillaries (Fig. 1B). The maxillaries and premaxillaries are attached to
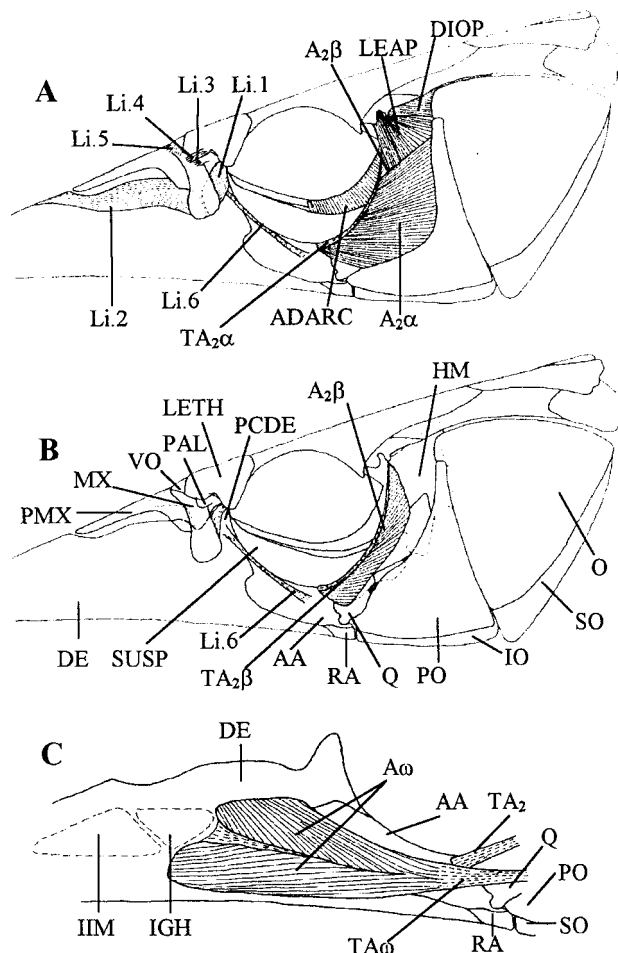

Fig. 1. – Zenarchopterus kampeni. A, left lateral view of the head, showing the musculature covering the suspensorium and several ligaments; interrupted lines show the limits of the ligaments. B, left lateral view of the head showing the positions of the $A_2\beta$ muscle and two ligaments; interrupted lines indicate the limits of certain bony structures. C, internal lateral view of the right half-mandible, showing the Aω muscle; interrupted lines indicate muscle insertion sites. On all three drawings, the anterior part of the mandible is not represented.

each other by very short fibres so as to form a single, rigid upper jaw. The maxillaries articulate with the anterior processes of the palatines and with the lateral ethmoids (Fig. 1B). A ligament (Li.3) connects the maxillaries to the front of the palatines and another (Li.4) connects them to the antero-dorsal face of the lateral ethmoids (Fig. 1A). Each palatine is firmly attached to the lateral ethmoid by very short fibres. Furthermore, a ligament (Li.5) connects the maxillaries and premaxillaries to the vomer (Fig. 1A). It consists of fibres increasing in length from the outer part to the middle of the vomer.

The mandible consists of the dentaries and articulo-angulars, fused to the retroarticulars (Fig. 1B). The dentaries are very elongated (Fig. 2), being very thin in front and broadening toward the rear. Their dorsal side is flat and their ventral side is rounded. Dorsally they are joined by short fibres up to the level of the upper jaw. From this level onward the distance between them increases. They bear three to four rows of little pointed teeth, located anteriorly and externally with respect to the premaxillaries. The coronoid processes are well developed (Fig. 1C).

The articulo-angulars, ensuring the articulation between the mandible and the quadrate, extend at the inner face of the dentaries, and their anterior tips penetrate a postero-mesial cavity of the dentaries. The dentaries and articulo-angulars are fused, making the posterior portion of each half-mandible very rigid.

The retroarticulars lean against the interoperculars and are connected with them by very short fibres. The interoperculars are joined by short fibres to the suboperculars.

Two large ligaments connect the lower jaw to the inner ventral face of the maxillaries: Li.1, attached to the coronoid process, and in front Li.2, which contributes to the lower lip. A long ligament (Li.6) links the outer posterior edge of the maxillary to the articulo-angular.

Musculature

The intermandibular muscle is wide and thick (Fig. 1C). The protractor hyoidei muscles insert to the front on the inner face of the dentaries (Fig. 1C) and to the rear on the hyoid bars. Posteriorly, the sternohyoid muscle extends between the scapular girdle and a long, fine urohyal (Fig. 5A).

The cheek is occupied principally by the adductor mandibulae. According to Winterbottom's nomenclature (1974), this is bundle A_2 divided into $A_2\alpha$ and $A_2\beta$ (Fig. 1A,B). $A_2\alpha$, the larger, more external bundle (Fig. 1A), is attached posteriorly to the preopercular, the metaptery-goid, the symplectic, and the quadrate. In front it is attached via a tendon to a spur on the articulo-angular (Fig. 1A,C). $A_2\beta$ is attached on the one hand to the hyomandibular and pterygoid and on the other hand it is extended by a tendon that fuses with the $A_2\alpha$ tendon (Fig. 1B,C).

On the inner face of the mandible lies a bipennate $A\omega$ adductor bundle. It is attached to the inner faces of the dentary and articulo-angular and continued by a tendon, which passes above the quadrato-mandibular joint and attaches to the inner face of the quadrate (Fig. 1C).

There is no levator operculi. The rest of the cephalic musculature shows no special features.

Movements

A 10° lowering of the mandible (which seems to be a maximum) causes a 30° rotation of the upper jaw and makes the interopercular move backward, causing the operculum to rotate around its articulation with the hyomandibular (Fig. 2).
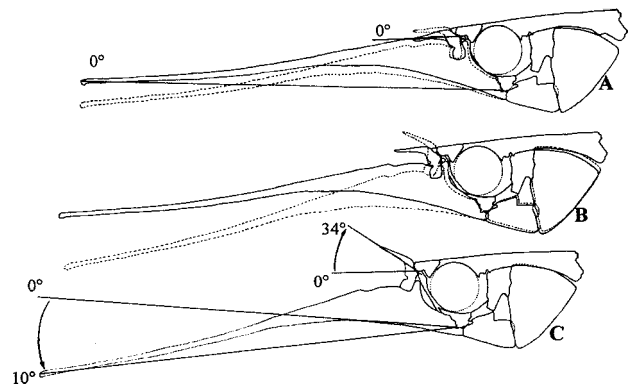

Fig. 2. – *Zenarchopterus kampeni*. Lateral view of the head. The preopercular is not represented. A, mouth closed (full lines) and mouth half-open (interrupted lines); B, mouth half-open (full lines) and mouth wide open (interrupted lines); C, mouth wide open.

Pharyngeal apparatus

Skeleton

The first branchial arch has no pharyngobranchials. The first epibranchials are tapered and point inward. Their cartilaginous extremities are bound by a short ligament to the parasphenoid (Fig. 5A) and their posterior parts articulate with the pharyngobranchials of the second arch.

The second and third branchial arches are complete. The second pharyngobranchials are independent (Fig. 5B). They are narrow and pointed in front and are wider on the back side (Fig. 5B). In front they hang from the parasphenoid by loose fibres and each bears a tooth plate limited to the wider part (Fig. 3B). The teeth are numerous, small, and conical and they curve slightly backward. The second pharyngobranchials articulate laterally with the second epibranchials. Caudally, they are connected to the third pharyngobranchials by the pharyngeal epithelium and connective tissue. These pharyngobranchials are fused, forming a single tooth-bearing pharyngeal bone (Fig. 3B,C,D) with two anterior points. A straight suture is visible between the two halves, although the two bones

cannot be separated. The teeth are large and tricuspid, but the lateral cusps can be rather slight. (Fig. 4B). The median cusp of the longest teeth extends backward in a kind of ridge. This pharyngeal bone has two long, straight dorsal ridges running from front to back. These ridges fit into two grooves on the posterior base of the neurocranium (Fig. 3D), at the level of the prootic, parasphenoid, and basioccipital. The third and fourth epibranchials articulate with the third pharyngobranchials. The second and third pharyngobranchials together constitute the upper pharyngeal jaws (Fig. 3A,B,C,D).

The fifth ceratobranchials are fused into a triangular tooth-bearing lower pharyngeal jaw (Fig. 3A). Tooth size decreases from front to rear (Fig. 4A) and from without to within. The dorsal faces of the largest teeth have a medial groove and a rather sharp tip pointing backward (Fig. 4A). In the back, the pharyngeal jaw bears two latero-posterior processes by which it abuts against the anterior face of the cleithra (Fig. 3C). The inner part of these processes is linked to the scapular girdle by a large ligament (Li.9) (Fig. 5A). Ventrally, the lower jaw bears an wing shaped like a keel (Fig. 3A).
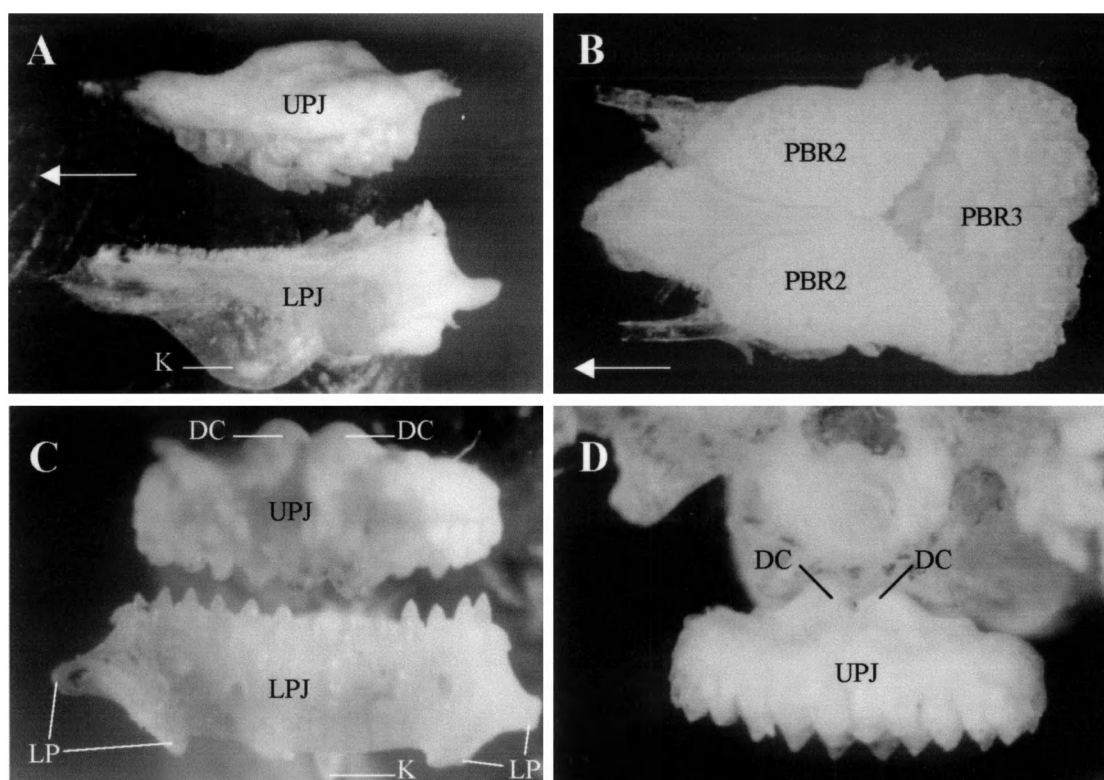

Fig. 3. – *Zenarchopterus kampeni*. Photos of the pharyngeal jaws. A, lateral view of the pharyngeal jaws; B, ventral views of the upper pharyngeal elements; C, posterior view of the pharyngeal jaws; D, posterior view of the third pharyngobranchials and lower part of the neurocranium. Arrows indicate the front.
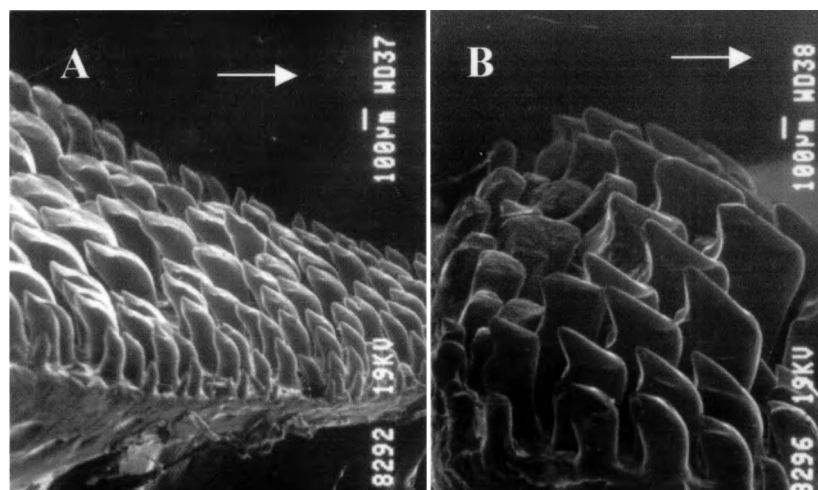

Fig. 4. – *Zenarchopterus kampeni*. Photos taken with a scanning electron microscope, showing part of the dentition of the lower jaw in A and of the third pharyngobranchials in B. Arrows indicate the front.

Musculature

The branchial musculature is original in several respects. The pharyngoclaviculares interni and externi are highly developed and connect the lower pharyngeal jaw to the scapular girdle (Fig. 5A). The outer muscles are attached to the ventral face of the pharyngeal jaw, the inner ones to the keel. The levatores interni 3 and externi 4 tilt markedly forward. The adductores branchiales 5 are very thick and attached on the one hand to the lower jaw and on the other hand to the ceratobranchials and epibranchials of the fourth arch (Fig. 5A). The levatores posteriores present a double ventral insertion on the ceratobranchials 4 and on the latero-posterior processes of the lower pharyngeal jaw. The retractores dorsales are particularly developed and insert on one side on the third pharyngobranchials and beneath the parapophyses and bodies of the third and fourth vertebrae (Fig. 5A).

Lastly, in addition to these dorsal retractores there are other retractores, inserting in front by a tendon onto the narrow anterior part of each second pharyngobranchial and caudally, on the parasphenoid end (Fig. 5B).
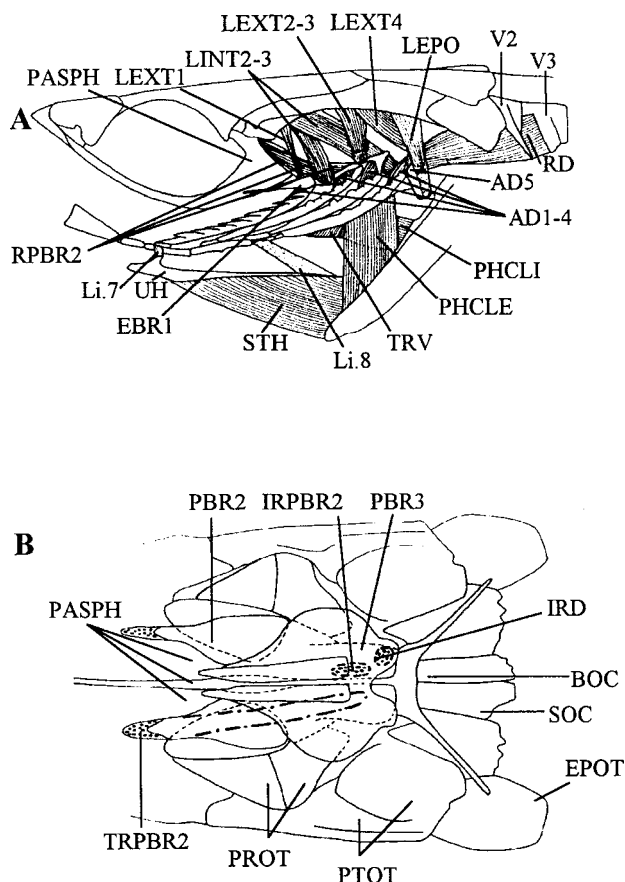

Fig. 5. – *Zenarchopterus kampeni*. A, lateral view of the neurocranium and branchial basket, showing much of the branchial musculature; B, ventral view of the back of the neurocranium, showing the pharyngobranchials and the second retractor dorsalis (thick interrupted line).

DISCUSSION

Buccal parts

Nearly all highly evolved fish have superimposed premaxillaries and maxillaries (GREENWOOD et al., 1966; OSSE, 1969; LIEM, 1970, 1991; VANDEWALLE, 1972; LAUDER, 1982, 1983). Laterally and posteriorly, the maxillaries cover the premaxillaries on the outside; mesially, they have an anterior process covering the premaxillaries and they articulate posteriorly with the palatines and ethmoid region (ALEXANDER, 1967a; LIEM, 1970; VANDEWALLE et al., 1995). The premaxillaries consist of a horizontal process (which usually bears teeth) bordering the mouth opening and a processus ascendens associated with a rostral cartilage surmounting the front of the neurocranium (GREENWOOD et al., 1966; NELSON, 1994). Ligaments hold the whole structure together (OSSE, 1969; LIEM, 1970; BENMOUNA et al., 1984; VANDEWALLE et al., 1995). When the mouth opens, the mandible is lowered, possibly by contraction of the levator operculi, sternohyoideus, protractor hyoidei, epaxials, and/or hypaxials (OSSE, 1969; LIEM, 1970; VANDEWALLE, 1978). It sets in motion the upper jaw: the premaxillaries move away from the maxillaries mesially by sliding over the front of the neurocranium, while the maxillaries remain in contact with the palatines and front of the neurocranium (ALEXANDER, 1967a; ELSHOUD-OLDENHAVE & OSSE, 1976; VAN HASSELT, 1978; LIEM, 1979; MOTTA, 1984; WESTNEAT & WAINWRIGHT, 1989). The mouth is closed by the adductor mandibulae bundles inserted on the maxillary (A_1) and lower jaw (A_2, A_3). Insertion of A_1 on the maxillary notably allows modulation of protrusion and mouth opening (ALEXANDER, 1967a; LIEM, 1991, 1993). The intermandibular is very small and probably slightly modifies the distance between the two half-mandibles (VANDEWALLE, 1972). This type of protrusible upper jaw is found in some Atherinomorpha species (sensu ROSEN & PARENTI, 1981) (ALEXANDER, 1967b) but the organisation of adductor mandibulae bundles seems variable: according to ALEXANDER (1967b), *Atherina presbyter* has an organisation like that of the Perciformes, with A_1 located dorsally with respect to A_2, whereas ROSEN (1964) describes in several Atherinomorpha species a crossing of the (outer) A_1 and (inner) A_2 bundles as in the Cypriniformes (ALEXANDER, 1966; BALLINTIJN et al., 1972; VANDEWALLE, 1975). ALEXANDER (1967b) does not describe the adductor mandibulae in *Dermogenys* sp.

In *Z. kampeni* as in other hemiramphids (ALEXANDER, 1967b) and also in belonids (BOUGHTON et al., 1991), the superposed maxillaries and premaxillaries are closely bound together over their entire length by very short fibres. Contrary to what ALEXANDER (1967b) describes in *Dermogenys* sp., there is no true processus ascendens or rostral cartilage in *Z. kampeni*.

In *Z. kampeni*, the mandible can only be lowered by the ventral and epiaxial musculature, since the levator oper-

culi is absent. The movements of the mandible cause in fact the operculum elevation and lowering. When the mandible is lowered, the upper jaw behaves like a single element. The mandible, acting via ligament Li.2, pulls on the upper jaw, which rotates upwards around a transversal axis running between the front of the left and right palatines and lateral ethmoids. With respect to the vomer, this movement is possible because ligament Li.5 has longer median fibres than outer fibres. No protrusion is possible. A 10° lowering of the mandible causes a considerable rotation of the upper jaw. This rotation is greater in *Z. kampeni* (over 30°) than in *Dermogenys* sp. (20°) (ALEXANDER, 1967b). A slight lowering of the mandible causing a greater rotation of the upper jaw is explainable only by the fact that the distance between (1) the articulation of the maxillary with the palatine and the front of the neurocranium and (2) the point where ligament Li.2 exerts its traction , is markedly shorter than the distance between the quadrato-mandibular joint and the coronoid process of the dentaries.

The mouth is closed by contraction of the A_2 and $A\omega$ bundles. Contraction of the latter raises the mandible, which pulls on the upper jaw via ligaments Li.1 and Li.5. The upper jaw moves backward and downward. The absence of the A1 bundle is probably related to the fact that the bones of the upper jaw cannot move with respect to each other. Given this rigidity of the upper jaw, this fish is probably unable to modulate the opening of its mouth as do other highly evolved teleosts (ALEXANDER, 1967a; LIEM, 1991). Only the intermandibular muscle might exert some modulation, being particularly large. Its contraction might bring closer together the ventral edges of the mandible, and thus move the coronoid processes apart. This in turn could widen the mouth and/or favour rotation of the upper jaw. It should also bring the anterior parts of the suspensoria closer together, somewhat reducing the volume of the buccal cavity.

Pharyngeal jaws

ROSEN (1964) described in hemiramphids a single lower pharyngeal jaw very similar to that of the Cichlidae and Embiotocidae, but with an additional ventral wing. This description is incomplete. In *Z. kampeni*, this jaw has an additional feature: it articulates with the scapular girdle like those of the most evolved Pharyngognathi, the Labridae and Scaridae (LIEM & GREENWOOD, 1981; LIEM & SANDERSON, 1986; MONOD et al., 1994). As in these fish, there is no pharyngohyoideus muscle. The ventral wing is the insertion site of the pharyngoclaviculares interni and not of the sternohyoid muscle as described by ROSEN (1964).

In Scaridae species, NELSON (1969), GOBALET (1989) and MONOD et al. (1994) described upper pharygeal jaws closely bound together by connective fibres. This, according to LIEM & GREENWOOD (1981), constitutes the final stage in the transformation of the upper pharyngeal jaws

in Pharyngognathi. Fused third pharyngobranchials have been described only in four Exocoetoidei species (ROSEN & PATTERSON, 1969; ROSEN & PARENTI, 1981). *Z. kampeni* is an addition to this list. Yet this species seems to be the only one with two dorsal ridges fitting into gutters at the base of the neurocranium. This arrangement seems unique. In Pharyngognathi, the upper pharyngeal jaws have always been described as articulating with the neurocranium and animated by swinging movements (AERTS et al., 1986; LIEM, 1986; LIEM & SANDERSON, 1986; CLAES & DE VREE, 1989, 1991). In *Z. kampeni*, the upper jaw is divided in two parts: the posterior part constituted by the third blended pharyngobranchials, can only slide back and forth in the neurocranial gutters, movements initiated by all the retractores muscles; the second pharygobranchials are free from one another and loosely fixed to the third ones by small fibers, and their position and orientation can be modified by the contraction of their second retractor bundles during the antero-posterior displacements of all the upper pharyngeal jaws.

The shapes of the largest upper and lower pharyngeal teeth show clearly that they can coapt: the ridges of the upper ones fit into the concave parts of the lower ones.

Among the Pharyngognathi, scarids possess the most powerful pharyngeal system (LIEM & GREENWOOD, 1981; GOBALET, 1989; MONOD et al., 1994; BULLOCK & MONOD, 1997). *Z. kampeni's* is even more remarkable. Opposite to a single triangular lower jaw articulating with the girdle are the second pharyngobranchials, bearing teeth as in most acanthopterygians, followed by a single large, broad pharyngeal bone. We propose the following hypothesis regarding the functional participation of this system in feeding. The upper parts protrude and the front of the lower jaw tilts downward. Upon arrival of a prey between the pharyngeal elements, the lower jaw would be raised by contraction of adductors 5, possibly associated with that of the levatores posteriores and externi 4 and with a forward rotation of the scapular girdle. The prey would be seized between the lower jaw and the second phryngobranchials which can be relieved by the contraction of their retractor muscles. It would then be crushed between the jaws by successive lowering movements due to contraction of the pharyngoclaviculares muscles, followed by elevation of the lower pharyngeal jaws. Then the retractores dorsales associated with the retractors of the second pharyngobranchials would pull the dorsal elements backward, the upper pharyngeal bone sliding in the neurocranial gutters, only the relative position and orientation of the second pharyngobranchial can be modulated. This movement would move the food backward while shearing it. Lastly, the pharyngocleithrales would depress the lower jaw (SIBBING, 1982) and the levatores interni 3 and externi 4 (principally) would protrude the upper jaws, guided by the neurocranial gutters. This pharyngeal system seems rigid, allowing only amplitude variations in the movements of its different components, contrary to what has been observed in Pharyngognathi (AERTS et al., 1986;

LIEM, 1986; LIEM & SANDERSON, 1986; CLAES & DE VREE, 1989, 1991). In the latter the mastication cycles, notably, differ from the transport and swallowing cycles. The upper pharyngeal jaw movements in the Pharyngognathi appear to follow several motor patterns or even a single pattern that can be modulated. There is probably no modulation in the third pharyngobranchial movements in *Z. kampeni*. By contrast, a variability in the second pharyngobranchial movements is possible because these elements are loosely connected to the third pharyngobranchials.

Comment on feeding behaviour

During the fishing expedition, some of the *Z. kampeni* specimens were caught near the water surface. Once in the aquarium, specimens often stayed horizontal near the surface (personal observation). This supports ALEXANDER's (1967b) hypothesis (see introduction), further supported by the observation of ALLEN (1991) and ALLEN & SWAINSTON (1992) that halfbeaks eat floating insects. Yet these same authors report that captured halfbeaks also eat aquatic insect larvae, prawns, or fishes. These prey can be either pelagic or benthic. Feeding on benthic animals could be related to foraging behaviour: the lower jaw could rummage through the sediment and send particles and organisms into temporary suspension. Whether the prey is an insect or a crustacean, the buccal jaws should only be able to seize the prey. The teeth of these jaws are very small and the upper ones are behind the lower ones. The upper jaw does not appear to have the size and solidity that would make it a good tool for crushing. This would be the task of the pharyngeal jaws, with powerful musculature and bearing many teeth. The prey is probably seized between the lower pharyngeal jaw and the second pharyngobranchials, and reduced principally by the third pharyngobranchials and the lower jaw before transporting it to the oesophagus.

ACKNOWLEDGEMENTS

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