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Morphology of the buccal apparatus and related structures in four species of Carapidae

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Abstract

The aims of this study were (1) to compare the morphology of the buccal apparatus, the suspensorium and the opercle in four species of Carapidae (*Carapus acus*, *Encheliophis boraborensis*, *Encheliophis homei* and *Encheliophis gracilis*) and (2) to investigate the relationships between their cranial anatomy, their carnivorous diet, and their well known ability to enter holothurians.

The complex and strong dentition and the wide hyomandibular with thickenings that seem to suit the constraints of the adductor mandibulae muscles partly inserted on the neurocranium are signs of a carnivorous diet.

C. acus, *E. boraborensis* and *E. homei* have extremely strong buccal pieces and can protrude their upper jaws. However, in *E. gracilis*, the jaws are more slender, and the insertions of the A_1 along the entire length of the maxillary associated with the lack of mobility between the maxillary and the premaxillary prevent buccal protrusion. These differences could be related to the diet: *C. acus*, *E. boraborensis* and *E. homei* can feed on fishes and crustaceans, whereas *E. gracilis* feeds only on holothurian tissue.

The cephalic morphology of the four species is not incompatible with entering the host. However, the neutralisation of the suboperculum spine by 'cartilaginous' tissue could be considered to be a particular adaptation to this behaviour.

Introduction

Most fishes in the Carapidae are well known to have a commensal or parasitic relationship with an echinoderm (holothuroid or asteroid) and/or mollusc (bivalve) host: Arnold (1953), Hipeau-Jacquotte (1967) and Trott (1970), for example, have documented the entry of carapids into a holothurian echinoderm host. Carapids are also carnivorous: the remains of crustaceans, fishes (including juvenile carapids), and holothurian tissues (Smith 1964; Hipeau-Jacquotte 1967; Smith and Tyler 1969; Smith *et al.* 1981) have been found in their stomach contents. The aims of the present study were (1) to compare the skeleton and musculature of the head in four carapid species and (2) to investigate whether the anatomy of the head displays any particular features that reflect this dual aspect of the carapid lifestyle: carnivorous diet and the ability to enter an echinoderm host.

Most studies on carapids provide little morphological information. The teeth of some species have been described (Arnold 1953; Smith 1955; Trott 1970; Williams 1984; Shen and Yeh 1987; Markle and Olney 1990) and there is some specific data on the position of the bones forming the suspensorium and jaws (Emery 1880; Markle and Olney 1990). The musculature in relation to the buccal parts, cheeks, and opercles has not been described. The mode of penetration in the host has largely been described by several authors (Hipeau-Jacquotte 1967; Trott 1970; Gustato 1976). Briefly, in most cases, once the host is located, the adult carapid (1) exerts pressure on the host's anus with its snout, (2) rapidly reverses its body and enters the host first with its caudal extremity, and (3) makes use of lateral body movements in order to move backwards in the host.

The four carapid species selected were: *Carapus acus* (Brunnich, 1768), *Encheliophis boraborensis* (Kaup, 1856) (formerly *Carapus parvipinnis*), *Encheliophis homei* (Richardson, 1844) (formerly *Carapus homei*), and *Encheliophis gracilis* (Bleeker, 1856). These species names are those recognised by Markle and Olney (1990). *Encheliophis boraborensis* is believed

to eat only crustaceans and fishes (Trott 1970; Van Den Spiegel and Jangoux 1989), *Encheliophis homei* and *Carapus acus* feed not only on crustaceans and fishes (Smith 1964; Trott 1970; Trott and Trott 1972) but are also thought to consume the gonads, viscera, and respiratory trees of the host (Arnold 1953; Hipeau-Jacquotte 1967), and *Encheliophis gracilis* is believed to feed solely on parts of the host (Smith 1964; Trott 1970; Van Den Spiegel and Jangoux 1989).

The nomenclature used to designate parts of the skeleton and musculature is based on Winterbottom (1974), Markle and Olney (1990) and Howes (1992).

Materials and Methods

Specimens of *Encheliophis boraborensis*, *E. homei* and *E. gracilis* were collected in Hansa Bay (Bismarck's sea, North of Papua New Guinea) and in Moorea (French Polynesia). They were found inside specimens of *Bohadschia argus* (a holothurian).

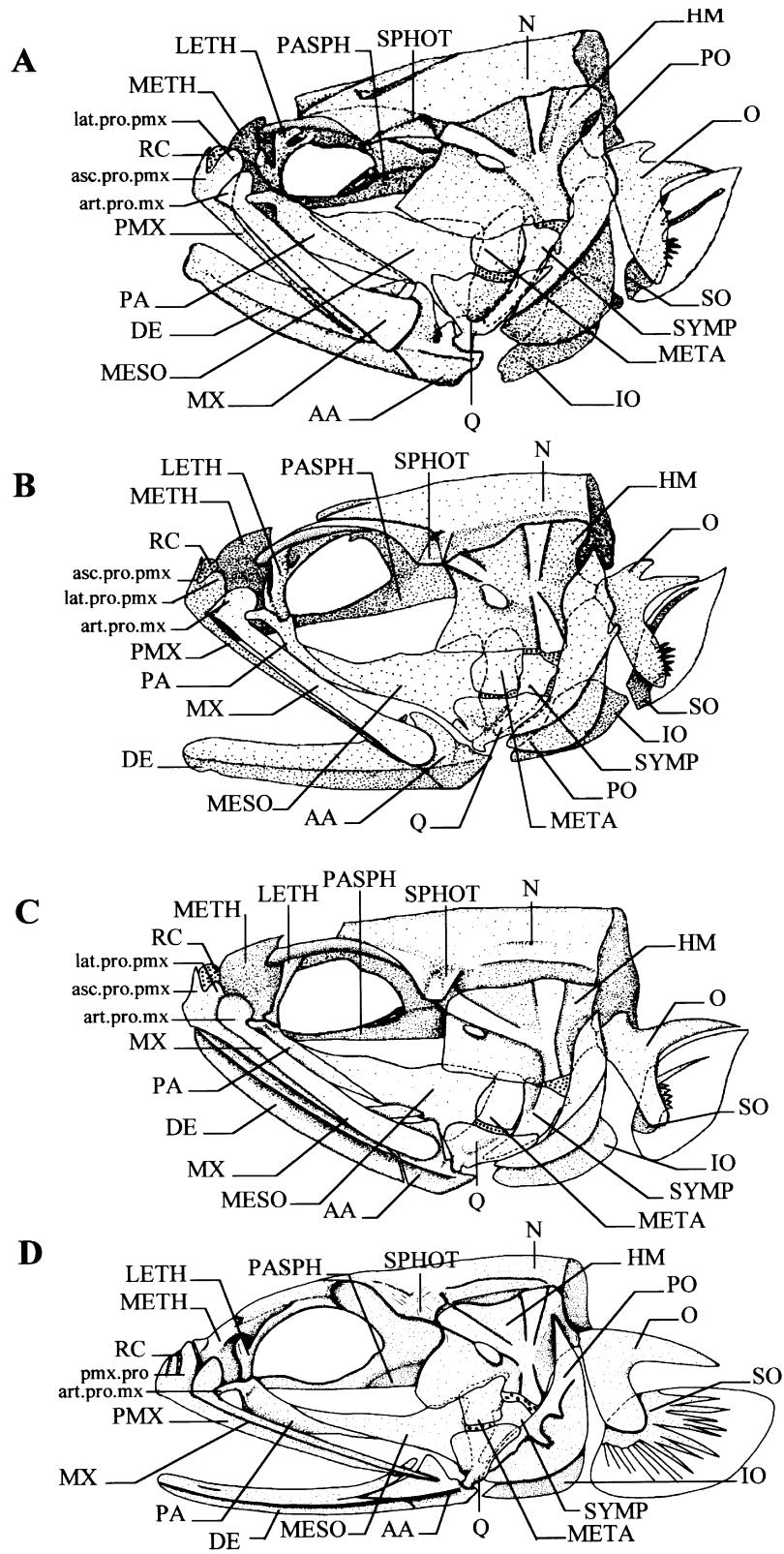
The specimens of *Carapus acus* come from the Mediterranean sea (STARESO station, Calvi, Corsica). They were found in specimens of *Holothuria forskälli* (a holothurian). The carapids were preserved in formalin (5%) or frozen at -20°C . Twelve *E. boraborensis* (total length, TL: 13–30 cm), 13 *E. homei* (TL: 8–17 cm), 8 *C. acus* (TL: 7–15 cm) and 5 *E. gracilis* (TL: 16–24 cm) were examined. Two individuals of each species were stained with Alizarin and/or Alcian blue using the method of Taylor and Van Dijk (1985) to reveal the skeletal structures. All the fish were dissected and examined using a Wild M10 binocular microscope with a camera lucida attached.

The mouth was opened simply by lowering the mandible of defrosted specimens (3 *C. acus*, 4 *E. boraborensis*, 3 *E. homei* and 2 *E. gracilis*).

List of abbreviations

AA: articuloangular	LEOPant: levator operculi (anterior part)
ADARC: arcus palatini adductor muscle	LEOPpost: levator operculi (posterior part)
art.pro.mx.: articular process of the maxillary	LETH: lateral ethmoid
asc.pro.pmx: ascending process of the premaxillary	lig. ω , 1–14: ligaments (see text)
A ₁ α : adductor mandibulae A ₁ α	meck c.: Meckel's cartilage
A ₁ β : adductor mandibulae A ₁ β	MESO: mesopterygoid
A ₂ α : adductor mandibulae A ₂ α	META: metapterygoid
A ₂ β : adductor mandibulae A ₂ β	METH: mesethmoid
A ₃ α : adductor mandibulae A ₃ α	MX: maxillary
A ₃ β : adductor mandibulae A ₃ β	N: neurocranium
A ω : adductor mandibulae A ω	O: operculum
c.: cartilage	PA: palatine
COMECK: corono-Meckelian	PASPH: parasphenoid
DE: dentary	PMX: premaxillary
DIOP: dilatator operculi	PO: preoperculum
DIOPp: dilatator operculi, deep bundle	pro.pa: palatine process
DIOPs: dilatator operculi, superficial bundle	Q: quadrate
HM: hyomandibular	R: retroarticular
IO: interoperculum	RC: rostral cartilage
lat.pro.pmx: lateral process of the premaxillary	SO: suboperculum
LEAP: levator arcus palatini	SOP: primary sound-producing muscle
LEOP: levator operculi	SPHOT: sphenotic
	SYMP: symplectic
	te 1–4: tendons 1–4

Fig. 1. Lateral view of the cephalic skull of *Encheliophis boraborensis* (A), *Encheliophis homei* (B), *Carapus acus* (C), and *Encheliophis gracilis* (D). The suborbital range is not represented.



Results

Skull

In *E. boraborensis*, *E. homei* and *C. acus*, the premaxillary has a row of external cardiform teeth and 2–3 rows of conical internal teeth. It has a slim, horizontal, rod-like process, a small ascending process, and a lateral process. A rostral cartilage lies beneath the ascending process. The premaxillary of *E. gracilis* has only one row of cardiform teeth and its ascending process is very small, leaving the rostral cartilage visible dorsally.

In all four species, the maxillary has a horseshoe-shaped articular process in front that caps the premaxillary. It is surmounted by the anterior process of the palatine (Figs 1, 3). Ligament 1 connects the articular process of the maxillary to the rostral cartilage (Fig. 2), except in *E. gracilis* where this is missing. In *E. boraborensis*, *E. homei* and *C. acus*, the maxillary widens towards the rear into a plate that partly conceals the coronoid processes of the inner jaw. In *E. gracilis*, on the other hand, the posterior end of the maxillary is tapered and the maxillary and premaxillary are interdependent along their entire length due to the presence of short connective fibres (ligament 11) (Fig. 2). In all four species, a ligament (ligament 2) is attached to the base of each articular process of the maxillary. This divides into two branches, an anterior branch attached to the base of the opposite premaxillary ascending process and a posterior branch attached to the mesethmoid (Figs 2, 5). Two other ligaments are inserted on the maxillary: ligaments 3 and 4, which are respectively inserted on the anterior process of the palatine and on the articuloangular, near the joint with the quadrate (Figs 2, 5). Ligament 4 is absent in

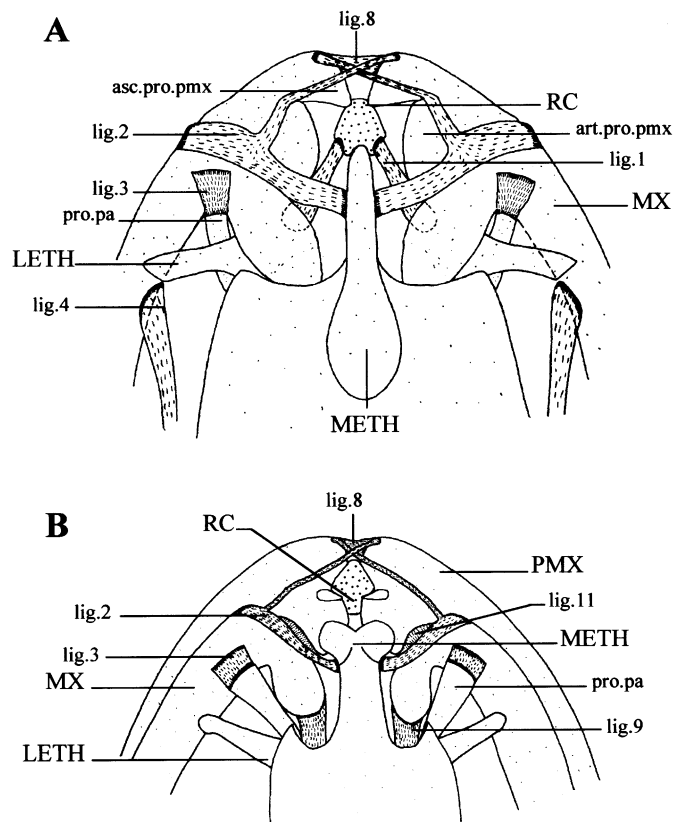


Fig. 2. Dorsal view of the front of the cephalic skull, with the ligaments, in *Encheliophis boraborensis* (A) and *Encheliophis gracilis* (B).

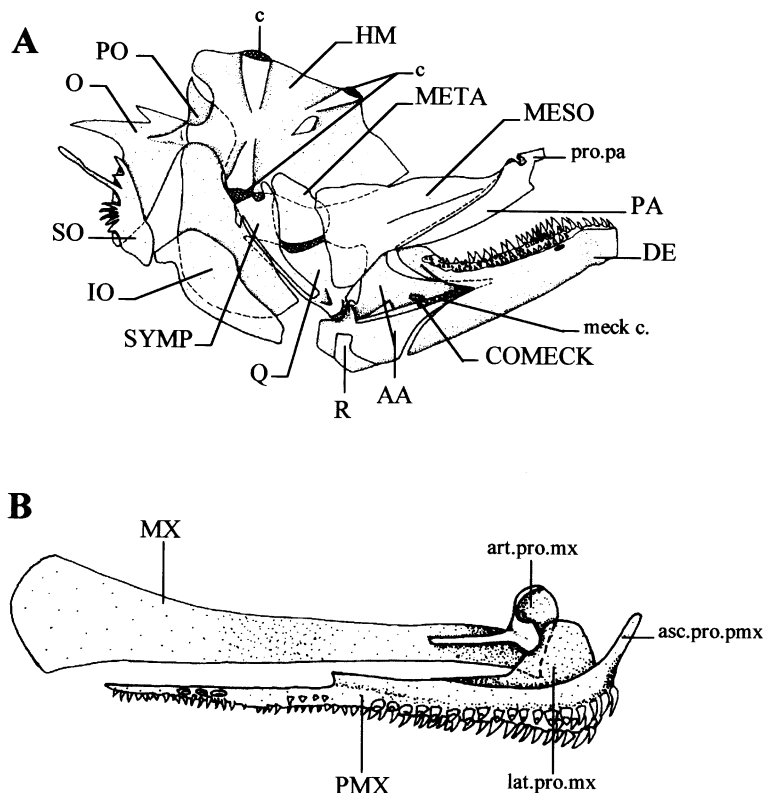


Fig. 3. Inner lateral view of the left suspensorium (A) and left mandible (B) in *Encheliophis boraborensis*.

E. gracilis. However, this species does have a ligament (fig. 9) attached, at one end, to the articular process of the maxillary and, at other end, to the lateral ethmoid (Fig. 2).

In all four species, the mandibular symphysis is rigid and makes the half-mandibles interdependent. The robust and toothed dentary is furrowed at the rear with a cavity housing the anterior tip of the articuloangular (Fig. 3). The two bones are joined by horizontal fibres that are shorter in front, inside the dento-angular cavity, and longer towards the rear. These fibres allow lateral and vertical displacement of the articuloangular with respect to the dentary. The dentary and articuloangular have short but conspicuous coronoid processes. The dentary is connected to the posterior parts of the maxillary and the premaxillary by ligament 10, and the articuloangular is attached to the quadrate by ligament 5 (Fig. 5). There is a small corono-Meckelian on the inner side of the articuloangular. It is in contact with Meckel's cartilage. Finally, the retroarticular constitutes the lower posterior corner of the mandible (Figs 1, 5). It is connected to the interopercle by ligament 6 (Fig. 5).

E. boraborensis has the most robust jaws and proportionately the most developed coronoid processes. By contrast, the buccal parts of *E. gracilis* are the most slender (Fig. 1).

In all four species, the suspensorium is characterised by a very wide hyomandibular that lends great importance to the posterior part of the jaw (Figs 1, 3). Its articulation with the neurocranium extends over the entire length of the very elongated otic region, from the front of the sphenotic to the back of the pterotic, and has two articular condyles: an anterior one in a rounded socket of the sphenotic and a posterior one in a groove in a protuberance of the pterotic. Both condyles are extended by thickenings that converge towards a third, extending the symplectic. A fourth thickening points towards the hyomandibular–operculum joint (Figs 1, 3).

A narrow but thick cartilaginous zone separates the hyomandibular from the symplectic (Fig. 3), the lower portion of which is largely covered by the quadrate. In the continuation of the symplectic, the quadrate displays a thickening that ends in the condyle in the joint with the mandible (Figs 1, 3). A cartilaginous plate separates the quadrate from the metapterygoid. The

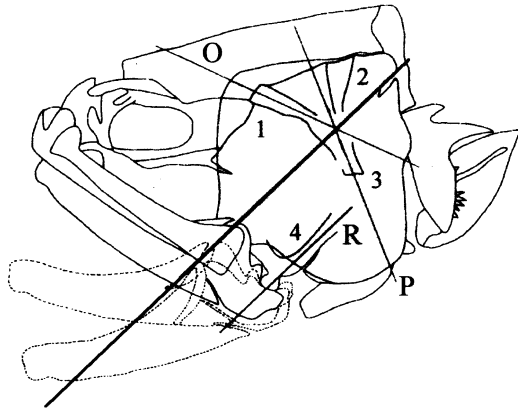


Fig. 4. Simplified lateral view of the head in *Encheliophis boraborensis*. Numbers 1–4 indicate the suspensorium thickenings. The grey surface represents the position of the A2–A3 muscles. The bold line is the bisector of the angle formed by O and P. R is parallel to the bisector running through the quadrate–mandible joint.

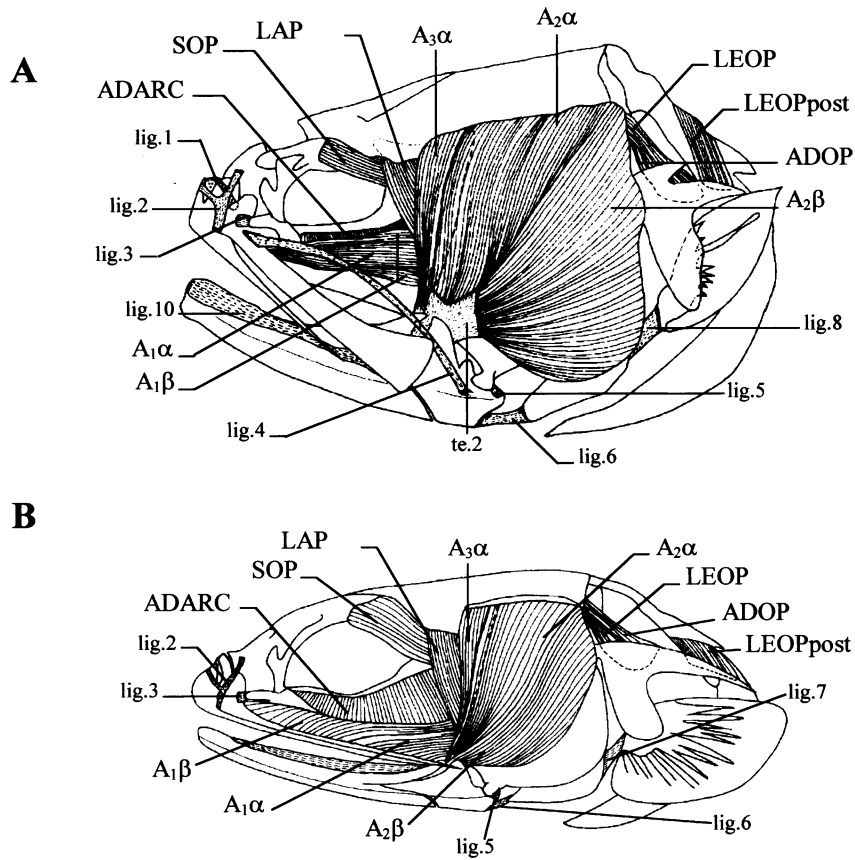


Fig. 5. Lateral view of the head musculature in *Encheliophis boraborensis* (A) and *Encheliophis gracilis* (B).

latter is covered dorsally by the hyomandibular. The mesopterygoid is covered posteriorly by the hyomandibular, metapterygoid, and quadrate, and it borders the palatine in front. The palatine possesses an oval joint socket into which fits the lateral ethmoid and it is prolonged in front by a process attached to the maxillary.

On a lateral view of *E. boraborensis*, *E. homei* or *C. acus*, it is possible to draw a straight line passing through the anterior palatine joint and the double posterior hyomandibular joint between the suspensorium and the neurocranium (Fig. 4). This is not the case in *E. gracilis*. In ventral view, these two articulations are situated on the same line in all four species.

The opercle comprises the bones usually present in teleosts. However, the suboperculum is peculiar in that it consists of a spinous bony anterior part extended backwards by a flexible, compact, cartilage-like zone (intensely stained by Alcyan blue). The operculum, suboperculum, and interoperculum are only slightly interdependent (Figs 1, 3), as they are linked only by ligaments and connective tissue.

Musculature

The adductor mandibulae muscles include the A₁ bundles inserted on the upper jaw, the A₂ bundles attached to the mandible, the A₃ bundles attached to the inner side of the mandible, and A_∞ on the inner side of the mandible (Winterbottom 1974).

In the species examined, adductor A₂ is the most external (Fig. 5). It is very thick and divided into two bundles: A₂α is inserted on the pterotic and hyomandibular and A₂β on the

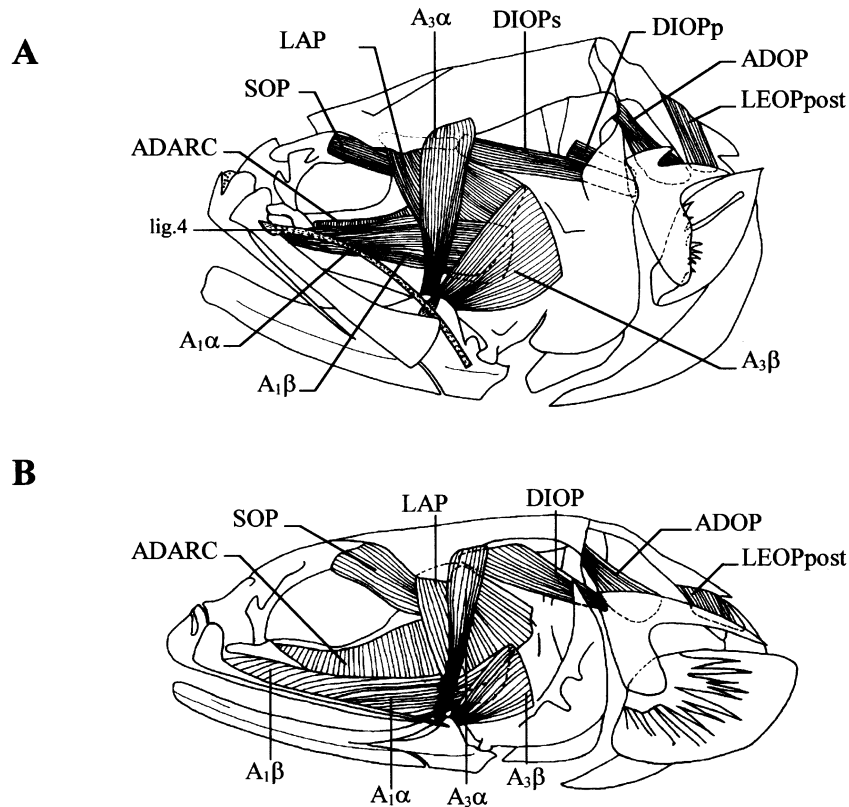


Fig. 6. Lateral view of the head musculature when A₂α and A₂β are removed in *Encheliophis boraborensis* (A) and *Encheliophis gracilis* (B).

hyomandibular, pterotic and preoperculum. Both bundles are attached by a tendon (te2) to the inner side of the coronoid process of the dentary.

Muscle A_3 (Figs 5, 6), under A_2 , is a thin layer of fibres divided into two bundles. $A_{3\alpha}$ is inserted dorsally on the sphenotic and is ventrally in contact with muscle A_ω via a tendon (te3 α) (Fig. 8). In *E. homei*, unlike the other three species, the $A_{3\alpha}$ fibres are totally covered by $A_{2\alpha}$ fibres. $A_{3\beta}$ is situated under $A_2\beta$ and is inserted on the central part of the suspensorium (hyomandibular, metapterygoid and symplectic) and on tendon 3 β , which passes beneath tendon 3 α to reach muscle A_ω (Figs 5, 6, 8).

In *E. boraborensis*, *E. homei* and *C. acus*, A_1 (Figs 5–7) is also divided into two distinct bundles. $A_{1\alpha}$, which is shaped like a recumbent cone, is inserted on the metapterygoid on one side and on ligament 4 on the other (Fig. 5). This ligament extends from the external side of the articuloangular to the front of the maxillary. $A_{1\beta}$ is shorter and is inserted at the rear on the mesopterygoid and at the front on the maxillary. These two bundles press between them the anterior part of the levator hyomandibulae. In *E. gracilis*, $A_{1\alpha}$ is attached to the metapterygoid and to the rear part of the maxillary, while $A_{1\beta}$ is inserted on the upper edge of the metapterygoid and the anterior part of the maxillary.

A_ω (Fig. 8) is pinnate in *E. homei* and *C. acus* but not in the two other species. It is inserted on the dentary and Meckel's cartilage, and on tendons 3 α and 3 β . The outermost fibres of A_ω are attached to a ligament (fig. 11), which extends, in the four species, from the dentary to the quadrate.

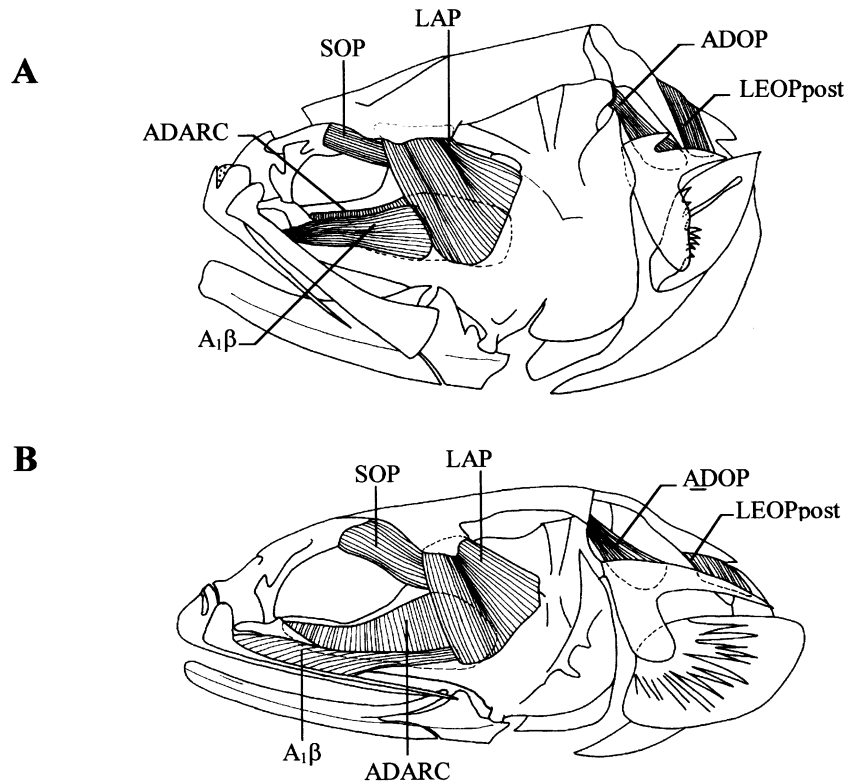


Fig. 7. Lateral view of the head musculature when $A_{1\alpha}$, $A_{2\alpha}$, $A_{2\beta}$, $A_{3\alpha}$, and $A_{3\beta}$ are removed in *Encheliophis boraborensis* (A) and *Encheliophis gracilis* (B). The dotted line delimits the ADARC on the inner side of the suspensorium.

The levator arcus palatini (Figs 6, 7) originates behind the orbit roof on the inner face of the sphenotic. It is almost entirely covered by A_2 fibres and is inserted on the hyomandibular, the mesopterygoid, and the metapterygoid.

Its antagonist, the adductor arcus palatini (Fig. 8), is a long muscle inserted medially on a major part of the parasphenoid and externally on the inner sides of all suspensorium bones

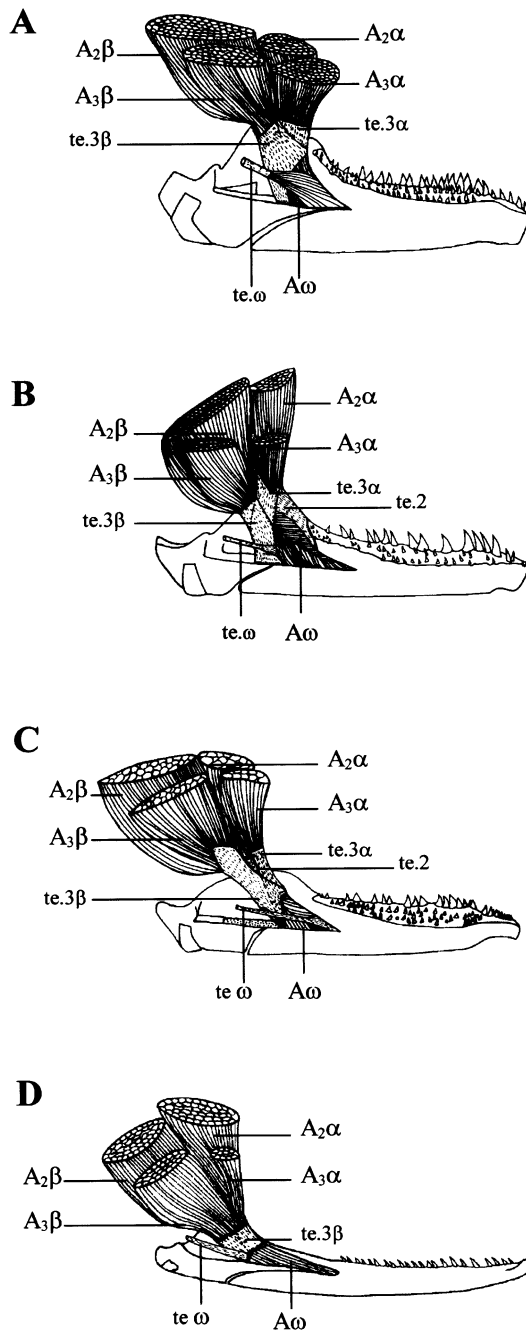


Fig. 8. Inner lateral view of the left mandible and of the organisation of the anterior A_2 , A_3 , and $A\omega$ in *Encheliophis boraborensis* (A), *Encheliophis homei* (B), *Carapus acus* (C), and *Encheliophis gracilis* (D).

except the quadrate and symplectic. It covers the entire orbit floor. There is no individualised adductor hyomandibulae.

The dilatator operculi (Fig. 7) is divided into two bundles in *E. boraborensis*, *E. homei* and *C. acus*. The more superficial part is inserted on the posterior crest of the sphenotic, skirts the levator hyomandibulae, runs between the upper parts of the hyomandibular and the preoperculum and is attached to the outer side of the operculum. The deep part consists of short fibres that start at the hyomandibular, pass below the preoperculum, and are inserted on the operculum, above the superficial bundle. There is only one dilatator operculi bundle in *E. gracilis*.

The levator operculi (Fig. 5) is in an original position in the four species. It has oblique fibres that are inserted on the upper crest of the operculum and on the upper posterior corner of the hyomandibular. In *E. boraborensis* and *E. gracilis*, there is also a bundle (LEOPpost) that is attached to the inner side of the operculum and to the supracleithrum (Fig. 5). The adductor operculi, situated beneath the anterior part of the levator operculi (Fig. 6), has oblique fibres inserted on the upper inner side of the operculum and on the pterotic and intercalar. *E. homei* and *C. acus* have only the anterior part of the levator operculi.

Functional features

Opening the mouth simply by lowering the mandible reveals the following features in *E. boraborensis*, *E. homei* and *C. acus*:

- (i) When the mandible is lowered, the posterior parts of the maxillary and premaxillary tilt downward and forward.
- (ii) At a certain mouth aperture, the lowering of the mandible is accompanied by forward projection of the upper part of the premaxillary. This movement is also accompanied by a lateral movement of posterior parts of the two upper jaw bones.
- (iii) The mandible can be lowered further after the premaxillary moves forward and the upper jaw expands

In *E. gracilis*, the mouth seemed to open less widely. We observed no projection of the premaxillaries upon opening of the mouth, and it was difficult to gauge any expansion of the upper jaws.

Discussion

The cephalic anatomy of the four species shows a series of characters that reflect their carnivorous lifestyle. The mouth is widely split and has strong buccal pieces. The dentition of the jaws, vomer and palatines is complex and strong (Smith 1955; Trott 1970; Shen and Yeh 1987; Markle and Olney 1990).

The adductor mandibulae are well developed. A_2 and A_3 form a strong muscle group inserted not only on the suspensorium, as is the case in most teleosts (Liem 1970; Lauder and Liem 1981; Vandewalle *et al.* 1995), but also on the neurocranium. This arrangement of the adductor could be related to feeding by grasping (Vandewalle *et al.* 1982).

At the front, A_2 is inserted on the coronoid process of the dentary and A_3 on the inner side of the articuloangular by means of $A\omega$. Contraction of A_2 , A_3 and $A\omega$ would result in the raising of the mandible. Because of the mobility between the dentary and the articuloangular, contraction of A_2 can raise the dentary still further, which would crush prey.

The sturdiness of the head is further demonstrated by the hyomandibular thickenings. According to Osse (1969) and Vandewalle (1978), a strengthened suspensorium is a response to physical necessity, preventing bone deformation. The bisector of the angle formed by thickenings 1 and 3 (Fig. 4) points towards the coronoid processes of the mandible (short and near the quadrate joint), the position of which varies little when the mouth opens. The direction of this bisector represents the force exerted on the hyomandibular and mandible by the

contraction of A_2 and A_3 . In these circumstances, thickenings 1 and 3 might be a response to the stresses imposed by these muscles. The hypothesis that the force exerted by A_2 and A_3 is in the direction of the above-mentioned bisector is supported by the fact that the latter is also virtually parallel to the quadrate thickening (4), except in *E. gracilis*. While thickenings 1, 3, and 4 seem easily explainable, thickening 2 of the hyomandibular is more difficult to explain. Its presence probably reflects, at least, the accumulated effects not only of the contraction of the A_2 and A_3 muscles, but also that of the levator hyomandibulae, adductor palatini, dilatator operculi, and even the levator operculi. However, it is difficult to determine the muscle whose impact could explain this thickening. In addition to the thickenings, numerous overlappings between thin bones probably also contribute to strengthening the suspensorium.

Raising the opercle usually results in opening of the mouth and in the creation of suction stream water (Vandewalle 1978; Motta 1984; Howes 1988). In the four species, the effect of raising the opercle is weak because the three opercular bones are loosely joined. This reinforces the hypothesis that the fishes catch their prey mainly by grasping.

Although the cephalic organisation shows that the four species are carnivorous, it also highlights differences as regards particular features of the diet of each species. The carnivorous features are most pronounced in *E. boraborensis*, whose musculature, jaws and suspensorium are the most developed and probably able to process 'tough' prey. This is in keeping with the stomach contents of this species, as no soft elements have been found (Smith and Tyler 1969; Trott 1970; Smith *et al.* 1981; Van Den Spiegel and Jangoux 1989). *E. gracilis*, on the other hand, has the least developed carnivorous aspect. The buccal parts are thinner, and the tooth sets on the jaws and palatines are uniserial (Williams 1984; Shen and Yeh 1987; Markle and Olney 1990). This morphology correlates with the diet, which consists of softer food (Smith 1964; Trott 1970; Van Den Spiegel and Jangoux 1989). The skeletal and muscular organisation of *E. homei* and *C. acus* is similar to that of *E. boraborensis*, but is less developed and could explain a diet comprising both hard and soft prey (Hipeau-Jacquotte 1967; Trott 1970; Van Den Spiegel and Jangoux 1989).

There are two major differences between *E. gracilis* and the three other species: the mouth-opening mechanism and the ability to obtain a wide mouth opening. These seem to be related to the anatomical organisation of the buccal pieces and of the muscles that activate them.

E. boraborensis, *E. homei* and *C. acus* can protrude their upper jaws, but this is not the case with *E. gracilis* or with most Paracanthopterygians (Greenwood *et al.* 1966; Rosen and Patterson 1969; Howes 1988). According to Casinos (1981) and Howes (1988), however, the premaxillary does protrude slightly in some gadiforms.

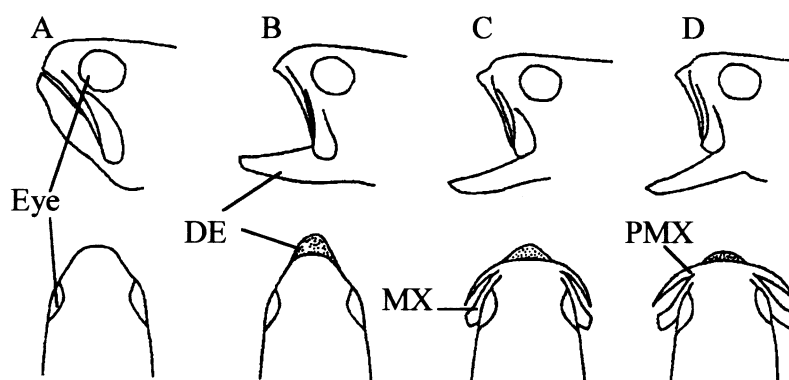


Fig. 9. Diagrams showing mouth opening from lateral and dorsal view in *Encheliophis boraborensis*. A, closed mouth; B, mouth position before upper jaw protrusion; C, mouth position after protrusion; D, maximum mouth opening.

The following mechanism might account for protrusion of the premaxillaries and expansion of the upper jaws in *E. boraborensis*, *E. homei* and *C. acus* (Fig. 9). (1) Depression of the jaw could occur by the standard mechanisms encountered in teleosts (Vandewalle 1978; Gosline 1987; Howes 1988). (2) Since the mandible, maxillary, and premaxillary are joined by ligament 10 and the lips, depression of the mandible causes the rear part of the upper jaw to move downward and forward and the premaxillary and maxillary to rotate, respectively, around the ethmoid region and the anterior process of the palatine. (3) At a certain aperture, the upper part of the premaxillary, which is independent of the maxillary, moves forward. This can be explained as follows: ligament 3 might reach full extension before ligament 1; sustained depression of the mandible would lead, via the lips, to a forward movement of the single premaxillary to the full extension of ligament 1. This protrusion of the upper jaw would generate tension in cross-ligament 2 (Figs 2, 5), causing the two upper jaw bones to move apart. Ligament 3 would limit this spacing. (4) The fact that further depression of the mandible is possible is probably due to the elasticity of the lips and the morphology of the articulation with the quadrate.

In *E. gracilis*, the lack of protrusion could be related, on the one hand, to the ascending and articular processes of the premaxillary, which are attached to the ethmoid region, and, on the other hand, to the fact that the premaxillary and maxillary are firmly joined together by dense connective tissue (ligament 11). In most teleosts, a wide mouth opening would be possible only if the buccal pieces had a substantial degree of independence (Alexander 1967; Lauder and Liem 1981).

Furthermore, *E. gracilis* differs from the other three species in the distribution of the A₁ insertion on the maxillary. According to Casinos (1981), the spreading out of a muscle insertion site is a factor that limits movement. In addition to the lack of protrusion of the upper jaws, these features would, moreover, be the cause of a small mouth opening in this fish compared with the three other species.

This capacity of the upper jaws to protrude is likely to be related to diet: *Encheliophis gracilis* is the only species to feed solely on holothurian tissues (Smith 1964; Trott 1970; Van Den Spiegel and Jangoux 1989). Its adaptation to a parasitic life, where the risk of losing prey is reduced, could be coupled with a simplification and a secondary reduction of the feeding system, as is the case in some Percoidei (Gosline 1989). In the three other species, the ability to protrude the upper jaws would enable them to catch elusive food more effectively.

Only the opercle seems to be adapted to the habit of entering the echinoderm host. The spinous suboperculum is bordered by a strong but supple tissue that would enable it to eliminate all the roughness that could prevent it from entering the host. In fact, the usual behaviour is to locate the host's anus with the head, then to bend and turn over entirely in order to enter with the caudal end first (Arnold 1953; Hipeau-Jacquotte 1967; Trott 1970). However, the species has been observed entering the host head-first on several occasions, indicating that the general shape of the head is not an obstacle to this behaviour in carapids.

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