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Morphological comparison of the buccal apparatus in two bivalve commensal Teleostei, *Encheliophis dubius* and *Onuxodon fowleri* (Ophidiiformes, Carapidae)

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Abstract *Onuxodon fowleri* and *Encheliophis dubius* are two Carapidae species that live in bivalve hosts and their diet is made of the same type of prey. The aim of this study is to compare their cephalic morphology to see whether: (1) the head anatomy of both species is related to the constraints of their way of life and (2) there are differences between these species and commensal carapids that shelter in other invertebrates. The components of their skeletons and muscles are similar, but differ in size and are arranged differently. In *O. fowleri*, the buccal cavity is smaller than in *E. dubius*, the jaws (bearing very large anterior teeth) are larger, the quadrato-mandibular joint lies further to the rear and the fibres of muscle bundles $A_3\alpha$, $A_2\alpha$ and $A_2\beta$ are more vertical and insert higher on the neurocranium. The buccal system of *O. fowleri* appears better suited for ingesting food by biting and grasping. That of *E. dubius* seems better adapted to a feeding mechanism where sucking would have a more important role. The *E. dubius* head morphology is more similar to the cephalic anatomy of non-bivalve commensal species than to *O. fowleri* features. Diet constraints may have greater influence than the different host constraints on the head construction. A simulated backwards rotation of the posterior part of the *E. dubius* suspensorium around the posterior joint between the hyomandibular and the neurocranium brings the jaws and the cheeks to coincide with those of *O. fowleri*. This model could be indicative of how structure modifications and their influences on annex pieces could in part have a role in the biodiversity.

A. Introduction

Several species of the Carapidae (*Onuxodon* sp., *Carapus* sp. and *Encheliophis* sp.) have commensal or parasitic relationships with echinoderms or bivalves (Trott 1970, 1981; Williams 1984; Shen and Yeh 1987; Markle and Olney 1990). Among the commensal Carapini, *Carapus acus* (Brunnich, 1768), *Encheliophis boraborensis* (Kaup, 1856) and *Encheliophis homei* (Richardson, 1844) display carnivorous traits, enabling them to ingest hard prey: the buccal parts are robust, the dentition is well developed, the mouth opens widely and the premaxillaries can project slightly frontwards (Parmentier et al. 1998). These carnivorous traits are also present, but less developed, in the parasitic species *Encheliophis gracilis* (Bleeker, 1856), which feeds solely on the soft tissues of its host (Strasburg 1961; Smith 1964; Trott 1970; Trott and Trott 1972; Parmentier et al. 1998). The mouth of this species opens less widely, protraction of the maxillaries is absent and the dentition is less impressive (Markle and Olney 1990; Parmentier et al. 1998).

The three species of the genus *Onuxodon* (Echinodontini) and the species *Encheliophis dubius* (Putnam, 1874) are the only Carapidae species known to live principally in bivalves, between the mantle and the shell (Munro 1967; Trott 1970; Tyler 1970; Trott and Trott 1972; Markle and Olney 1990; Castro-Aguirre et al. 1996). They are considered commensal (Trott 1981; Markle and Olney 1990). The genus *Onuxodon* is characterised notably by the presence of a pair of large anterior teeth on each jaw, a very compressed body and the presence of a 'rocker bone' in front of the swim bladder (Fowler 1927; Arnold 1956; Courtenay and McKittrick 1970; Tyler 1970; Markle and Olney 1990). *E. dubius* has an external morphology very similar to that of the holothurian commensal Carapini (Trott 1970; Markle and Olney 1990).

In this study, the diets, cephalic skeletons and musculatures of *Onuxodon fowleri* (Smith, 1955) and *E. dubius* are compared with each other and with those of other commensal Carapini living in holothurians (Parmentier et al. 1998). The aim is to compare the cephalic mor-

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phology of both species to see how it responds to the demands of their particular way of life (bivalve host and diet) and to see if they are modifications in comparison with other holothurian commensal Carapidae. Since the cephalic structures of several Carapini have already been described (Parmentier et al. 1998), the description of *E. dubius* will be limited to how it differs from *O. fowleri*.

B. Materials and methods

Twenty-seven *O. fowleri* specimens, 57–90 mm total length, were collected in Hansa Bay (Bismarck Sea) in Papua New Guinea. They were found in representatives of *Pinctada margaritifera* (Linné, 1758) (Bivalvia, Pteriidae) and were preserved in formaldehyde (5%) or frozen at -20°C . The cephalic structures of 14 specimens, 4 of which were alizarin stained according to Taylor and Van Dijk (1985), were dissected, examined and drawn with the help of a coupled binocular (Wild M10). The buccal movements described were obtained by manipulations of unfrozen specimens. The stomach contents of 23 specimens were collected.

The morphological data pertaining to *E. dubius* (90–120 mm) were compiled from specimens from the following institutions: American Museum of Natural History (AMNH), New York; California Academy of Sciences (CAS), California; Natural History Museum of Los Angeles County (LACM), California; Scripps Institution of Oceanography (SIO), California; Florida Museum of Natural History (UF), Florida. The *E. dubius* specimens are listed as follows: Colombia: AMNH 16090 (1); Mexico: CAS 102506 (2); Panama: UF 219384 (1); Costa Rica: LACM 32479–3 (1); SIO 66–492 (1); SIO 71–53 (1C & S). As we were unable to obtain frozen *E. dubius* specimens, it was not possible to open the mouth of this species manually. The stomach contents of 17 other specimens were studied. These (total length 91–108 mm) came from the waters surrounding Espiritu Santo Island in the Bay of la Paz (Gulf of California, Pacific Ocean).

To compare the cephalic structures of the two species we referred their neurocrania to the same reference length, the distance between the mesethmoid and the basioccipital. The various diagrams pertaining to the cranial transformations were produced with the help of DesignCad 2-D, version 7.0 (ViaGrafic Corporation).

C. Results

I. Stomach contents

1. *O. fowleri*

Among the 23 digestive tracts examined, 9 were empty, 3 contained remains of Ostracoda and Amphipoda, 8 contained remains of Annelida and 2 contained unidentifiable soft tissues. The prey appeared to be shredded.

2. *E. dubius*

Among the 17 stomachs examined, 6 were empty and 11 contained Amphipoda and/or Mysidae. One contained Annelida remains.

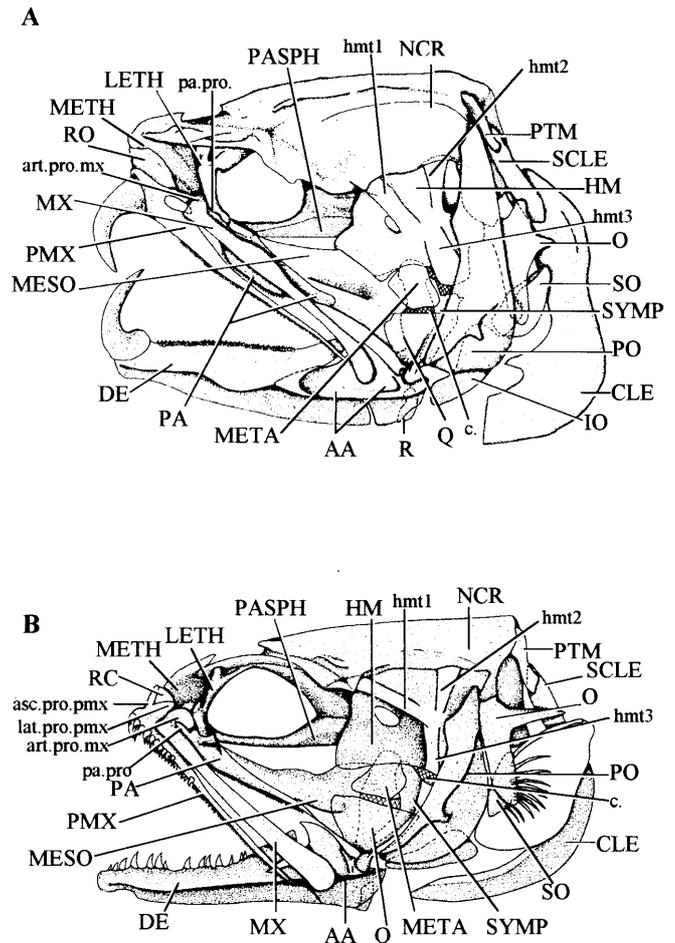


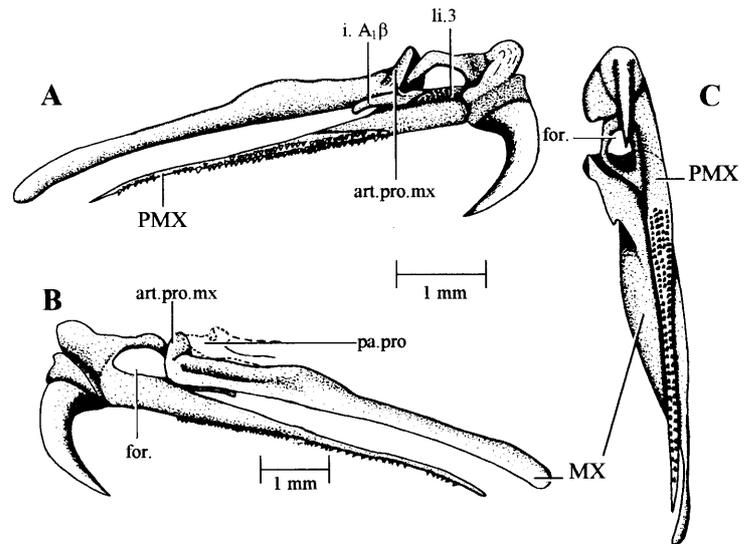
Fig. 1 Lateral view of the cephalic skull of *Onuxodon fowleri* (A) and *Encheliophis dubius* (B). The suborbital range and branchiostegal rays are not represented. AA Articulo-angular, art.pro.mx articular process of the maxillary, asc.pro.pmx ascending process of the premaxillary, c. cartilage, CLE cleithrum, DE dentary, HM hyomandibular, hmt hyomandibular thickening, IO interoperculum, lat.pro.pmx lateral process of the premaxillary, LETH lateral ethmoid, MESO mesopterygoid, META metapterygoid, METH mesethmoid, MX maxillary, NCR neurocranium, O operculum, pa.pro palatine process, PA palatine, PASPH paraspheonoid, PMX premaxillary, PO preoperculum, PTM posttemporal, Q quadrate, R retroarticular, RC rostral cartilage, RO rostral bone, SCLE supracleithrum, SO suboperculum, SYMP symplectic

II. Skull

1. *O. fowleri*

The maximum height of the neurocranium represented about 45% of the length between the mesethmoid and the basioccipital. In front, the concave mesethmoid lies above the vomer which bears a set of small conical teeth. The lateral ethmoid slants slightly backwards and displays two dorsal processes that press ventrally and medially against the frontal (Fig. 1A). The otico-occipital region is the highest in the neurocranium; it shows a broad insertion area for the *adductores mandibulae*. The premaxillaries and dentaries each bear in front a broad, backward-curving tooth (Fig. 2). It is broad at its base,

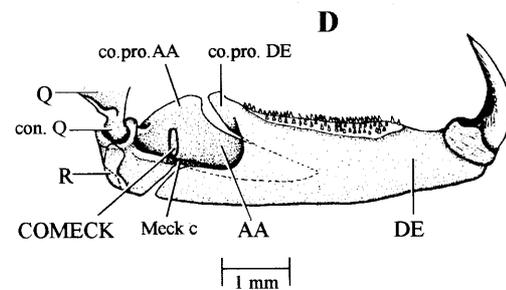
Fig. 2 Inner lateral (A), outer lateral (B) and ventral (C) views of the left maxillary and premaxillary, and inner lateral view of the left mandible (D) in *O. fowleri*. COMECK Coronomeckelian, *con. Q* condyle of the quadrate, *co.pro.AA* coronoid process of the AA, *co.pro.DE* coronoid process of the DE, *for.* foramen, *i. A₁β* insertion of A₁β, *li.* ligament, *Meck c* Meckel's cartilage



then flattens and tapers to form a sharp blade with a parasagittal orientation. It is separated by a diastema from numerous small, conical teeth surmounted by a dome and arranged in several rows of unequal length. The teeth of the premaxillary are external with respect to those borne by the mandible.

The premaxillaries have no ascending process (Figs. 1A, 2). Their lateral process is extended at the front and pierced by a large foramen (Fig. 2) into which the large tooth of the corresponding dentary penetrates. The left and right premaxillaries are firmly interconnected and connected by short connective fibres to an uneven rostral bone (in *O. parvibrachium* called X bone by Tyler 1970). The rostral displays a posterior groove into which the mesethmoid fits. The anterior ridge of this bone is concave and ventrally ends in a bump; the rostral and the anterior parts of the maxillaries and premaxillaries are situated beneath the mesethmoid (Fig. 1A). Overlapping the front of each maxillary is the articular process of the palatine. Slightly behind the articular process on the inner face of the maxillary, a small bump forms the anterior insertion process of the *adductor mandibulae* A₁β.

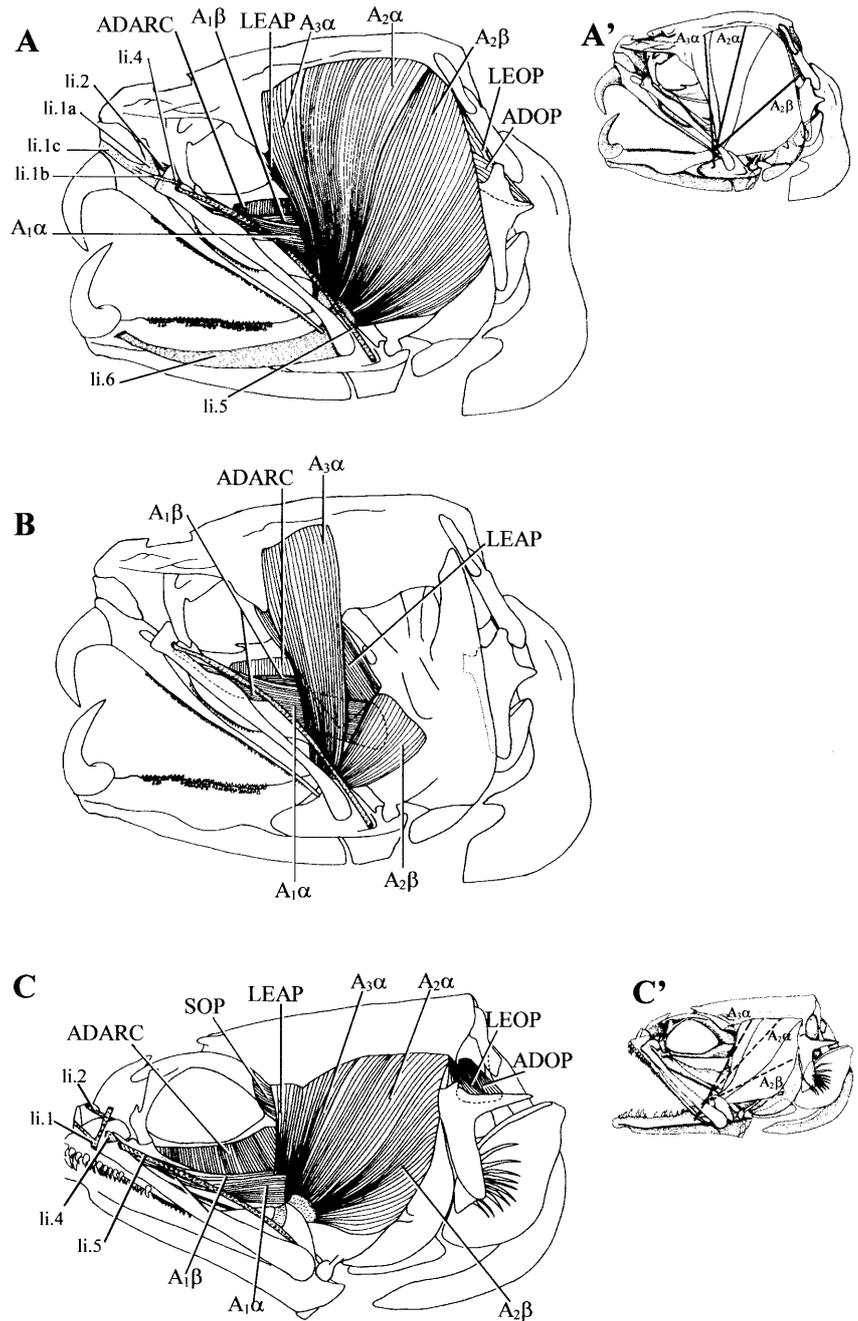
A large branched ligament (Fig. 3) extends from the articular process of the left maxillary to its right-hand counterpart (li.1c). On each side, a branch (li.1a) of this ligament is attached dorsally to the mesethmoid and another ramification (li.1b) starts on li.1c to attach to the anterior palatine process (Fig. 3). The front of the maxillary is also used as a point of attachment for other ligaments: ligament 2 is attached on the one hand to the inner side of the articular process of the maxillary and on the other hand to the back of the rostral; ligament 3 joins the inner base of the articular process of the maxillary to the inner side of the premaxillary; ligament 4 connects the external side of the articular process of the maxillary to the anterior process of the palatine; ligament 5, attached to the maxillary under ligament 4, extends to the external side of the articulo-angular (Figs. 1A, 3).



The dentary is robust and has a hollow cavity at the back into which the anterior head of the articulo-angular fits (Figs. 1A, 4). The two bones are rendered interdependent by horizontal fibres which afford them a small degree of vertical and lateral mobility. The dentary and articulo-angular have short but distinct coronoid processes. The dentary is connected to the posterior parts of the maxillary and premaxillary by ligament 6 (Fig. 3A). The quadrato-mandibular joint is situated clearly behind the posterior ends of the maxillary and premaxillary. A small coronomeckelian is situated on the inner side of the articulo-angular. It is in contact with Meckel's cartilage. Finally, the posterior lower corner of the mandible is formed by the retroarticular (Fig. 1A).

The hyomandibular is broad and its double joint with the neurocranium slants forward (Fig. 1). The two condyle heads of the articulation facet of the hyomandibular with the neurocranium are extended by thickenings (hmt1 and hmt2) that converge towards a third thickening (hmt3) in continuation of the symplectic. Angles hmt1/hmt2, hmt1/hmt3 and hmt2/hmt3 measure about 43, 159 and 136°, respectively. The symplectic is separated from the hyomandibular by a cartilaginous zone and is situated almost entirely ventral to the neighbouring bones. The quadrato-mandibular joint is large and situated at the level of the centre of the joint between the hyomandibular and the neurocranium.

Fig. 3 Left lateral view of the head musculature in *O. fowleri* (A) and when $A_2\alpha$ and $A_2\beta$ are removed (B). Left lateral view of the head musculature in *E. dubius* (C). The average orientations of bundles $A_2\alpha$, $A_2\beta$ and $A_3\alpha$ are represented by solid lines for *O. fowleri* (A') and by dotted lines for *E. dubius* (C') (corresponds to the solid and dotted lines in Fig. 7). $A_1\alpha$ Adductor mandibulae $A_1\alpha$, $A_1\beta$ adductor mandibulae $A_1\beta$, $A_2\alpha$ adductor mandibulae $A_2\alpha$, $A_2\beta$ adductor mandibulae $A_2\beta$, $A_3\alpha$ adductor mandibulae $A_3\alpha$, ADARC arcus palatini adductor, ADOP adductor operculi, LEAP levator arcus palatini, LEOP levator operculi, SOP primary sound-producing muscle



A cartilaginous plate separates the quadrate from the metapterygoid, the latter partly covered by the hyomandibular (Fig. 1). The mesopterygoid connects the hyomandibular, metapterygoid and quadrate at the back to the palatine in the front. Behind its anterior process, the palatine shows a depression into which the lateral ethmoid fits to form the anterior joint between suspensorium and neurocranium (Fig. 1). On the inner, ventral side of the palatine, four rows of small, sharp-pointed teeth of unequal length face the dentary teeth.

The operculum displays a small posterior process and surmounts the small suboperculum characterised by a long dorsal spike and a long series of small posterior

denticles. These elements are continued by a dense material. Ventrally, the interoperculum is connected to the mandible and subopercular by two ligaments.

2. *E. dubius*

The cephalic skeleton of *E. dubius* has the same bony components as that of *O. fowleri*; the differences between the crania of these two species lie in the proportions, arrangement and shape of their components. The neurocranium of *E. dubius* is less elevated than that of *O. fowleri* (its height represents approximately 30% of

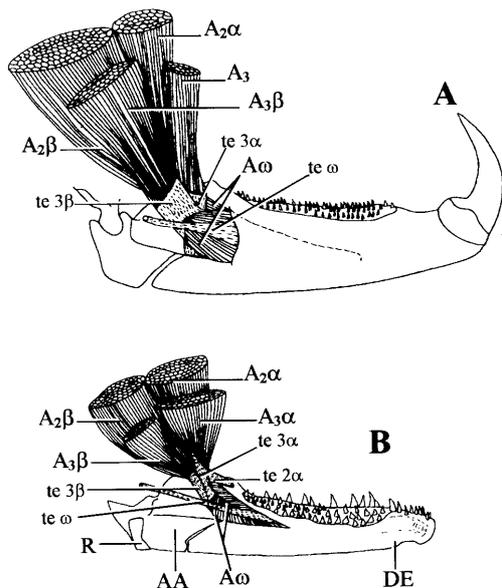


Fig. 4 Inner lateral view of the organisation of the anterior A_2 , A_3 and $A\omega$ bundles in *O. fowleri* (A) and *E. dubius* (B). $A\omega$ Adductor mandibulae $A\omega$, $A_3\beta$ adductor mandibulae $A_3\beta$, te tendons

the length of the cranium). Unlike the latter, it possesses a convex mesethmoid. Sagittally, the vomer bears large, backward-curving, conical teeth surrounded by a series of little teeth. The lateral ethmoid possesses a lateral process in addition to the two dorsal processes, and it slants slightly frontward (Fig. 1B). The otico-occipital region has an insertion area for the *adductores mandibulae*, the mandible being less developed. The joint between the maxillary and premaxillary lies in front of the ethmoid region and these bones are proportionately lower with respect to the neurocranium. The premaxilla has a separate small ascending process and a lateral process; these partly conceal a cartilaginous rostral (Fig. 1B).

As regards the dentition of *E. dubius* (Fig. 1B), the premaxillary displays, at the front, a short row of external cardiform teeth and two more internal anterior conical teeth that curve inwards. They are followed by four unequal rows of small teeth similar to those of *O. fowleri*, extending along the entire length of the premaxillary. The dentary displays an external row of backward- and inward-curving conical teeth, and three internal rows of small teeth similar to those of the premaxillaries. The palatine has small sharp-pointed teeth as in *O. fowleri*, but the vomer bears three or four central main teeth surrounded by small conical teeth. The li.1b ramification is missing in *E. dubius*. Because of the more anterior position of the maxillary on the premaxillary, the li.1a ramification has a dorsoventral orientation.

In *E. dubius*, the quadrato-mandibular joint lies beneath the anterior condyle of the hyomandibular at its joint with the neurocranium. The anterior part of the suspensorium (palatine, mesopterygoid) is situated further to the front (Fig. 1B). The joint between the hyomandibular and the neurocranium is almost horizontal. In both species the posterior condyles at the joint between the

hyomandibular and the neurocranium are at the same distance from the parasphenoid, but they are further apart in *E. dubius* (the angle hmt1/hmt2 measures about 80°) than in *O. fowleri*. Furthermore, the ventral thickening of the hyomandibular (hmt3) is almost vertical in *E. dubius* and has a backward orientation in *O. fowleri* (Fig. 1). The angle hmt1/hmt3 is about 100° in *E. dubius* and hmt2/hmt3 is about 168° .

The *E. dubius* operculum displays a larger posterior process. The suboperculum also appears more developed than in *O. fowleri*: the dorsal spike and denticles are longer and the dense structure continuing this region is larger.

III. Musculature

1. *O. fowleri*

The *adductor mandibulae* includes the A_1 , A_2 , A_3 , and $A\omega$ bundles (Fig. 3A). A_2 is the most external (Fig. 3A). It is very thick and divided into two bundles: at the back, $A_2\alpha$ is attached to the sphenotic and pterotic, and $A_2\beta$ to the pterotic, preoperculum and hyomandibular. Both bundles are attached ventrally by two tendons (2α and 2β) to the inner side of the coronoid process of the dentary.

A_3 consists of two thinner bundles (Figs. 3B, 4A). $A_3\alpha$ is attached dorsally to the sphenotic and ventrally to $A\omega$ via a tendon (3α). $A_3\beta$, situated under $A_2\beta$, is attached on the one hand to the central part of the suspensorium (hyomandibular, metapterygoid, symplectic) and on the other hand to tendon 3 (3α and 3β) connecting muscle $A\omega$ to Meckel's cartilage (Fig. 4). The average orientation of $A_2\alpha$, $A_2\beta$ and $A_3\alpha$ (Fig. 3A') is arbitrarily defined by their insertion on the lower jaw on the one hand and the middle of their insertion on the neurocranium and/or suspensorium. $A\omega$ is attached to the dentary and to Meckel's cartilage and, at the back, to tendons 3α and 3β . A tendon (ω) extends from $A\omega$ up to the quadrate (Fig. 4A).

A_1 also consists of two distinct bundles (Fig. 3A,B). $A_1\alpha$ is attached to the metapterygoid on one side and to ligament 5 on the other. $A_1\beta$ is attached to the mesopterygoid and hyomandibular behind and to the bump of the maxillary in front (Fig. 3B).

The *levator arcus palatini* is attached, on the one hand, to the orbit roof, to the frontal and sphenotic, and on the other hand, to the hyomandibular, mesopterygoid and metapterygoid. The *adductor arcus palatini* is attached to a major part of the parasphenoid and to the inner sides of the palatine, mesopterygoid and hyomandibular.

The *dilatator operculi* is divided into two bundles. The outermost of these is attached to a small bump of the sphenotic, passes behind the preoperculum and attaches to the outer side of the operculum. The second, made of shorter fibres, is attached to the posterior part of the hyomandibular and to the operculum, above the fibres of its analogue. Two other muscles are attached to the opercu-

lum, the *levator operculi* on the upper posterior crest of the hyomandibular and the *adductor operculi* attached to the rear of the neurocranium.

The *geniohyoideus* extends from the anterior part of the dentary to the ceratohyal, and the *sternohyoideus* from the urohyal to the pectoral arch, on the cleithrum. The *abductor hyohyoideus* connects the first branchiostegal ray to the inner edge of the opposite ceratohyal and the *adductor hyohyoideus* interconnects the different branchiostegal rays, the last part extending from branchiostegal ray 7 to the inner side of the operculum. *O. fowleri* does not have any intermandibular muscles.

2. *E. dubius*

Few differences exist in the composition of the upper jaw musculature. The division into bundles of the *adductores mandibulae* is the same in both species. With a smaller neurocranium and with the coronoid processes lying further to the front, the fibres of adductors $A_2\alpha$, $A_2\beta$ and $A_3\alpha$ insert lower on the neurocranium (Fig. 3C) and generally tilt more markedly backwards (Fig. 3C'). The rest of the cephalic musculature of *E. dubius* resembles that of *O. fowleri*.

IV. Movements

In *O. fowleri*, when the mouth is closed, the jaws point upwards and the tips of their large teeth point more or less backwards. The large teeth of the premaxillary are in front of those of the dentary (Fig. 5A). The latter are housed in the premaxillary foramen. In this position, the small premaxillary teeth are external and there is occlusion between those on the dentary and those borne by the palatines. Lowering of the mandible induces, via ligament 6, a downwards and forwards movement of the rear of the maxillaries and premaxillaries. The front of the maxillary turns while the rostral, and thus also the anterior part of the premaxillary, slides downwards and rotates around the mesethmoid as far as the ventral bump of the latter (Fig. 6). This bump accentuates the rotational movement. Simultaneously, the upper jaws move slightly away from the body's axis. At maximum opening (Fig. 5B,D), the tips of the large teeth of the premaxillary point forwards and downwards, and those of the mandible teeth point forwards and upwards. The large teeth of the lower jaw then occupy a more anterior position than those of the premaxillaries (Fig. 5B,D). This is related to the fact that the mandible is longer than the upper jaw parts, and that the mandible teeth are appreciably further from the point of rotation with the quadrate than the premaxillary teeth of the rostral. When the mouth closes, the premaxillary teeth pivot backwards whereas the mandible teeth are raised and set back behind those of the upper jaws. The latter execute a greater anterior-posterior movement than the upper teeth.

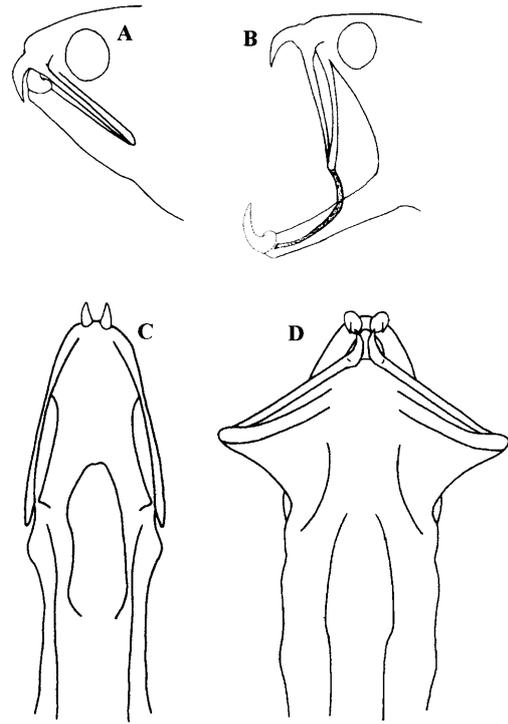


Fig. 5 Diagrams showing lateral and dorsal views of *O. fowleri* with its mouth closed (A,C) or wide open (B,D; maximum mouth opening)

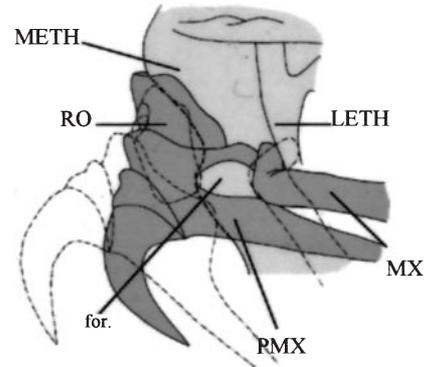


Fig. 6 Positions of the premaxillary, maxillary and rostral of *O. fowleri* when the mouth is closed and wide open (dotted line)

D. Discussion

The skeletal, muscular and ligamentary organisation of the *E. dubius* head is as described by Parmentier et al. (1998) for the commensal Carapini *E. homei*, *E. boraborensis* and *C. acus*. Although manual mouth opening could not be carried out on the *E. dubius* specimens, the full similarity of the cephalic organisation between this Carapidae species on the one hand and *E. boraborensis*, *E. homei* and *C. acus* on the other makes it reasonable to assume that *E. dubius* can open its mouth widely with slight protrusion of the premaxillaries. A widely cleaved mouth, a well-developed dentition, a reinforced hyomandibular, robust jaws and a powerful musculature confirm

the carnivorous diet of these four Carapini (Parmentier et al. 1998). The feeding mechanism probably first involves grasping and then sucking (Kotrschal 1989; Vandewalle et al. 1995; Parmentier et al. 1998). The shape and organisation of the *O. fowleri* head contrasts markedly with this picture: the dentition is peculiar, the jaws are stronger and longer, the joint between the suspensorium and neurocranium is more slanted, the quadrato-mandibular joint lies further backwards, the operculum is smaller and the *adductores mandibulae* are more upright and longer.

The aquatic diet intake is characterised by a suction (Lauder 1980). It is realised by two series of movements: (1) mouth opening followed by lowering of the pharyngeal floor, the suspensoria spacing and finally the opercle abduction and (2) mouth closing followed by raising of the pharyngeal floor and adduction of the suspensoria and the opercles. This succession of movements generates a water flow due to a depression set in the buccal and opercular cavity. This water flow causes a suction mode that represents a diet factor. The suction is more efficient when the buccal cavity is shaped like a large cone with a small circular mouth opening (Alexander 1967; Liem 1978; Lauder 1980; Lauder and Lanyon 1980; Vandewalle and Chardon 1981; Drucker and Jencksen 1991). From this point of view, the suction is probably weak in both species because the mouth remains broadly split. However, a small buccal cavity and a narrow operculum suggest that when *O. fowleri* ingests a prey, sucking plays a minor role when compared to *E. dubius*. On the other hand, *O. fowleri* should be better at grasping its prey. When the mouth is wide open, the large upper teeth point forwards (Fig. 5). The characteristic position of the upper jaw beneath the ethmoid region (Fig. 1) determines a firm fulcrum on the neurocranium that should facilitate penetration of the large teeth into the prey when the mouth closes (Barel 1983; Otten 1983; Turingan 1994). During gradual closing of the mouth, the large premaxillary teeth must pivot and should clamp into the prey, and the mandible teeth, which move further upwards and backwards, should shear it.

This idea is reinforced by the position and the orientation of the $A_3\alpha$, $A_2\alpha$ and $A_2\beta$. According to Barel (1983) and Turingan (1994), the efficiency of muscle contraction is maximal when the muscles are perpendicular to the axis passing through their insertion on the jaw and the joint between the jaw and the quadrate. Figure 7 represents schematically the average orientations of bundles $A_3\alpha$, $A_2\alpha$ and $A_2\beta$ and the orientations of the insertion-joint axes (axis 1 for $A_3\alpha$ and axis 2 for $A_2\alpha$ and $A_2\beta$) for five mandible positions in both species. In *O. fowleri*, the average orientation of the $A_2\alpha$ fibres is perpendicular to axis 2 when the mouth opening is between 45 and 30°, that of $A_3\alpha$ is perpendicular to axis 1 when the opening is between 30 and 15°, and that of $A_2\beta$ is perpendicular to axis 1 when the mouth is closed. In *E. dubius*, only $A_2\alpha$ can be almost perpendicular to the corresponding axis (axis 2) and solely when the mouth is closed. From

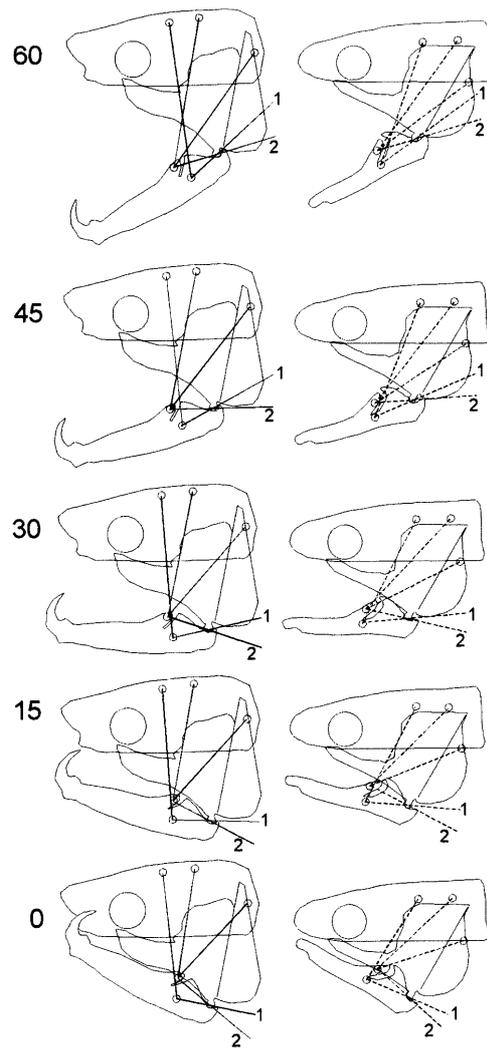


Fig. 7 Diagram showing the average positions of bundles $A_3\alpha$, $A_2\alpha$ and $A_2\beta$ at five stages as the mouth closes. Solid lines *O. fowleri*, dotted lines *E. dubius* (corresponds to the solid and dotted lines in Fig. 3A',C')

this point of view, the generally more erect orientation of $A_2\alpha$, $A_2\beta$ and $A_3\alpha$ bundles is thus better adapted to the necessity of seizing their prey when the mouth closes.

Any change in the size or position of a component can affect partly or entirely the organisation of the skull and its biomechanics (Vandewalle and Chardon 1981; Barel 1983; Gosline 1987; Galis and Drucker 1996). In this context, it is possible to formulate a model regarding the transformation of a buccal system like that of *E. dubius* into that of *O. fowleri*. The suspensorium can be divided into two parts: (1) a posterior part consisting of the hyomandibular, the metapterygoid, the symplectic, the quadrate and the preopercular and (2) an anterior part including the palatine and the mesopterygoid (Fig. 8A₁). If the posterior part of the *E. dubius* suspensorium undergoes a rotation of approximately 19° around the posterior joint between the hyomandibular and the neurocranium (Fig. 8A₁), and if simultaneously the palatine and

Fig. 8 Imagined transformation of the *E. dubius* suspensorium (A) leading to a suspensorium like that of *O. fowleri* (B). Line α Floor of the neurocranium, open circle point around which the suspensorium is rotated

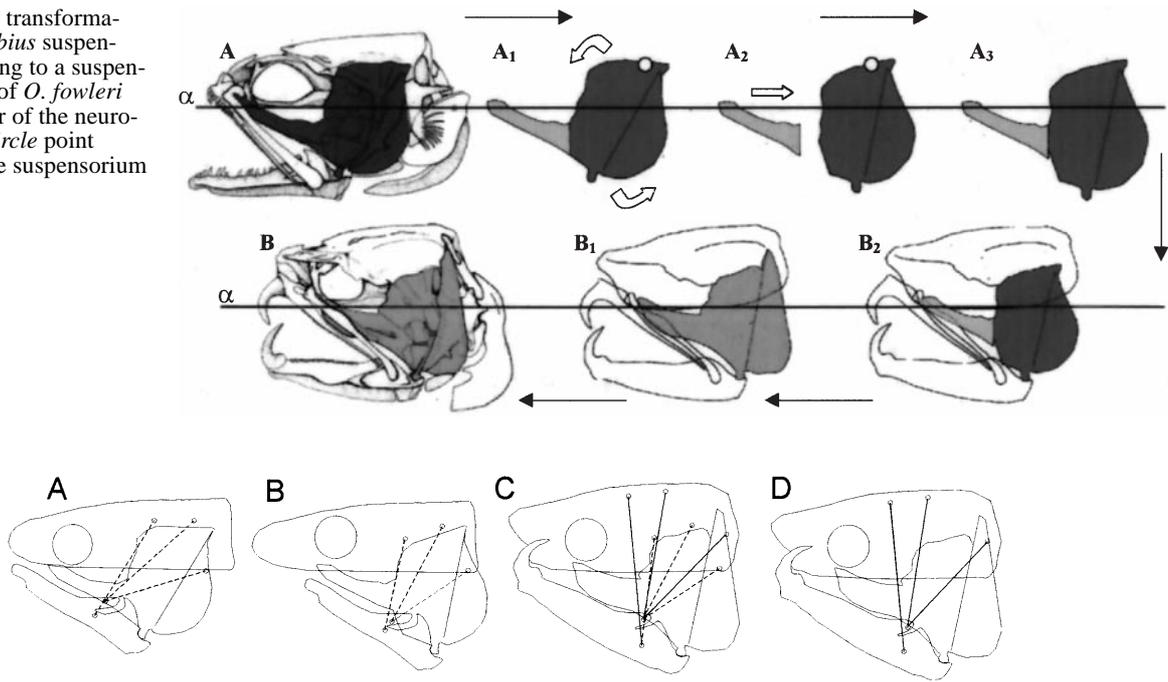


Fig. 9A–D Diagram representing the positions of the cranium, suspensorium, mandible and bundles $A_2\alpha$, $A_2\beta$ and $A_3\alpha$ (cf. Fig. 3). **A** in *E. dubius*; **D** in *O. fowleri*; **B** in *E. dubius*, after modification of the suspensorium (cf. Fig. 8) and bundles; in **C**, the displaced bundles of *E. dubius* (dotted lines) are placed on the cranium of *O. fowleri*

mesopterygoid slide horizontally along the neurocranium (Fig. 8A₂), the resulting new suspensorium can be brought to coincide with that of *O. fowleri* (Fig. 8B₁, B₂). These displacements in *E. dubius* have additional consequences: (1) the jaws are pulled backwards, the upper jaw sliding beneath the ethmoid region, (2) the preopercular becomes more erect and (3) the volume of the buccal cavity is reduced. Applied to $A_2\alpha$, $A_3\alpha$ and $A_2\beta$, however, a 19° rotation brings these bundles to a more erect position without making them coincide with those of *O. fowleri* (Fig. 9). The reorganisation simulation (rotation and translation) of this part of the *E. dubius* skull induces it to look like the head of *O. fowleri*: in this case, they could have approximately the same performances. The real differences between both species represent compromises among different constraints. The causes of such modifications are difficult to explain but the latter could be revealing a mechanism of the biodiversity. It is interesting to note that *Onuxodon*-like form is restricted to bivalves whereas *E. dubius*-like types are able to adapt to different hosts: holothurian, asterian, ascidian and bivalve (Arnold 1956; Trott 1970; Markle and Olney 1990) and appears thus to be more tolerant.

Although the cephalic morphology is different in *E. dubius* and *O. fowleri*, the same types of prey are found in their stomachs. Like the holothuroid commensal Carapini, *O. fowleri* and *E. dubius* eat crustaceans and annelids (Munro 1967; Branch 1969; Trott 1970; Meyer-Rochow 1979; Van Den Spiegel and Jangoux 1989).

Consequently, differences in the prey-seizing apparatus are not necessarily related to different diets but it could reflect strategies of prey seizing adapted to the same type of prey but with different performances (velocity, tegument hardness) (Barel 1983; Kotschal 1989; Turingan 1994).

In conclusion, although both *O. fowleri* and *E. dubius* live in bivalve hosts, the buccal anatomy of this latter is closely related to that of Carapini which are commensal within holothurians, asterians and ascidians. The buccal anatomy of these species seems more dependent on the different dietary constraints than the occupation of a particular host.

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