MORPHOLOGICAL PARTICULARITIES OF THE HEAD
IN FOUR CARAPIDAE (OPHIDIIFORMES)

by

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ABSTRACT. - A study of the skull and the musculature of the oral and pharyngeal region of four adult Carapidae species (*Encheliophis boraborensis, E. homei, E. gracilis* and *Carapus acus*) has been undertaken to compare it with the diet related characters. The cephalic organization of *E. boraborensis* and *E. gracilis* seems related to diet (mainly fishes and shrimps for the first one and holothurian tissues for the other): these species are respectively commensal and parasitic. Although the feeding characters of *E. homei* and *C. acus* are closely similar to those of *E. boraborensis*, there are sparse observations of holothurian tissues in their stomach contents. It is suggested that these fishes are commensal when they are adults and have parasitic tendency when they are juveniles.

RÉSUMÉ. - Particularités morphologiques de la tête chez quatre Carapidae (Ophidiiformes).
Une étude du squelette et de la musculature des régions orale et pharyngienne de quatre espèces adultes de Carapidae (*Encheliophis boraborensis, E. homei, E. gracilis* and *Carapus acus*) a été réalisée afin de les comparer avec le régime alimentaire. L'organisation céphalique de *E. boraborensis* et *E. gracilis* semble être le reflet de leur alimentation (composée principalement de crustacés et de poissons pour le premier et de tissus d'holothuries pour le second): ils sont respectivement commensal et parasite. Bien que les caractères en relation avec la prise de nourriture d'*E. homei* et *C. acus* soient très semblables à ceux de *E. boraborensis*, quelques données ponctuelles rapportent la présence de tissus d'holothuries dans leurs contenus stomacaux. Ces poissons seraient des commensaux à l'état adulte et auraient des tendances parasitaires lorsqu'ils sont juvéniles.

Key-words. - Carapidae, *Carapus acus, Encheliophis boraborensis, Encheliophis homei, Encheliophis gracilis*, Cephalic morphology, Diet, Commensalism, Parasitism.

Most species of the Carapidae family have commensal or parasitic relationships either with an invertebrate echinoderm (Holothuroid or Asteroid) and/or a mollusc host (Markle and Olney, 1990). Stomach contents examination reveals their carnivorous lifestyle (Smith, 1964; Hipeau-Jacquotte, 1967; Trott, 1970; Dawson, 1971; Trott and Trott, 1972; Seymour, 1974; Gustato, 1976; Meyer-Rochow, 1977; Gustato *et al.*, 1979; Van Den Spiegel and Jangoux, 1989). Using a morphological approach, our aim is to contribute to the comprehension of carapids / holothurian host relationship. By studying the skeleton and the musculature of the oral and pharyngeal jaws in four carapids (*Encheliophis boraborensis, E. homei, E. gracilis* and *Carapus acus*), it is possible to

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confirm the diet and if a species is commensal or parasitic. Our choice was based on the availability of these four species and on their essentially similar behaviour towards their host. Moreover the three *Encheliophis* species are found inside the same holothurian species (*Bohadschia argus*). *E. boraborensis* is believed to eat mainly crustaceans and fishes (Trott, 1970; Van Den Spiegel and Jangoux, 1989), *E. homei* and *C. acus*, are thought to additionally consume the gonads, viscera, and respiratory trees of their host (Arnold, 1953; Smith, 1964; Hipeau-Jacquotte, 1967; Trott, 1970; Trott and Trott, 1972; Van Den Spiegel and Jangoux, 1989), and *E. gracilis* to feed solely on parts of the host (Strasburg, 1961; Smith, 1964; Branch, 1969; Trott, 1970; Van Den Spiegel and Jangoux, 1989).

MATERIALS AND METHODS

Twelve *Encheliophis boraborensis* (TL: 13 to 30 cm), 13 *E. homei* (TL: 8 to 17 cm), and 5 *E. gracilis* (TL: 16 to 24 cm) adult specimens were collected in Hansa bay (Bismarck'sea, North of Papua New Guinea). They were found inside specimens of *Bohadschia argus* (a holothurian). The 8 specimens of *Carapus acus* (TL: 7 to 15 cm) were found in *Holothuria forskali* from the Mediterranean sea (S.T.A.R.E.S.O. station, Calvi, Corsica).

The carapids were preserved in 5% formaline or frozen at -20°C. Three individuals of each species were stained with Alizarin and Alcian blue according to Taylor and Van Dijk (1985) to reveal the skeletal structures. All fish were dissected and examined with a Wild M10 binocular coupled with a camera lucida.

Abbreviations

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A : adductor mandibulae A	A_1 : adductor mandibulae A_1	A_1 : adductor mandibulae A_1
A_2 : adductor mandibulae A_2	A_2 : adductor mandibulae A_2	A_3 : adductor mandibulae A_3
A_3 : adductor mandibulae A_3	AA : articuloangular	art.pro.mx.: articular process of the maxillary
asc.pro.pmx : ascending process of the premaxillary	BBR 1-4 : basibranchial 1 to 4	BH : basihyal
CBR 1-5 : ceratobranchial 1 to 5	DE : dentary	EBR 1-5 : epibranchial 1 to 4
HBR 1-3 : hypobranchial 1 to 3	HM : hyomandibular	HM pos. : Hyomandibular position
INEL : interarcual element	IO : interoperculum	lat.pro.pmx : lateral process of the premaxillary
LEAP : levator arcus palatini	LETH : lateral ethmoid	LEXT 1-4 : levator externus 1 to 4
Li. : ligament	LINT 2 : levator internus 2	LINT 4 : levator internus 4
MESO : mesopterygoid	META : metapterygoid	MX : maxillary
NCR: neurocranium	O : operculum	PA : palatine
PBR 1 : pharyngobranchial 1	PBR 2-4 : pharyngobranchial 2 to 4	PMX : premaxillary
PO: preoperculum	pa. pro : palatine process	Q : quadrate
R : rib	RC : rostral cartilage	RD : retractor dorsalis
SB : swim bladder	SCAP : pectoral girdle	SO : suboperculum
SOP : primary sound-producing muscle	SYMP : symplectic	I, II, III, IV : vertebra
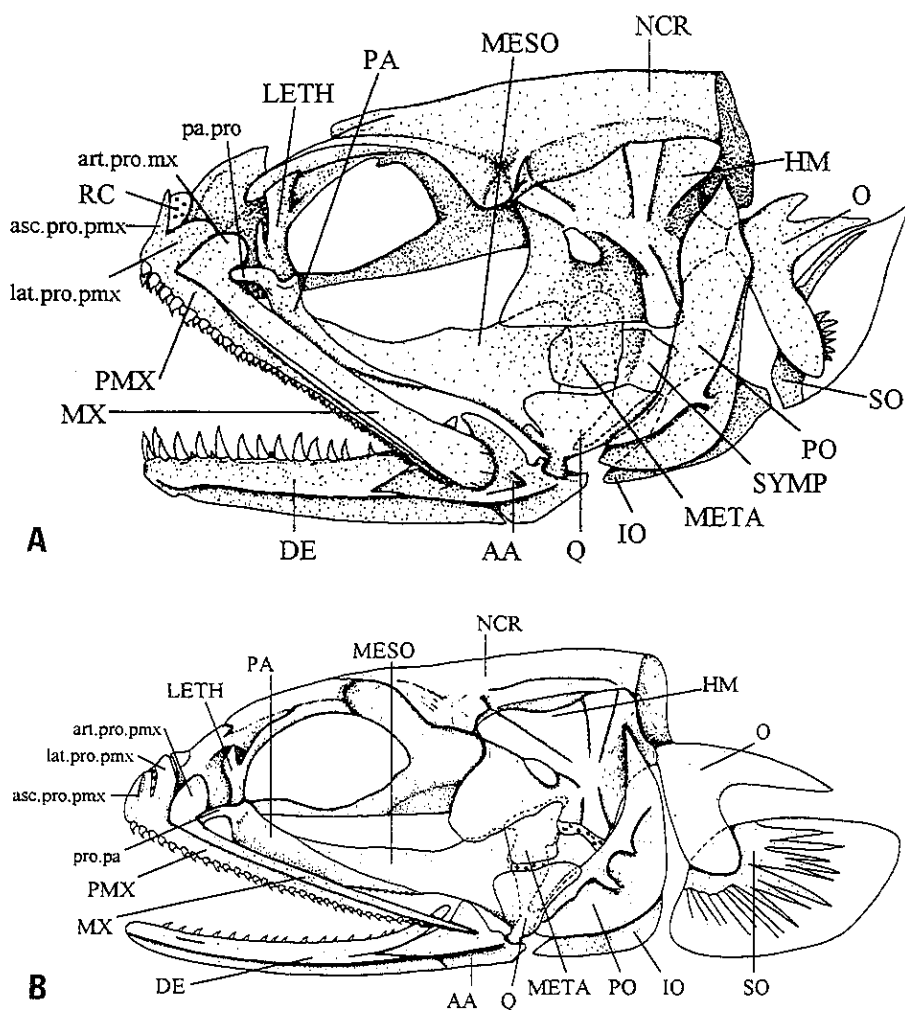
Fig. 1. - Lateral view of the cephalic skull in *Encheliophis homei* (A) and *E. gracilis* (B).

RESULTS

Skull of the oral region

In all four species, the premaxillary bears a row of external cardiform teeth (Fig. 1) and an additional two or three rows of conical internal teeth in *Encheliophis boraborensis*, *E. homei* and *Carapus acus*. The premaxillary of *E. gracilis* is also distinctive from the three other species by its close ascending and lateral processes (Fig. 1B). The articular process of the maxillary articulates on the anterior process of the palatine and caps the premaxillary. The ethmoid region of the four species has two ligaments (Li. 1 and 2) in common (Fig. 2). Li. 1 divides into two branches: the first branch attaches on the mesethmoid and on the base of the maxillary articular process and the sec-
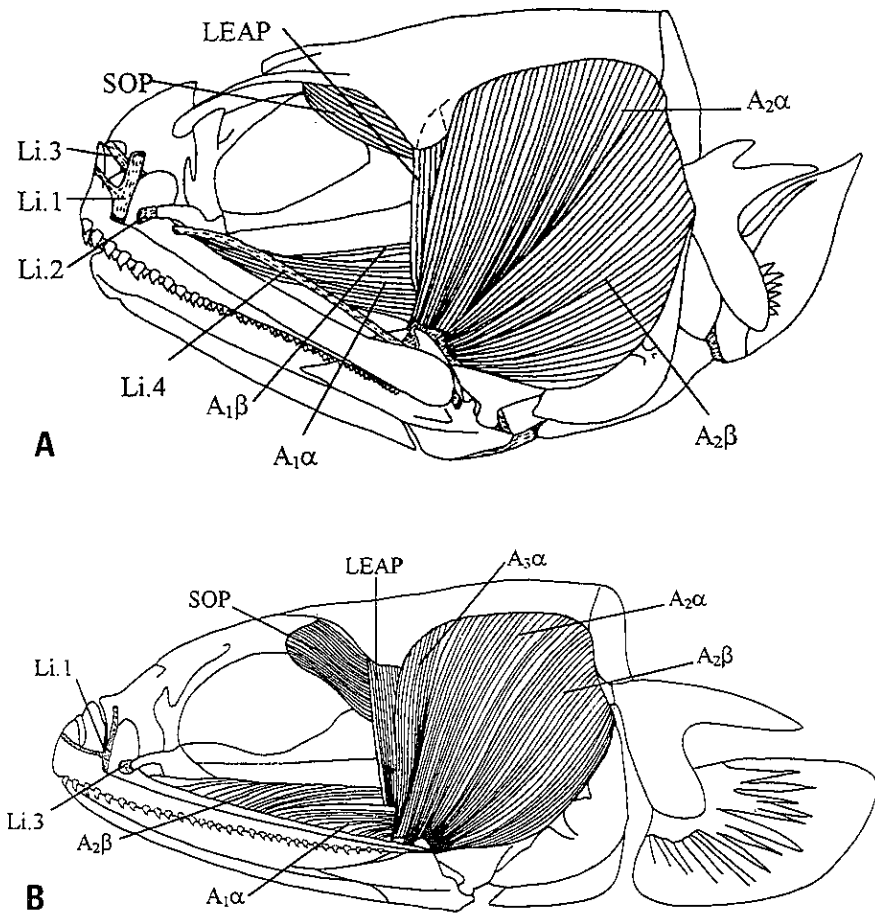
Fig. 2. - Lateral view of the *adductor mandibulae* muscles and of the *levator arcus palatini* muscle in *Encheliophis homei* (A) and *E. gracilis* (B).

ond branch originates on the first branch and runs to the opposite premaxillary ascending process. Li. 2 joins the anterior process of the palatine and the upper part of the maxillary. In addition there are two other common ligaments in *E. boraborensis, E. homei* and *C. acus*: the first one (Li. 3) attaches on the maxillary articular process and on the rostral cartilage; the second one (Li. 4) is fixed below the Li. 3 and attaches to the articulo-angular (Fig. 2A). The latter two are missing in *E. gracilis*. On the other hand, *E. gracilis* possesses short connective fibres (Li. 5) spread along the maxillary and premaxillary length that do not permit a separation between the upper jaw elements.

The dentaries are robust and toothed. *Encheliophis boraborensis, E. homei* (Fig. 1A) and *Carapus acus* possess a row of large external, incurved conical teeth and several smaller internal teeth; *E. gracilis* possesses only external teeth (Fig. 1B). Proportionately, the lower jaws of the latter are slender (less thick and the coronoid processes less developed).
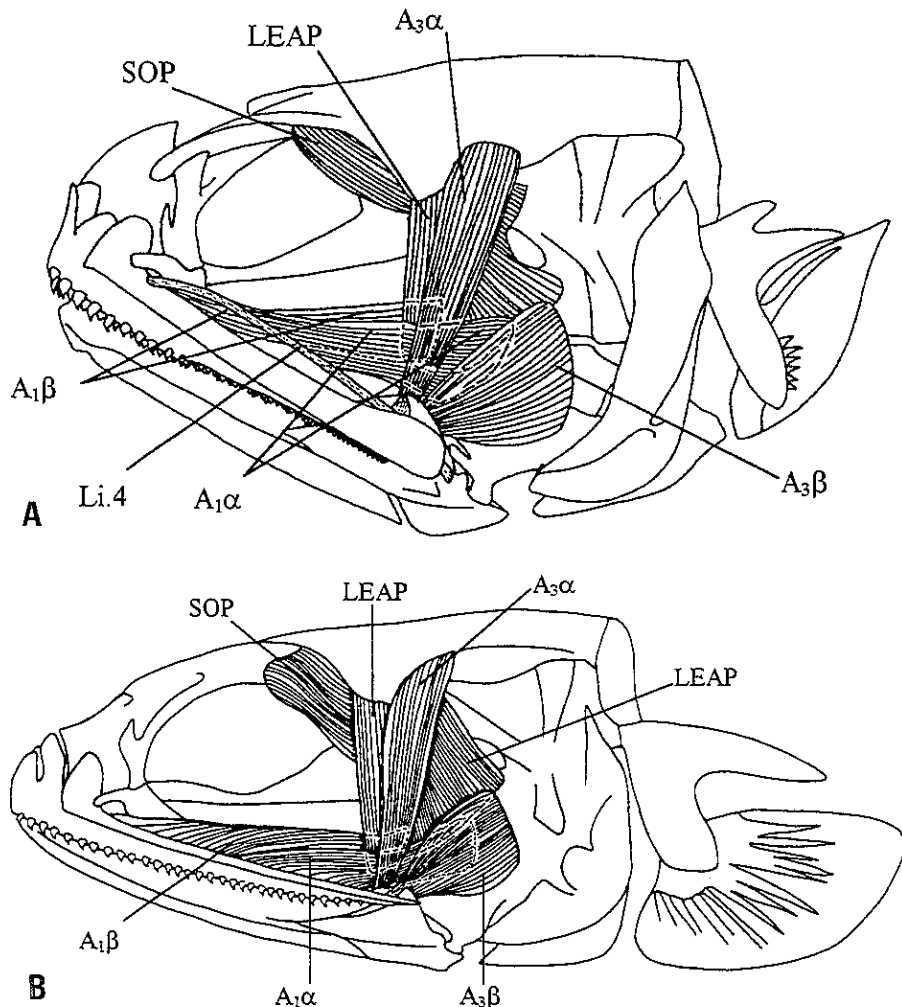
Fig. 3. - Lateral view of the *adductor mandibulae* muscles and of the *levator arcus palatini* in *Encheliophis homei* (A) and *E. gracilis* (B) when A_2 bundles are removed.

In all four species the major characteristic of the suspensorium is in the large and reinforced hyomandibular. It articulates with the neurocranium along the otic region and displays two articular condyles: one on the sphenotic and the second on the pterotic. Both condyles are extended by thickenings that converge toward a third extending toward the symplectic. The quadrate shows a thickening in the continuation of the symplectic.

Musculature of the oral region

The *adductor mandibulae* muscle of the examined species has six bundles. Adductor A_2 is the most external and is separated in two bundles: $A_2\alpha$ and $A_2\beta$ (Fig. 2). These muscles extend from the inner side of the dentary coronoid process to the pterotic and hyomandibular respectively. Adductor A_3 lies under A_2 and is divided in two bundles
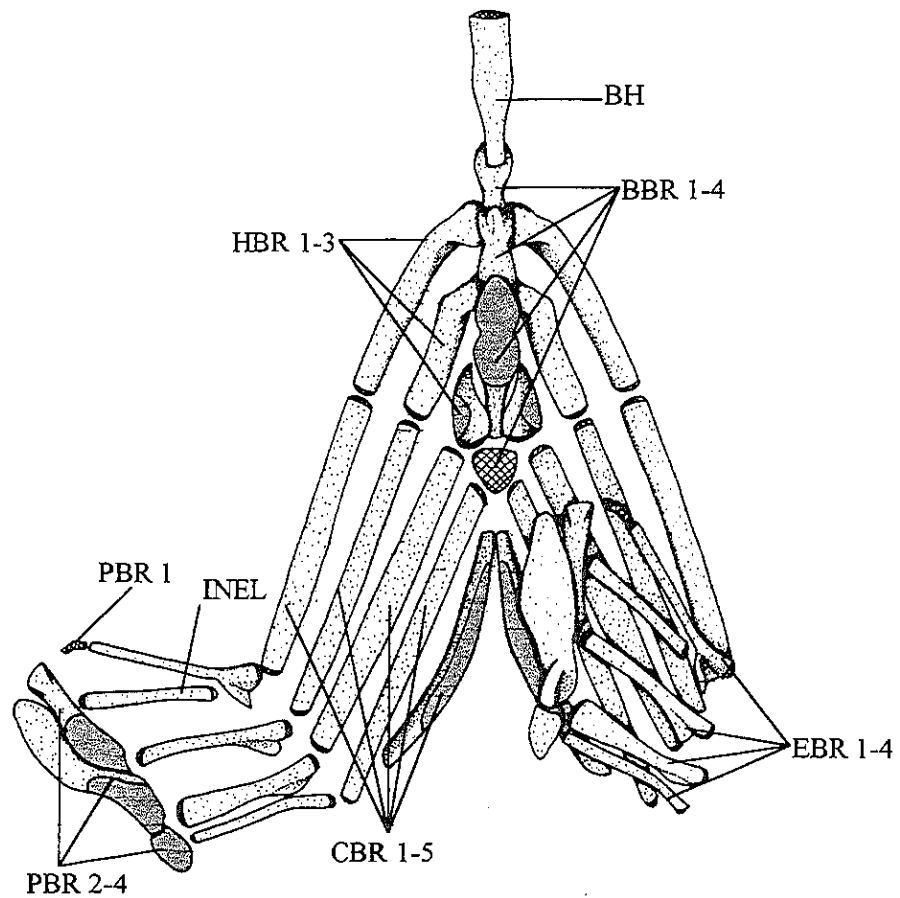
Fig. 4. - Dorsal view of the branchial basket in *Encheliophis boraborensis*. Grey surfaces represent the teeth positions and hatched surfaces the cartilage.

(Figs 2, 3). The first one (A$_3$α) inserts dorsally on the sphenotic and is ventrally in contact with Aω adductor and the second one (A$_3$β) inserts on the central part on the suspensorium (hyomandibular, metapterygoid and symplectic) and on A.

A new major difference appears with the disposition of the A$_1$ bundles (A$_1$α and A$_1$β) between *E. gracilis* and the three other species (Figs 2, 3). In *E. boraborensis*, *E. homei* and *C. acus*, A$_1$α inserts on the metapterygoid posteriorly and on ligament 4 (Li. 4) anteriorly. A$_1$β extends from the mesopterygoid to the inner face of the maxillary. In *E. gracilis*, insertions on the suspensorium are similar but none anterior, the two bundles insert along most of the length of the maxillary.

Functional features of the oral region

In *Encheliophis boraborensis*, *E. homei* and *Carapus acus*, the mouth opening shows a forward projection of the upper part of the premaxillary when the dentary is lowered. In addition to this movement, the posterior parts of the upper jaws move laterally. In
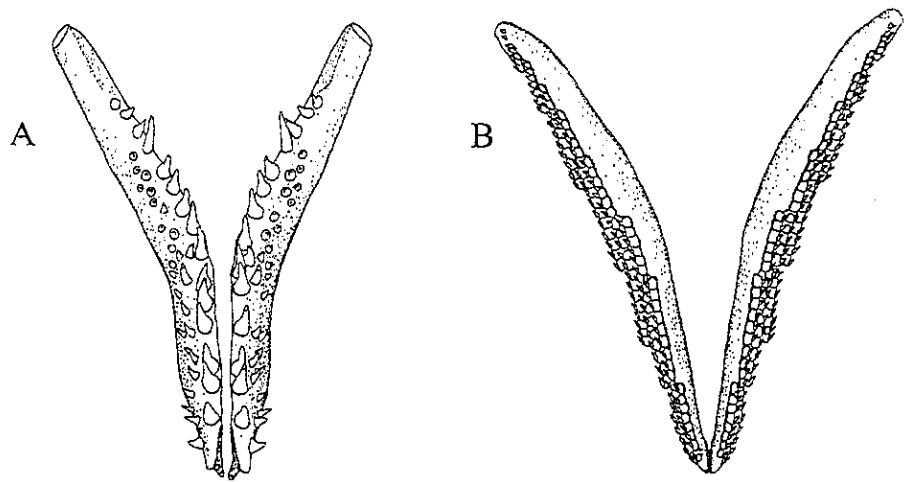
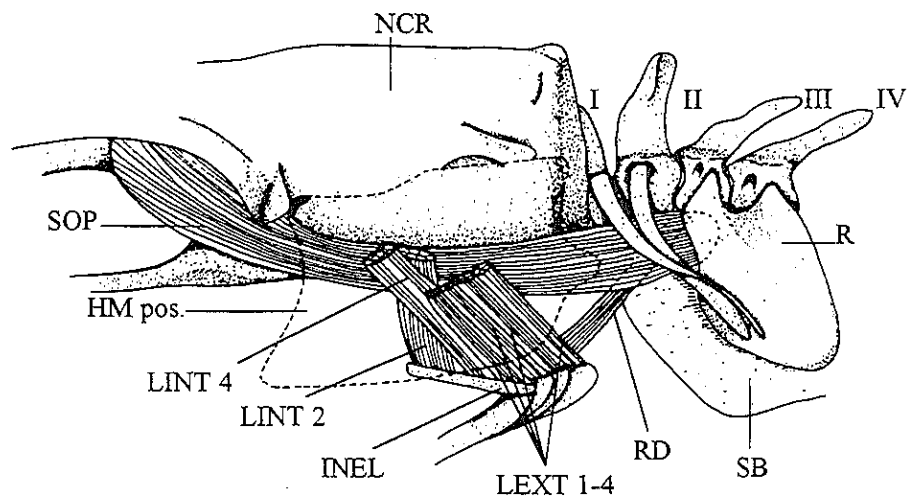Fig. 5. - Dorsal view of the 5th pharyngobranchial in *Encheliophis boraborensis* (A) and *E. gracilis* (B).

Fig. 6. - Lateral view of the upper pharyngeal muscles and of the sound-producing muscles in *E. homei*.

E. gracilis, there is no projection of the premaxillaries upon mouth opening and the mouth opens less widely. Furthermore, the premaxillaries and maxillaries do not show interdependent movements.

Skull of the pharyngeal region (Fig. 4)

The disposition and the form of the fifth ceratobranchials (= lower pharyngeal jaws, LPJ) differ between the four species examined. Generally speaking, in *Encheliophis boraborensis*, *E. homei* and *Carapus acus*, the 5th ceratobranchials are robust, their upper surface has big teeth on the inner side and small teeth on the outer side (Fig. 5A). These teeth are conical and are directed toward the back of the buccopharyngeal cavity. In *E.*

gracilis, the 5th ceratobranchials are flattened and separated from each other posteriorly. From a dorsal view, they slope laterally and have only cardiform teeth on their inner dorsal surfaces (Fig. 5B). In these four species, a membrane joins the right and left ceratobranchials.

In all four species, the 2nd, 3rd and 4th pharyngobranchials form the upper pharyngeal jaws (UPJ). *Carapus acus* has the largest 2nd pharyngobranchials. This element is smaller in *E. boraborensis* and *E. homei*, and *E. gracilis* has greatly reduced 2nd pharyngobranchials. In *E. gracilis*, the 4th pharyngobranchials are larger compared to the other species. Teeth are more numerous and more tapered in *E. gracilis*.

In all examined species, there are two characteristics (Fig. 4): (A) the 1st epibranchial does not connect with the 2nd pharyngobranchial. This role is assumed by an interarcual element (Allis, 1915) articulated on the one hand on the 1st epibranchial and on the other hand on the 2nd pharyngobranchial; (B) the 1st pharyngobranchial does not connect the neurocranium but is reduced and lost in conjunctive tissue.

Note: *E. boraborensis* and *C. acus* also have teeth on the 3rd basibranchial and on the 3rd hypobranchials, whereas *E. homei* only has teeth on the 3rd basibranchial. These teeth are missing in *E. gracilis*.

Musculature of the pharyngeal region (Fig. 6)

The ventral musculature of the branchial basket is that usually encountered in the Teleostei and is not described here. However, it is important to note that (A) the *levator interni* and *externi* originate on the inner side of the hyomandibular (except some fibres of the 3rd *levator internus* that attach to the neurocranium); (B) there is no *levator posterior* and (C) the *retractores dorsalis* muscles run obliquely between the primary sound-producing muscles and are attached posteriorly to the lower surface of the 2nd and 3rd vertebrae.

DISCUSSION

Several characters are indicative of a carnivorous lifestyle in all four species. (1) There are major sets of conical teeth on the vomer (Arnold, 1953; Trott, 1970; Williams, 1984) palatines and jaws (Fig. 1); (2) There is a wide-split mouth with robust dentaries; and (3) A_2 and A_3 form a very powerful set of muscles inserting on the suspensorium, as in most teleosts (Liem, 1970; Lauder and Liem, 1981; Vandewalle *et al.*, 1995), but also with fibres on the neurocranium (Fig. 2). Vandewalle *et al.* (1982) suppose that such insertions are indicative of a prey catching by grasping. In addition, the powerful *adductores mandibulae* are associated with hyomandibular thickenings that are believed to be necessary to prevent bone deformation (Osse, 1969; Dutta, 1975; Vandewalle, 1978). The bisector of the angle formed by thickenings 1 and 3 points toward the coronoid processes of the dentary (short and near the quadrate); its position varies little during mouth opening (Fig. 7). The direction of this bisector is thus probably that of the force exerted on the hyomandibular and mandible by contraction of A_2 and A_3. If so, the 1 and 3 thickenings might a response to the stress 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 practically parallel to the quadrate thickening. It seems more difficult to explain thickening 2. Its presence probably reflects the added effects not only of A_2 and A_3 muscle contraction and the contraction of *levator arcus palatini*, and *adductor palatini*.
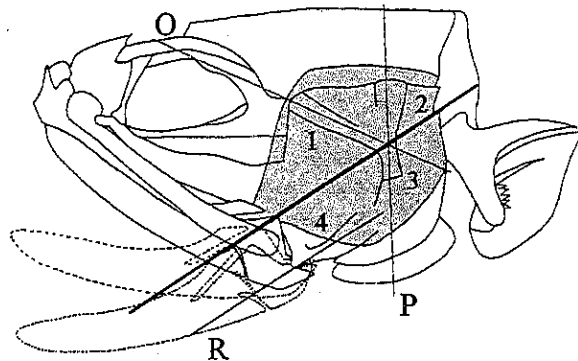
Fig. 7. - Simplified lateral view of the head in *Carapus acus*. Numbers 1 to 4 indicate the suspensorium thickenings; the grey surface represents the position of the A_2-A_3 muscles. The bold line is the bisector of the angle formed by O and P; R is the parallel to the bisector running through the quadrate-dentary joint.

Among these four species, anatomical characters seem related to their way of life. Carnivorous features are more pronounced in *Encheliophis boraborensis*, whose musculature, jaws, and suspensorium are the best developed, allowing the capture of "tough" prey, such as fishes and crustaceans. This is in keeping with stomach contents analyses of this species. Although these characters are somewhat less developped in *Carapus acus* and *E. homei*, they should be able to feed on prey with an endo-and/or exoskeleton. On the other hand, *E. gracilis* has thin buccal parts, uniserial set of teeth on the jaws and palatines, and maxillary ending in a spine (Fig. 1B). This morphology suits the diet which consists of soft food (holothurian tissues). These diet differences among species also relate to the mouth opening. The fact that *E. boraborensis*, *E. homei* and *C. acus* can protrude their upper jaw allows them to have a wide mouth opening. This protrusion is possible because the buccal parts are quite independent (Schaeffer and Rosen, 1961; Alexander, 1967; Lauder and Liem, 1981). On the other hand, *E. gracilis* displays no protrusion and no wide opening mouth. The most important factor of this feature seems to be the lack of mobility between maxillaries and premaxillaries: they are joined by dense connective tissues (Li. 5) along their entire length. In addition, the upper jaws do not have much mobility because the A_1 bundles are inserted along the entire maxillary length and not on a ligament (Li. 4) and because they are concealed and confined by skin.

A wide mouth opening with a small protrusion is found in the three species that eat crustaceans and fishes. It permits the capture and retention of larger prey. On the other hand, a wide mouth opening is not necessary in the case of *E. gracilis*: in the host (and victim), there is no probability to lose the gonad or the viscera of the holothuroid. In addition the more numerous cardiform teeth of *E. gracilis* could consist in a sawing system that cuts soft tissue.

The four species possess two sound-producing muscles (Courtenay and McKittrick, 1970) that originate on the orbital roof, run ventrally alongside the neurocranium and attach to the swim bladder (Fig. 6). The topographic situation of the muscles could have two consequences at the branchial basket level. (1) It could indicate that the 1st pharyngobranchials are not involved in the suspension of the upper pharyngeal elements which do not have rigid suspension; (2) the remarkable origin sites of the *levatores* on the inner side of the hyomandibular and not on the neurocranium as is the case in all Teleosteans

known from this point of view (Holstvoogd, 1965; Nelson, 1967; Lauder, 1983; Liem and Sanderson, 1986; Claes and De Vree, 1992; Vandewalle *et al.*, 1995) is also probably linked to the presence of the sound-producing muscles. Their insertion on a mobile element could have functional implications. *Encheliophis boraborensis*, *E. homei* and *C. acus* all have the upper jaw teeth directed toward the rear and the inside, the strength of 5th ceratobranchials which have close-set sharp teeth, the thinness of the 4th *levator interni*, the presence of the *retractores dorsalis* on the one hand and the possible presence of entire prey in the stomach contents on the other hand suggest that the pharyngeal jaws are only able to transport food. In *E. gracilis*, weaker and more widely spread lower pharyngeal jaws with cardiform teeth as opposed to the longer teeth of the upper pharyngeal jaws could be related to cutting soft prey in addition to the transport movements.

All the *E. gracilis* stomach contents showed the exclusive presence of holothurian tissue as already reported in the literature (Strasburg, 1961; Smith, 1964; Branch, 1969; Trott, 1970; Van Den Spiegel and Jangoux, 1989). This is in accordance with our cephalic morphological study that shows poorly developed and somewhat different oral and pharyngeal carnivorous features in comparison with the three other species.

Encheliophis boraborensis has the most highly developed carnivorous characters and feeds only on non-holothurian tissues caught by grasping (Trott, 1970; Van Den Spiegel and Jangoux, 1989). Most authors have established that *C. acus* and *E. homei* feed on crustaceans or fishes (including cannibalism) (Arnold, 1956; Smith, 1964; Hipeau-Jacquotte, 1967; Trott, 1970; Trott and Trott, 1972; Van Den Spiegel and Jangoux, 1989). However, Arnold (1953) and Hipeau-Jacquotte (1967) mention the presence of holothurian tissues in, respectively, *C. acus* and *E. homei*, but these authors have combined data from juvenile and adult exemplars. It seems that young individuals feed on holothurian tissues then modification of the diet occurs in the adult stage when non-holothurian tissues are the principal source of food. Our cephalic examinations support this hypothesis because these fishes have morphological features closely similar to those of *E. boraborensis*: set of teeth on the dentaries, protrusion ability, muscular organization, etc. It would be interesting to know the diet of young *E. boraborensis* in order to see if they feed on holothurian tissues. If so, *E. boraborensis*, *E. homei* and *C. acus* have three ways of life during their life. They are free living and planktivorous (Williams, pers. com.) during their pelagic larval stage; they enter Holothuroid and are parasitic during their juvenile stage; they continue to enter Holothuroid during their adult stage but the host is used as a shelter. *Encheliophis gracilis* has lost this third way of life and is adapted to the parasitism.

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