Comparative analysis of the head morphology of Pacific temperate kyphosid fishes: a morpho-functional approach to prey-capture mechanisms

Análisis comparativo de la morfología cefálica de los peces kifósidos del
Pacífico templado: una aproximación morfo-funcional a los
mecanismos de captura de presas

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ABSTRACT

Vial & Ojeda (1990) proposed that the low diversity of herbivorous fishes observed among Percoids might be owing to the existence of morpho-functional restrictions of the feeding apparatus that hinder the acquisition of efficient mechanisms for cropping and ingesting plant material. The morphological and functional evidence presented therein for the herbivorous kyphoid *Girella laevifrons* indicates that its morphological specializations are related to structural decouplings of the anterior and posterior regions of the buccal cavity involving the jaw and the hyoid arch. Functionally, these decouplings allow the ingestion of algae in a continuous fashion at low energetic cost. In this study, we evaluate the general validity of the proposed model by means of a morphological and functional comparative analysis of the cephalic structures of the four most abundant Kyphosid species of the Chilean coast: the girellids *Girella laevifrons* (Tschudi), *Girella albostriata* Steindachner, and *Graus nigra* Philippi, and the scorpid *Scorpis chilensis* Guichenot. We found great osteological and myological similarities between the two strict herbivores, *G. albostriata* and *G. laevifrons*, thus suggesting that the mechanism previously described for the latter species corresponds very closely to that of the former. This mechanism provides for mandibular manipulation carried out independently by the upper jaw and for a decoupling of the lower jaw into two mechanical units. *Graus* and *Scorpis* display a somewhat different morphological design. Although both maintain the intrahyoid decoupling shared by all kyphosid species, they do not present mechanical independence between the upper and lower jaw, nor a capacity for intramandibular movements. In *Graus*, teeth are well developed, conical, and slightly curved toward the interior. These characteristics make possible a trophic mechanism primarily based on a strong biting especially well suited for carnivory. The structural plan of *Scorpis* appears more distant from species in the other two genera, althoug it shares with them characters such as the double tendon of the A1 muscle in the maxilla, the intrahyoid articulation, the type of teeth, their replacement system, and the general design of the suspensorium. The particular morphology of the adductor muscles, and the mandibular design of *Scorpis* suggest a trophic mechanism mainly based on a rapid suction. From a functional viewpoint, the structural differences encountered in the four species analyzed may be understood as modifications related to their different mechanisms of prey capture.

Key words: Kyphosidae, herbivory, head morphology, feeding apparatus, functional design.

RESUMEN

Vial & Ojeda (1990) propusieron que la baja diversidad de peces herbívoros observada en Percoideos podría deberse a la existencia de restricciones morfofuncionales del aparato alimentario que impedirían el desarrollo de mecanismos eficientes de captura e ingestión de algas. La evidencia morfológica y funcional presentada por Vial & Ojeda (1990) para el pez herbívoro *Girella laevifrons* indica que tales especializaciones morfológicas están relacionadas con desacoplamientos estructurales de las regiones anterior y posterior de la cavidad bucal que incluyen la mandíbula y el arco hioideo. Funcionalmente, estos desacoplamientos permiten la ingestión de algas en forma continua y con un bajo costo energético. En el presente estudio, evaluamos la validez general del modelo propuesto previamente a través de un análisis morfológico y funcional comparativo de las estructuras cefálicas de las cuatro especies de kifósidos más abundantes de la costa de Chile: los girélidos *Girella laevifrons* (Tschudi), *Girella albostriata* Steindachner y *Graus nigra* Philippi, y el escórpido *Scorpis chilensis* Guichenot. Se encontró una gran similitud osteológica y miológica entre los dos herbívoros estrictos, *G. laevifrons* y *G. albostriata*, lo cual sugiere que los mecanismos previamente descritos para la primera especie corresponden con exactitud a los de la última. Este mecanismo permitiría una manipulación mandibular llevada a cabo independientemente por la mandíbula superior y por el desacoplamiento de la mandíbula inferior en dos unidades mecánicas. *Graus* y *Scorpis* presentan un diseño diferente. Aunque ambas conservan un esquema hioideo desacoplado que es común en kifósidos, ellas no presentan independencia mecánica entre maxilar y mandíbula ni movimientos intramandibulares. En *Graus*, los dientes son fuertes, cónicos y curvados hacia el interior. Estas características hacen posible un

mecanismo trófico basado en una fuerte mordida especializada para la carnivoría. El plan estructural de *Scorpis* aparece más distante de las especies de los otros géneros, aunque comparte con ellas caracteres tales como una doble inserción del músculo Al en la maxila, la articulación intrahioidea, el tipo de dientes y su sistema de reemplazo, y el diseño general del suspensorium. La particular morfología de los músculos aductores y el diseño mandibular de *Scorpis* sugieren un mecanismo trófico basado principalmente en una succión rápida. Desde un punto de vista funcional, las diferencias estructurales observadas en las cuatro especies analizadas pueden ser comprendidas como modificaciones relacionadas con sus diferentes mecanismos de captura de presas.

Palabras claves: Kyphosidae, herbivoría, morfología cefálica, aparato alimentario, diseño funcional.

INTRODUCTION

Kyphosidae is a large Perciform family widely distributed in tropical and temperate waters (Nelson 1984). This family is also one of the few known percoid groups in which most of its members have strict herbivorous diets (Randall 1967). This is especially true for those species belonging to the subfamilies Kyphosinae and Girellinae (see Horn 1989).

The presence of non-herbivorous species within the Girellinae group, recently reported by Johnson & Fritzsche (1989), and the primarily omnivorous habits of most of the species included in the Scorpininae, the third subfamily (see Nelson 1984), make Kyphosids and unusual and interesting group in which to explore morphological specializations evolved in closed related species concerning prey-capture mechanisms. This approach may also serve to identify alternative explanations of the uncommon occurrence of herbivory among teleost fishes (see Liem & Osse 1975, Liem 1979).

In a recent paper, we (Vial & Ojeda 1990) proposed that the low diversity of herbivorous fishes observed among Percoids, may well be due to the existence of morpho-functional restrictions of the feeding apparatus hindering the acquisition of efficient mechanism for cropping and ingestion of plant material. The morphological and functional evidence presented for the herbivorous kyphosid *Girella laevifrons* indicates that the morphological specializations are related with structural decouplings of the anterior and posterior regions of the buccal cavity involving the jaw and the hyoid arch (Vial & Ojeda 1990). Functionally, these decouplings allow the ingestion of algae in a continuous fashion at low energetic cost. Furthermore, the structural organization described for *G.*

laevifrons —characterized by a unique articulation between the dentary and the articular— angular, and teeth more or less specialized, restricted to the anterior regions of the dentary and of the premaxilla - has been also found in other percoids groups having herbivorous representatives, such as Scarids, Blennies and Acanthurids (Tedman 1980, Vanderwalle *et al.* 1982, Gosline 1987).

The morphological specializations and feeding mechanism documented for *Girella laevifrons*, which may provide a general model explaining the herbivorous design in Kyphosidae, however, can only be evaluated by means of a morphological and functional comparative analysis of its members.

The main goals of this study were: (1) to carry out a comparative description of the cephalic anatomy of the four most abundant Kyphosid species of the Chilean coast: the girellids *Girella laevifrons* (Tschudi), *G. albostriata* Steindachner, and *Graus nigra* Philippi, and the scorpid *Scorpis chilensis* Guichenot and (2) to analyze the morpho-functional aspects that could represent exaptive modifications for effectively feeding on macroalgae.

MATERIALS AND METHODS

Observations of bones and cartilages of the cephalic region were based on specimens cleared and stained following the technique of Dingerkus & Uhler (1977). Muscle and ligament descriptions were made on individuals previously fixed and preserved in a 10% solution of buffered formalin-sea water mixture. Observations and analyses of mandibular movements were carried out by mechanical manipulations on fresh and stained specimens. All observations

and figures were made with the aid of a Wild M5 stereomicroscope and a drawing tube. The terminology used in this study follows that of Osse (1969) for bones, Stiassny (1986) for ligaments, and Winterbottom (1974) for muscles.

Material examined

Girella laevifrons: 8 specimens, 30-220 mm total length (TL), collected in tidepools at Quintay (33°11'S; 72°43'W) and Las Cruces (33°30'S; 71°38'W) Chile, March 1989.

Graus nigra: 5 specimens, 25-330 mm TL, collected in tidepools at Quintay (33°11'S; 72°43'W) and Las Cruces (33°30'S; 71°38'W), March 1989.

Girella albostriata: 3 specimens, 110-120 mm TL, collected off Juan Fernández Archipelago (33°77'S; 78°50'W) in December 1980.

Scorpis chilensis: 5 specimens, 35-350 mm TL, collected off Juan Fernández Archipelago (33°77'S; 78°50'W) in December 1980.

RESULTS

Osteological comparison

Splanchnocranium

The structural organization of the splanchnocranium presents a similar scheme in all four species (Fig. 1). It is characterized by the development of the opercular system, with relatively broad, high bones, and a preopercle with a posterior vertical arm about twice the length of the anterior arm, which runs horizontally. A large cartilaginous zone lies between the quadrate and metapterygoid and between the symplectic and the distal end of the hyomandibular. The entopterygoid and ectopterygoid are laminar, elongated, arranged almost vertically and weakly connected to the palatine. The symplectic is shaped like a thin rod, whose anterior end is located mesially in a depression on the quadrate which gives rise to the spine.

Some distinctive characters differentiate the species examined. At the level of the suspensorium, the hyomandibular of *Scorpis*

chilensis (Fig. 1D) has a narrower base than the rest of the species, while in *Graus nigra* (Fig. 1C) the base of this bone is wide and strong. The metapterygoid is triangular in *Scorpis* and quadrangular in the other species studied; the outer lamina in the posterior border of this bone is well developed in *Graus* and *Girella* and encloses a bundle of the palatine arch levator muscle.

In *S. chilensis*, the relationships between metapterygoid, entopterygoid, and ectopterygoid bones are direct and strong whereas in the other three species there is great flexibility among them, the same as in the case of the palatine. Only in *Scorpis* the ectopterygoid hold a dentate plate in its inner face.

Girella laevifrons, G. albostriata and *Graus nigra* present a very similar design in the palatines, maxillae and premaxillae: the palatine is robuts, with a wide triangular proximal base and a well developed cilindric distal end. In *S. chilensis* the base of this bone is elongated and its distal portion is smaller and weaker. The maxilla is long and thin in *Scorpis* while in the other species it is shorter and robust, with a well developed mesian process on the outer border. The premaxilla of *Graus* and *Girella* are similar, triangular in shape, very robust, with an ascending process of about the same size as the alveolar process and with a thickened anterior edge in relation to more developed anterior teeth. In *Scorpis* the premaxilla is weaker and its ascending process, much shorter than the dentate border; the anterior border is thin (Fig. 1).

The lower jaw is also similar in *Graus* and *Girella* (Fig. 1). It is composed of thick and strong bones; the dentaries have a thickened anterior border, and a wide firm symphysis, particularly in both *Girella* species where they form a specially large and firm anterior tranverse zone, in concordance to the arrangement of the teeth (Fig. 1). The jaw of *Graus* is more elongated than that of the former species. On the other hand, the jaw of *Scorpis*, has laminar bones and the dentaries have no thickened border; the symphysis is narrow and mobile (Fig. 1). The mobile
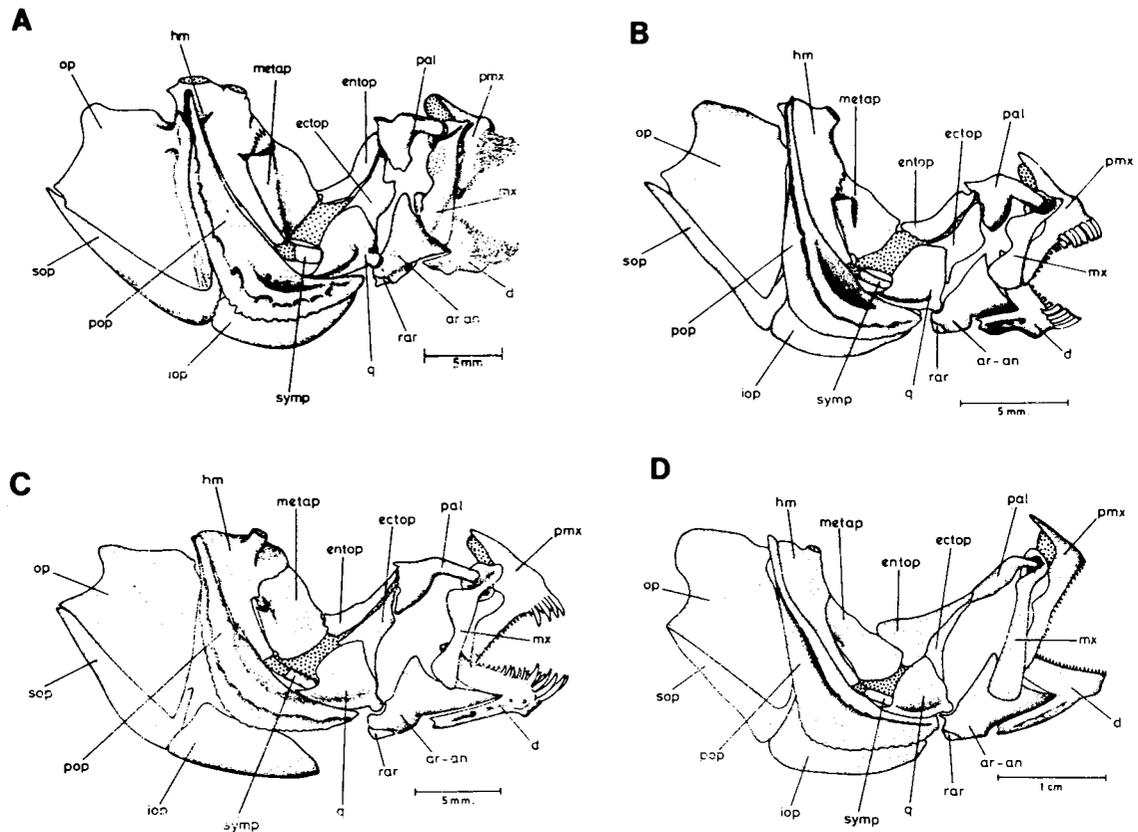
Fig. 1: External view of right splanchnocranium of *Girella laevifrons* (A), *Girella albostriata* (B), *Graus nigra* (C), and *Scorpis chilensis* (D). ar-an = articular-angular, d = dentary, ectop = ectopterygoid, entop = entopterygoid, hm = hyomandibular, iop = interopercle, metap = metapterygoid, mx = maxilla, op = opercle, pal = palatine, pmx = premaxilla, pop = preopercle, q = quadrate, rar = retroarticular, sop = subopercle, symp = symplectic.

Vista externa del esplacnocráneo derecho de *Girella laevifrons* (A), *Girella albostriata* (B), *Graus nigra* (C), y *Scorpis chilensis* (D). ar-an = articular-angular, d = dentario, ectop = ectopterigoides, entop = entopterigoides, hm = hiomandibular, iop = interopérculo, metap = metapterigoides, mx = maxilar, op = opérculo, pal = palatino, pmx = premaxilar, pop = preopérculo, q = cuadrado, rar = retroarticular, sob = subopérculo, symp = simpléctico.

joint between dentary and articular-angular described for *G. laevifrons* (Vial & Ojeda 1990) shows the same mobility in *G. albostriata*. In *Graus* and *Scorpis* there is no mobile joint between both bones.

The structure, design and arrangement of the teeth in premaxillae and dentaries display remarkable differences. All the species considered have two types of teeth. The first type are small, slightly tilted and arranged in several rows at the inner zone of the anterior border of premaxillae and dentaries, strongly attached to the bones; they have different patterns: tricuspid in *Girella*, with triangular border in *Scorpis*, and simple and conical in

Graus. The second type of teeth are arranged more externally, usually in a single row; they are larger and, in all species, present a replacement system from the outside (Johnson & Fritzsche 1989).

In both *Girella* species, the outer teeth are formed by two articulated segments: the cylindrical basal segment is not directly related to the bone; it is immersed in a matrix of fibrous tissue which fills the alveolar cavity of the anterior border of premaxillae and dentaries. The distal segment has an articular cavity on its outer border which is inserted in a condyle of the basal segment. The proximal part of this segment is laterally compressed, while

the distal end is flattened and curved toward inside, with tricuspid border in *Girella albostriata* and small specimens of *Girella laevifrons*; in bigger individuals of the latter species it adopts the shape of a curved spatula (Fuentes 1981, Vial & Ojeda 1990). In *Scorpis*, the outer teeth are slightly larger than the inner ones; the distal border is triangular, with a median sharp tip, not becoming strictly tricuspid. *Graus nigra* has well developed outer teeth, conical, slightly curved toward the interior and obliquely directed forward with respect to the bone border; there are no articulate segments and its proximal ends are strongly articulated to the bone.

Hyoid bar

In all four species studied, the hyoid bars are short and tall (Fig. 2). The ceratohyal presents an anterior ventral tip which articulates with the hypohyal by cartilage;

the dorsal border has a narrow cartilaginous band which extends from the articular zone with the epihyal. Near the dorsal border the ceratohyal shows an oblong foramen like that described by McAllister (1968) for Bericiforms fishes.

The most striking feature of the hyoid bar of these four species is the mobile articulation between the dorsal anterior border of ceratohyal and dorsal hypohyal, which allows the rotation of the ceratohyal along its longitudinal axis (see Fig. 2).

Scorpis has 7 branchiostegal rays, while the other three species have only 6.

Myological comparison

The musculature associated with the buccal system has multiple shared features among the four species studied.

The adductor mandibulae muscle A1 has two insertions to the maxillary bone, one
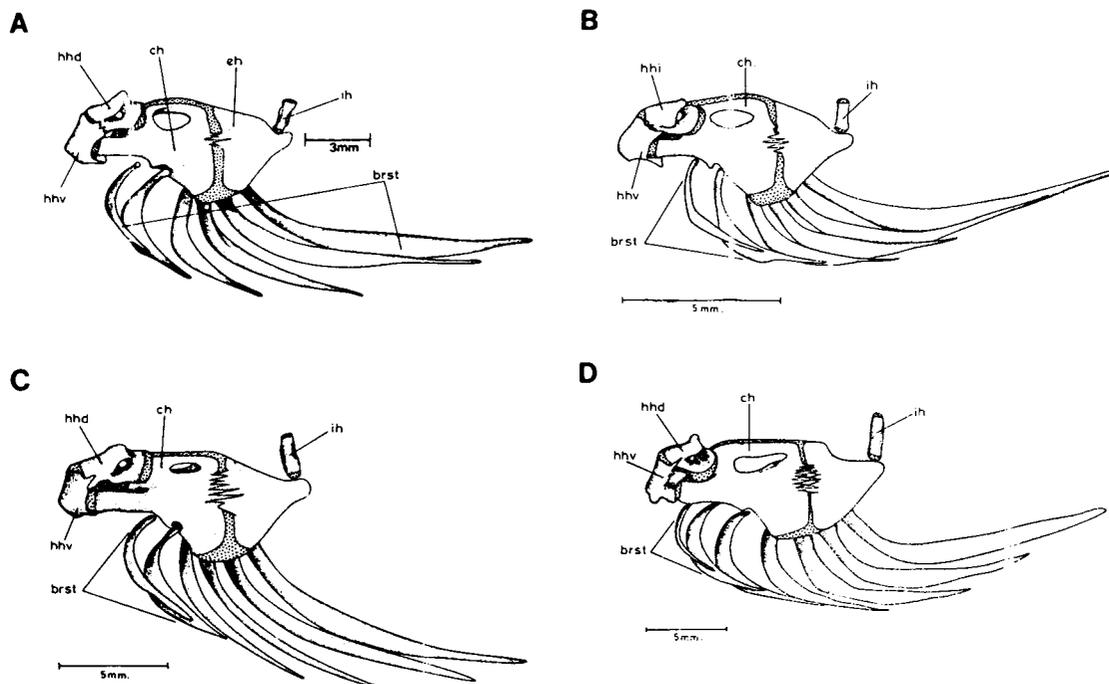

Fig. 2: Internal view of right hyoid arch of *Girella laevifrons* (A), *Girella albostriata* (B), *Graus nigra* (C), and *Scorpis chilensis* (D). brst = branchiostegal rays, ch = ceratohyal, eh = epihyal, hhd = dorsal hypohyal, hhv = ventral hypohyal, ih = interhyal.

Vista interna del arco hioideo derecho de *Girella laevifrons* (A), *Girella albostriata* (B), *Graus nigra* (C) y *Scorpis chilensis* (D). brst = radios branquiostegales, ch = ceratohial, eh = epihial, hhd = hipohial dorsal, hhv = hipohial ventral, ih = interhial.

in the outer face of the maxillary arm and the other in the inner face, very close to the maxillary head; furthermore, this muscle is related with the lower jaw through a tendon that reaches the inner face of the articular-angular near its ventral border.

In both *Girella* species the A1 muscle bears two anterior fascicles associated with each maxillary tendon (A1 α and A1 β). Further, *G. laevifrons* has fibers that are directly inserted in the outer face of the maxilla (Figs. 3 and 4). A1 is not related to the primordial ligament in either species.
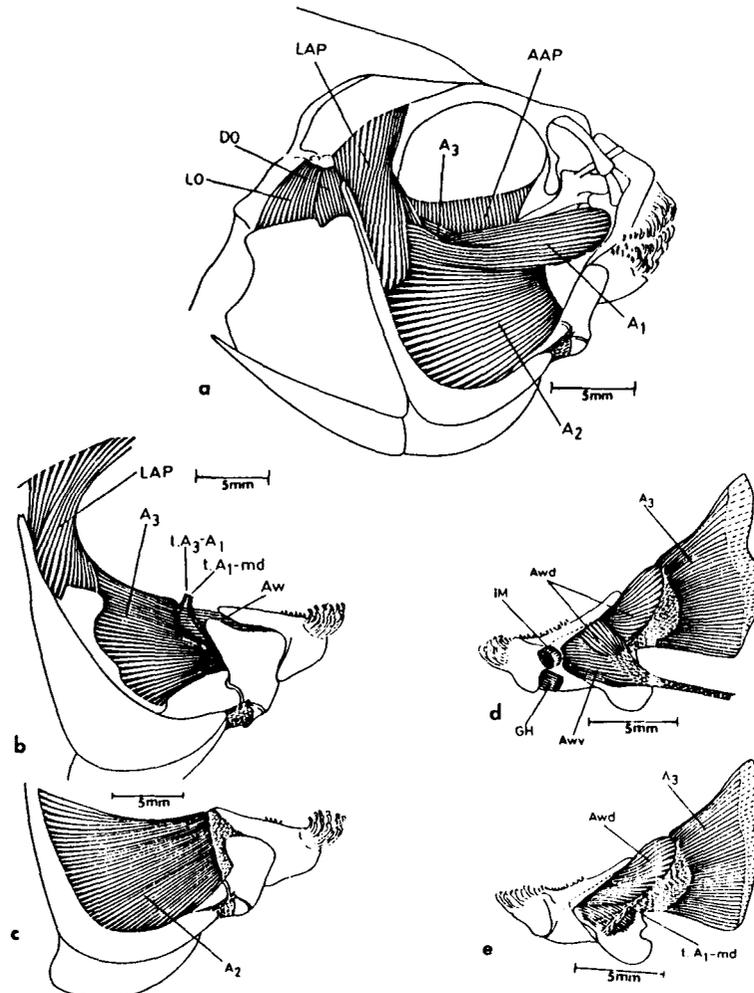

Fig. 3: *Girella laevifrons.* View of muscles of the right side of the head. (a) general lateral view; (b) lateral view of A3 adductor mandibulae muscle, note the A3-Aw connection; (c) A2 attachment on dentary and articular-angular; lateral (d) and (e) internal views of A3 and Aw adductor mandibulae muscles. A = adductor mandibulae (1-3), AAP = adductor arcus palatini, Aw = adductor mandibulae Aw (Awd = dorsal fascicle; Awv = ventral fascicle); DO = dilatator operculi, GH = geniohyoideus, IM = intermandibularis, LAP = levator arcus palatini, t A3-A1 = tendon of adductor mandibulae A1 and A3, t A1 md = tendon of adductor mandibulae A1 which is inserted on the lower jaw.

Girella laevifrons. Vista de los músculos del lado derecho de la cabeza. (a) vista lateral general, (b) vista lateral del músculo aductor mandibular A3; nótese la conexión A3-Aw, (c) vista lateral de la inserción del músculo A2 en el dentario y articular-angular, (d) y (e) vistas internas de los aductores mandibulares A3 y Aw. A = aductor mandibular (1-3), AAP = aductor arco palatino, Aw = aductor mandibular Aw (Awd = dorsal y Awv = ventral), DO = dilatador del opérculo, GH = geniohioideo, IM = intermandibularis, LAP = elevador del arco palatino, tA3-A1 = tendón de los aductores mandibulares A1 y A3, tA1md = tendón del aductor mandibular A1 que se inserta en la mandíbula inferior.
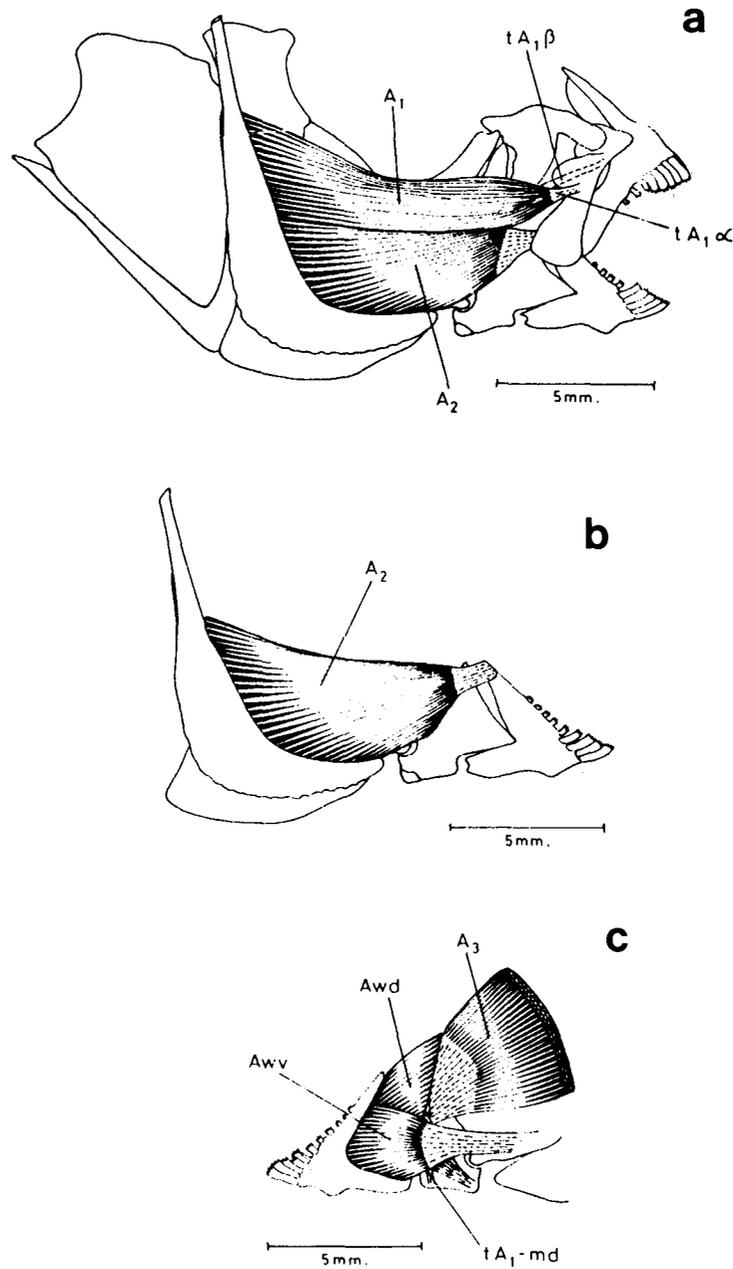
Fig. 4: Girella albostriata. View of the adductor mandibulae muscles of the right side of the head. (a) general lateral view; (b) lateral view of A2 adductor mandibulae muscle; (c) internal views of A3 and Aw adductor mandibulae muscles. See Figure 3 for other abbreviations.

Girella albostriata. Vista de los músculos aductores mandibulares del lado derecho de la cabeza. (a) vista lateral general; (b) vista lateral del músculo aductor mandibular A2; (c) vista interna de los músculos aductores mandibulares A3 y Aw. Las otras abreviaciones al igual que en Fig. 3.

In *Graus* and *Scorpis* the A1 muscle is not differentiated into distinct fascicles, though they maintain the double tendinous insertion on the maxilla (Figs. 5 and 6).

Moreover, in these species, the muscular fibres are associated with the primordial ligament which connect the maxilla with the articular-angular. The arrangement of
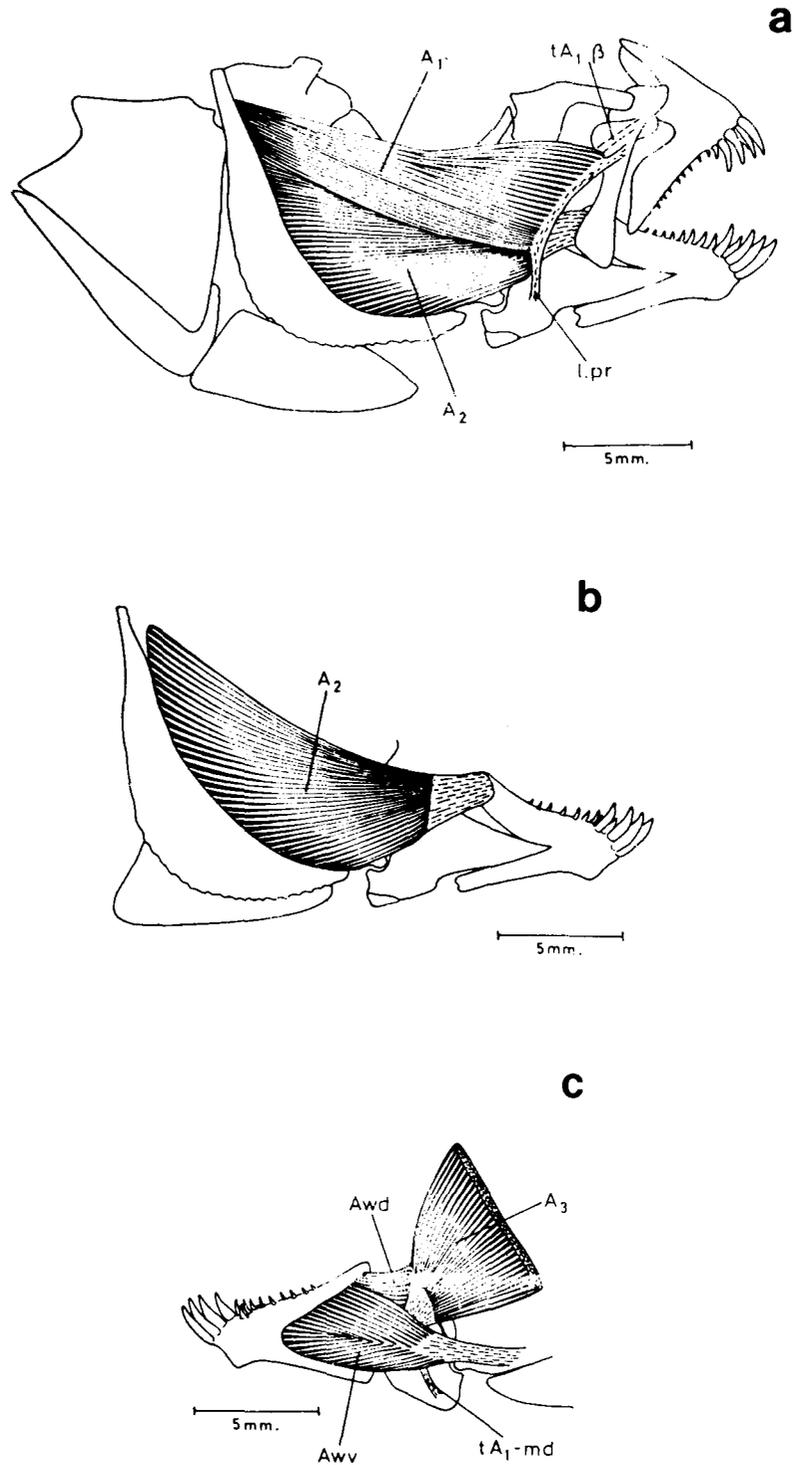
Fig. 5: Graus nigra. View of the adductor mandibulae muscles of the right side of the head. (a) general lateral view; (b) lateral view of A2 adductor mandibulae muscle; (c) internal views of A3 and Aw adductor mandibulae muscles. See Figure 3 for other abbreviations.

Graus nigra. Vista de los músculos aductores mandibulares del lado derecho de la cabeza. (a) vista lateral general; (b) vista lateral del músculo aductor mandibular A2; (c) vista interna de los músculos aductores mandibulares A3 y Aw. Las otras abreviaciones al igual que en Fig. 3.
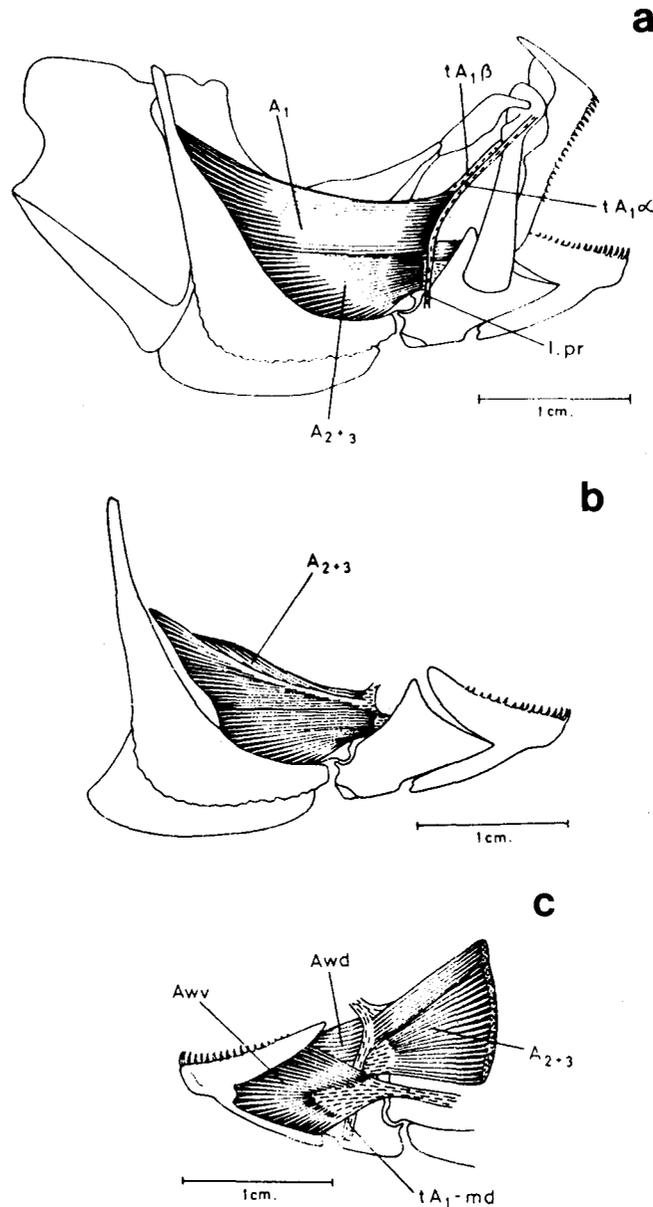
Fig. 6: Scorpis chilensis. View of the adductor mandibulae muscles of the right side of the head. (a) general lateral view; (b) lateral view of A2 adductor mandibulae muscle; (c) internal views of A3 and Aw adductor mandibulae muscles. See Figure 3 for other abbreviations.

Scorpis chilensis. Vista de los músculos aductores mandibulares del lado derecho de la cabeza. (a) vista lateral general; (b) vista lateral del músculo aductor mandibular A2; (c) vista interna de los músculos aductores mandibulares A3 y Aw. Las otras abreviaciones al igual que en Fig. 3.

A1 is similar in these two species, but the muscle is much more developed in *Graus.*

In *Girella* and *Graus,* the Adductor mandibulae muscle A2 presents a peculiar tendinous insertion in the dentary coronoid process. In *Scorpis,* however, the Adductor mandibulae muscles A2 and A3 are fused and inserted in the posterior border of the articular-angular (Figs. 3-6).

In all species studied the adductor mandibulae muscle A3 (A2 + A3 in *Scorpis*) is well developed and is inserted in the co-

ronomeckelian bone. Furthermore, in all of them, the dorsal fascicle of the Aw muscle, is posteriorly associated with the A3 (A2 + A3 in *Scorpis*), but it is more developed in both *Girella* species.

DISCUSSION

From a functional viewpoint, the structural differences encountered in the four analyzed species can be understood as modifications related to different mechanisms of prey capture.

The osteological and myological similarities between *Girella albostriata* and *G. laevifrons* suggest that the mechanism described by Vial & Ojeda (1990) for the latter species corresponds exactly to that of the former. This mechanism provides for mandibular manipulation carried out independently by the upper jaw and decoupling of the lower jaw into two mechanical units, together with the specialized teeth and the possibility of generating great suction for the capture and ingestion of macroalgae (Fig. 7).

The structural scheme of *Graus nigra* is somewhat unique, particularly in those features that have been considered as special adaptations to herbivory (Vial & Ojeda 1990). The connection of the A1 muscle to the lower jaw by means of the primordial ligament is and important determinant of the force exerted by this muscle to the action for mandibular closing. A mechanism for strong biting is obtained with the development of the suspensorium, particularly hyomandibular and metapterygoid (Fig. 1C), the higher development reached by the adductor muscles due to the increase of insertion areas in these bones (Fig. 5), the maintenance of the insertion of A2 in the dentary coronoid process which derives in a greater power arm of the muscle, and the firm design of the teeth. Since the movements of maxillary and lower jaw are connected by the primordial ligament, both jaws act mechanically like a system of very strong and precise pliers (Fig. 8A). The tilted arrangements of the outer primary teeth is related to this coordination in the movements of both jaws so that, when biting, the forces exerted follow the
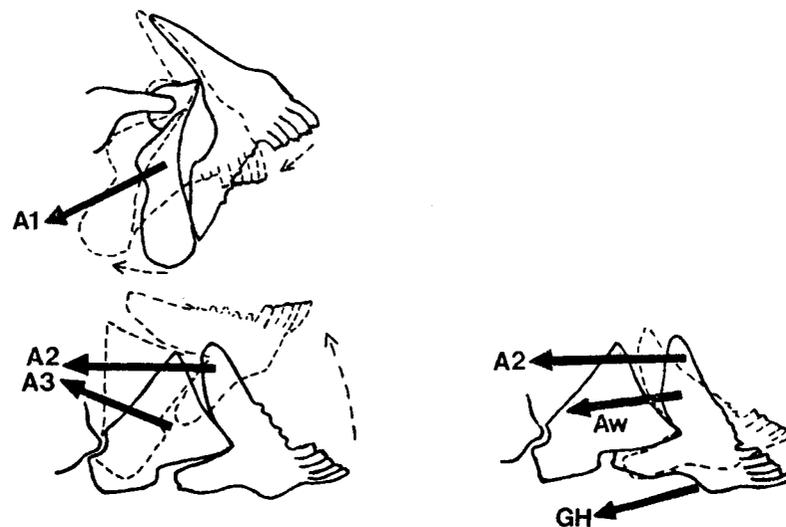
Girella albostriata

Fig. 7: Girella albostriata. Movements of the upper jaw (a), and lower jaw (b and c) mediated by the action of the adductor mandibulae muscles A1, A2, A3, Aw, and Genio-hyoideus (GH).

Girella albostriata. Movimientos de la mandíbula superior (a) y mandíbula inferior (b y c) mediadas por la acción de los músculos aductores mandibulares A1, A2, A3, Aw y Geniohioideo (GH).
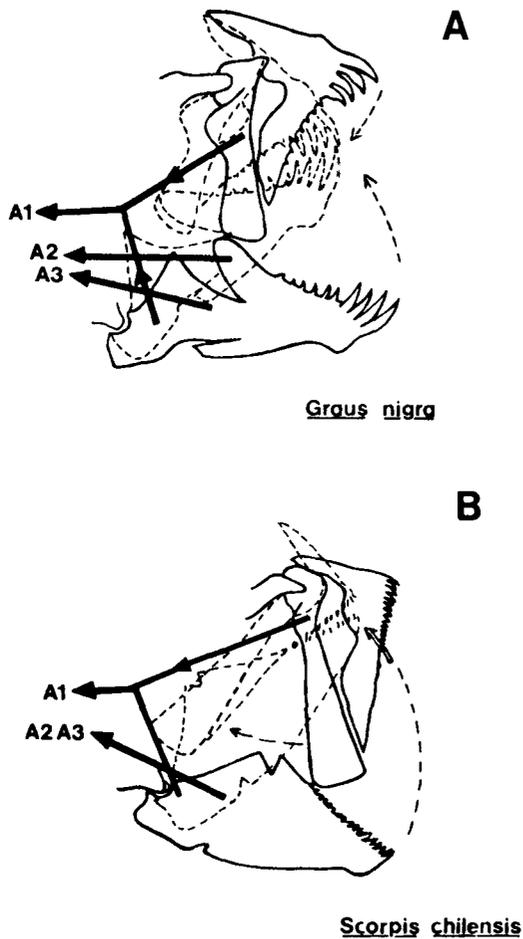
Graus nigra

Scorpis chilensis

Fig. 8(A): Graus nigra. Movements of the upper and lower jaw mediated by the action of the adductor mandibulae muscles A1, A2, and A3.

(A) Graus nigra. Movimientos de la mandíbula superior e inferior mediada por la acción de los músculos aductores mandibulares A1, A2 y A3.

(B): Scorpis chilensis. Movements of the upper and lower jaw mediated by the action of the adductor mandibulae muscles A1, and A2 + A3.

(B): Scorpis chilensis. Movimientos de la mandíbula superior e inferior mediada por la acción de los músculos aductores mandibulares A1 y A2+A3.

longitudinal axis of the teeth, thus giving them great power. This type of mechanism is in keeping with the feeding habits described for this exclusively carnivorous species which feeds mostly on echinoderms, crustaceans and mollusks (Moreno 1972, Fuentes 1982, Varas & Ojeda 1990).

On the other hand, the structural modifications observed in *Scorpis chilensis,*

suggest mechanical actions with quite a different result. Compared with the former species, the different proportions in the design of the mandibular pieces and their lesser strength, associated with a less developed muscular design with proximally displaced insertion points into the mobile elements (maxilla and jaw), indicate a tendency to performing wider movements of less strength and greater speed (Fig. 8B). Furthermore, the reduced development of the mandibular adductor muscles (Fig. 6) and the more slender design of the suspensorium (Fig. 1D) together with a greater freedom of movement to the mandibular symphysis allow the performance of wider and quicker lateral movements of the suspensorium, associated with a rapid suction mechanism (Barel 1983). The greater protrusion capacity created by the premaxillae of this species can be understood in the same sense. The maintenance of the intrahyoid articulation permits the suction carried out by *S. chilensis* to involve great volume of water. These peculiar structures and mechanical actions clearly diverge from those previously described for strict herbivorous species such as *Girella.* In turn, they determine more generalized feeding mechanisms, which are more closely related to an omnivorous diet. The primarily omnivorous habits consisting of small crustaceans and macroalgae (personal observations) of this species strongly support our conclusions.

The comparative structural and functional analysis of the cephalic morphologic elements related with mechanisms of prey capture also allows for some considerations about the phylogenetic relationships of this group. The structural schemes described for *Girella laevifrons* (previously allocated into *Doydixodon*) and *G. albostriata* are very close and supports the conclusions recently reached by Orton (1989) and Johnson & Fritzsche (1989) who included *D. laevifrons* within the genus *Girella.*

Despite the adaptive modifications related to the acquisition of carnivory by *Graus nigra,* the cephalic morphological plan of this species is similar to the former species (*Girella*), which justifies its incorporation

in the same group proposed by Johnson & Fritzsche (1989). These authors suggest that since herbivory is primitive for girellids, the generalized feeding morphology of *Graus* - characterized by the absence of specializations for gathering plant material - should be interpreted as an atavistic condition. The retention of an herbivorous behavior (Johnson & Fritzsche 1989) during a phase of its life history (from 80 to 240 mm SL), however, does not have much support in the recent literature. The studies of Varas & Ojeda (1990) and Stepien (1990) on intertidal fish ecology in central Chile, clearly demonstrate that individuals of *Graus nigra* with TL 24-211 mm (N = 72 and 211, respectively, in the above studies) prey exclusively on benthic invertebrate prey. No ontogenetic niche shift was detected and no algal material was reported in *Graus* diet's in these two studies.

The structural plan of *Scorpis chilensis* appears more distant from species of the other two genera, although it shares characters such as the double tendon of the A1 muscle in the maxilla, the intrahyoid articulation, the type of teeth, their replacement system, and the general design of the suspensorium.

In summary, we conclude that the acquisition of strict herbivory in *Girella laevifrons* and *G. albostriata* is related to the development of structural modifications that allow the performance of accurate mechanisms for the capture of macroalgae. The resultant manipulation and sucking, occurs with greater energetic efficiency by ingesting great volumes of food with low cost mechanics.

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