

Cephalic anatomy of the herbivorous fish *Girella laevisfrons* (Osteichthyes: Kyphosidae): mechanical considerations of its trophic function

Anatomía cefálica del pez herbívoro *Girella laevisfrons* (Osteichthyes: Kyphosidae): consideraciones mecánicas sobre su función trófica

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ABSTRACT

Structural and functional restrictions hindering the development of efficient mechanism for cropping and ingestion of algal material could constitute an explanatory hypothesis for the observed low diversity of herbivorous fishes. In this study, the cephalic structures of the herbivorous kyphosid fish *Girella laevisfrons* (Tschudi 1844) are described, including a functional analysis of its alimentary apparatus. This species can be characterized by having: (i) a great freedom of movement between the dentary and articular-angular, (ii) a double insertion of the muscle adductor mandibulae A1 in both faces of the maxilla, (iii) specialized teeth, long and flexible with a peculiar articular condyle at their anterior base, (iv) a mobile articulation between ceratohyal and dorsal hypohyal, and (v) a well developed branchiostegal system. A mechanism based on a mandibular manipulation associated with a slow suction of a large volume of water is proposed. This mechanism would allow the ingestion of large amounts of algae (as long stripes) in a continuous fashion. The combined activity of both an oral manipulation and buccal suction systems are possible by the existence of a decoupling of the anterior and posterior regions of the buccal cavity involving the jaw and the hyoid arch. The adaptive value of this mechanism is discussed in relation of the feeding strategies utilized by this species.

Key words: *Girella*; herbivory; head morphology; feeding apparatus; functional design.

RESUMEN

Restricciones estructurales y funcionales que impiden el desarrollo de mecanismos eficientes de captura e ingestión de algas, pueden constituir una hipótesis explicativa a la baja diversidad de peces herbívoros observada en este grupo. En este estudio se describe la anatomía cefálica del kifósido herbívoro *Girella laevisfrons* y se realiza un análisis funcional de su aparato alimentario. Esta especie se caracteriza por presentar: (i) gran libertad de movimiento entre el dentario y el articular-angular, (ii) doble inserción del músculo aductor mandíbula A1 en ambas caras del maxilar, (iii) dientes especializados largos y flexibles, con un peculiar cóndilo articular en su base, (iv) una articulación móvil entre el ceratohial e hipohial dorsal, y (v) un sistema branquiostegal bien desarrollado. Se propone un mecanismo basado en una manipulación mandibular asociado con una succión lenta y de gran volumen. Este mecanismo permitiría la ingestión de gran cantidad de algas (largos trozos sin cortar) en forma continua. La actividad combinada de una manipulación oral y una succión bucal es posible por la existencia de desacoplamiento en la región mandibular y arco hioideo. Se discute el valor adaptativo de este mecanismo en relación a la estrategia alimentaria utilizada por esta especie.

Palabras claves: *Girella*; herbivoría; morfología cefálica; aparato alimentario; diseño funcional.

INTRODUCTION

The phenomenon of fish herbivory in marine ecosystems has received increasing attention in recent years (Mead 1970, Earle 1972, Van Dyke & Sutton 1977, Wheeler 1980, Lobel 1981, Choat 1982, Horn *et al.* 1982, Horn 1989). Much of the discussion on this topic has been focused on the causes explaining the relatively

low diversity of species that feed exclusively on algae (Mead 1970, Horn 1989). In tropical coral reefs, herbivorous fishes represent not more than 25% of total fish diversity (Talbot 1965, Bakus 1966, Randall 1967, Sale 1977, Ogden & Lobel 1978) while in temperate waters they do not exceed 8% of the fish faunas (Bigelow & Schroeder 1953, Quast 1968, see also Choat 1982).

Although several approaches have been proposed to answer the question of why there are so few species of herbivorous

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fishes, including biogeographical and eco-physiological studies, little attention has been paid to functional morphology as an analytical tool to explore other hypotheses about fish herbivory. From a morpho-functional viewpoint, the phenomenon of fish herbivory should focus on the analysis of the extrinsic and intrinsic constraints imposed on the design (Lauder 1981, 1982a). Further, since functional demands imposed by feeding have been shown to have a decisive influence on the integration of the fish head (Liem & Osse 1975), such mechanical constraints have been studied specifically in relation to trophic function (Lauder 1981, 1982b, 1983; Liem & Sanderson 1986). In this context, the analysis of cephalic structures of herbivorous fishes is particularly interesting because structural constraints related to their feeding mechanisms may well serve as an alternative hypothesis explaining the relatively low number of herbivorous species among the teleosts.

Few studies in the literature document morphological aspects of herbivorous fishes. Most of them have dealt primarily with osteological and myological descriptions of the head (Springer 1968, Tedman 1980a, 1980b, Gosline 1987, Clements & Bellwood 1988) or with the study of morphological adaptations associated with a particular mode of biting or grazing (Liem 1979, Barel 1983) or with morphological descriptions of the alimentary canal (Suyehiro 1942, Al-Hussaini 1947, see Horn 1989). Kyphosidae is one of the few known percoid families in which most of its representatives are strict herbivores (Randall 1967), at least those belonging to Kyphosinae and Girellinae, although recently Johnson & Fritzsche (1989) have shown that *Graus nigra* Philippi 1887, an strict carnivorous species, is closely related to *Girella*. The morphologies and feeding mechanisms of these species, however, are almost completely unknown. The kyphosid fish *Girella laevis* (Tschudi 1844) (previously known as *Doydixodon laevis*; see Orton 1989) is an abundant and conspicuous herbivorous species inhabiting rocky nearshore habitats along the coast of Chile and Peru (Mann

1954, Chirichigno 1974, Varas & Ojeda 1990). The main goals of this paper are (1) to describe the cephalic anatomy of *Girella laevis*, and (2) to study the structural design of the head of this species as possible adaptations to herbivory by analyzing the functional potential of its morphological elements, and its mechanisms of prey capture.

MATERIALS AND METHODS

Seven specimens of *Girella laevis* were analyzed in this study; they ranged from 100 to 220 mm in total length (TL) and were collected in intertidal pools at two localities along the Chilean central coast, Quintay (33°11'S; 72°43'W) and Las Cruces (33°30'S; 71°38'W), during March 1989. For osteological analysis, four individuals previously fixed in a 10% solution of buffered formalin-sea water mixture, were double stained for bone and cartilage following the technique of Dingerkus and Uhler (1977). Another two preserved specimens were used for muscle and ligament descriptions while one fresh individual was examined for mechanical manipulation and determination of mandibular movements. 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.

RESULTS

Osteology

Neurocranium

The neurocranium is a well ossified structure, broad and tall on its anterior and posterior portions (Figs. 1, 2 and 3). The major modifications in relation to the percoid body plan (Osse 1969) are found in the ethmoid region. The mesethmoid is solid and large, rounded in shape in lateral view and quadrangular in a dorsal

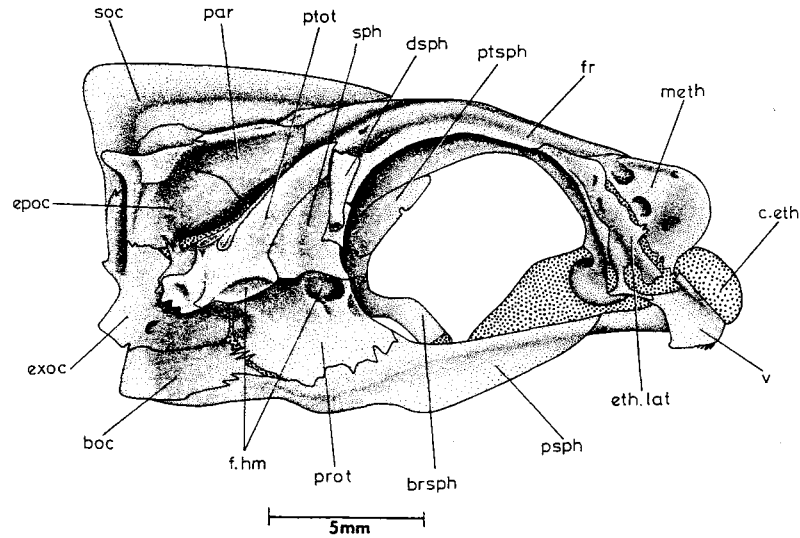


Fig. 1: Lateral view of neurocranium. boc = basioccipital; brsph = basisphenoid, c. eth = cartilaginous ethmoideal plate; dsph = dermosphenotic, epoc = epioccipital; eth. lat = lateral ethmoid; exoc = exoccipital; f. hm = articular fossa of hyomandibular; fr = frontal; meth = mesethmoid; par = parietal; prot = prootic; psph = parasphe-noid; ptot = pterotic; ptsph = pterosphenoid; soc = supraoccipital; sph = sphenotic; v = vomer.

Vista lateral del neuracrneo. boc = basioccipital; brsph = basisfenoides; c. eth = placa cartilaginosa etmoidal; dsph = dermoesfenotico; epoc = epioccipital; eth. lat = etmoides lateral; exoc = exoccipital; f. hm = fosa articular para el hiomandibular; fr = frontal; meth = mesetmoides; par = parietal; prot = prootico; psph = paraesfenoides; ptot = pterotico; ptsph = pteroesfenoides; soc = supraoccipital; sph = esfenotico; v = vomer.

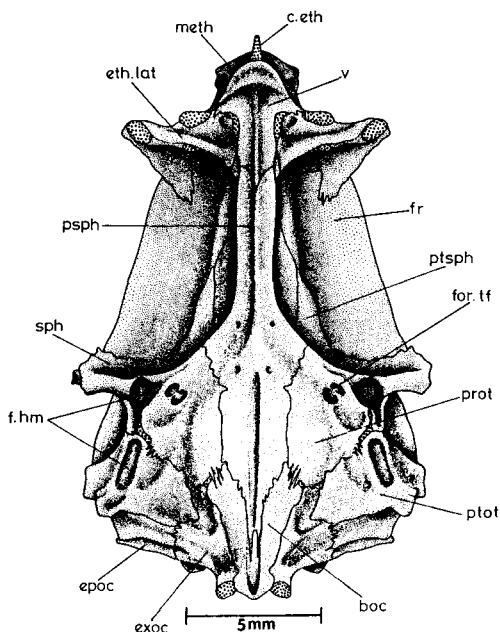


Fig. 2: Ventral view of neurocranium. for. tf = trigemino-facial foramen. See Figure 1 for other abbreviations.

Vista ventral del neuroacrneo. for. tf = foramen trigemino-facial. Las otras abreviaciones igual que en Fig. 1.

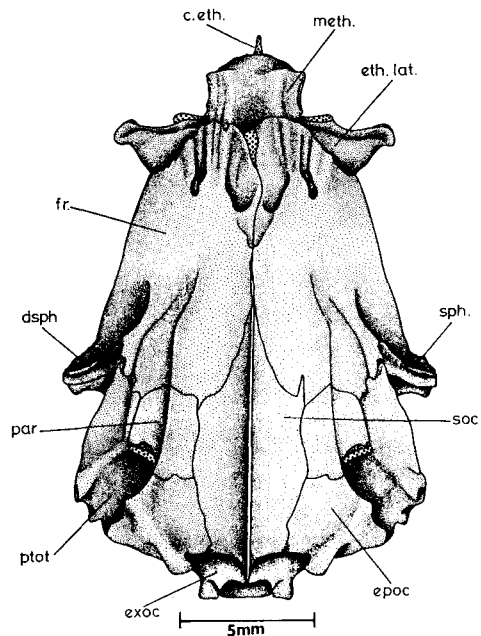


Fig. 3: Dorsal view of neurocranium. See Figure 1 for abbreviations.

Vista dorsal del neuroacrneo. Abreviaciones igual que en Fig. 1.

view; it is projected forward forming the anterior tip of the neurocranium (Fig. 1). Postero-dorsally there is a large overlap with the frontals. Laterally, it is associated with the lateral ethmoids by a narrow cartilaginous band; the antero-ventral surface is connected with a cartilaginous ethmoidal plate. The well ossified lateral ethmoids show a firm articulation with the frontals and with the postero-dorsal surface of the mesethmoid, connected with the rest of the anterior ossifications by means of cartilage (Fig. 1). The lateral processes are well developed and the antero-ventral surface articulates with the palatine. The antero-ventral end of the neurocranium is formed by the vomer, its head not projected farther forward than the mesethmoid, and presents an oblique anterior surface over which lies the prominent cartilaginous ethmoidal plate. Near the anterior edge of the ventral surface there are few vomerine teeth (5-10) of slender and conic shape (Fig. 1). The parasphenoid has a well developed medial ventral keel which gives it a tall aspect in the medial region (Fig. 1). The anterior portion presents a dorsal bed which continues as a plate-like projection of the ethmoidal cartilage. The ascending expansions are poorly developed (Figs. 1 and 2). The dorsal edge of the prootics with its respective sphenotic form the anterior articular fossa of the hyomandibular. The sphenotics have a prominent post-orbital process (Fig. 2). The dermosphenotics overlap dorsally with the sphenotics and are not fused. Each pterosphenoid is extended and laminar, dorsally articulated to the flange border of the frontals (Fig. 1). The posterior articular fossa for the hyomandibular is formed only by the pterotic (Fig. 2). In dorsal view, the exoccipitals have a posterior oblique process with an articular surface for the first vertebra (Fig. 2). The epioccipitals have wide posterior crests, short and obliquely directed (Fig. 3). The parietals are reduced, with a longitudinal ridge projected towards the frontals (Fig. 3). The supraoccipital projects forward to approximately the middle of the neurocranium, with a broad supraoccipital crest

that runs its entire length (Fig. 3). The postero-dorsal edge of the supraoccipital crest has a right angle shape (Fig. 1). The supraoccipital does not belong to the foramen magnum. The frontals are large and do not overlap the sphenotics posteriorly. Ventrally, they present a vertical crest which together with the pterophenoid form the dorsal edge of the interorbital septum (Fig. 1). The basisphenoid has a curved anterior medial projection and is associated with the parasphenoid by a cartilaginous tip (Fig. 1).

Suspensorium

Basically, it has 3 mechanical units that possess some flexibility between them: palatine, ectopterygoid-entopterygoid-quadrates-symplectic, and metapterygoid-hyomandibular (Fig. 4). The palatine has a robust triangular base, the postero-ventral portion bearing some acute conical teeth; the posterior edge is connected with the

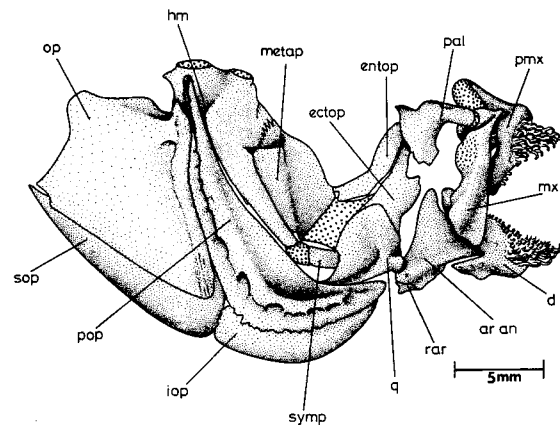


Fig. 4: External view of right splanchnocranium. ar-an = articular-angular; d = dentary; ectop = ectopterygoid; entop = entopterygoid; hm = hyomandibular; iop = interopercle; metap = metapterygoid; mx = maxilla; op = opercle; pal = palatine; pmx = premaxilla; pop = preopercle; q = quadrates; rar = retroarticular; sop = subopercle; symp = symplectic.

Vista externa del esplanocráneo derecho. 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.

ecto- and entopterygoid through ligaments; the anterior process is curved and bears an articular facet which articulates with the lateral ethmoids while its anterior cartilaginous tip is located over the maxillary palatinad facet (Figs. 4 and 5). The quadrate is triangular in shape with a short posterior spine; the ventral margin is thick, joined closely to the preopercle by a strong ligament; its articular condyle is about the level of the palatine (Figs. 4 and 5). The ectopterygoid and entopterygoids are laminar, of similar length, and arranged near vertically. The anterior edge of the ectopterygoid bears a concave dorsal edge which attaches to the palatine through a fibrous membrane that permits flexibility. Its ventral portion overlaps with the middle internal face of the quadrate. The symplectic is small and slender, arranged horizontally and both tips are cartilaginous (Figs. 4 and 5). The metapterygoid is rectangular, closely joined to the hyomandibular by its postero-ventral edge and through a dentate suture by its postero-dorsal border; anteriorly it is weakly connected to the entopterygoid, leaving a broad cartilaginous plate between it and the quadrate (Figs. 4 and 5). On its external face there is a conspicuous plate that lodges a fascicle of the levator arcus palatini muscle (Fig. 4). The hyomandibular has a broad base and a slender and long ventral process that is connected with the symplectic by cartilage (Figs. 4 and 5). It bears two condyles for the articulation to the neurocranium, the anterior is circular and the posterior oblong. The articular process for the opercle is short, thick, and postero-ventrally directed (Fig. 5). The opercular bones are large and very tall; the lower border of the preopercle is irregularly serrated (Fig. 4).

Lower Jaw

The lower jaw is triangular in shape, tall, short, and robust (Figs. 4 and 5). The dentary has a thick anterior border and is transversely oriented, showing an ample cavity for teeth reception. The mandibular symphysis is vertically oriented (Fig. 5) with a broad surface and abundant fi-

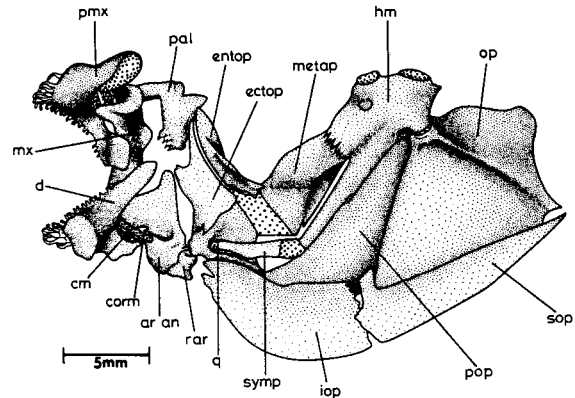


Fig. 5: Internal view of right splanchnocranium. cm = Meckel's cartilage; corm = coronomeckelian. See Figure 4 for other abbreviations.

Vista interna del esplanocráneo derecho. cm = cartilago de Meckel; cor = coronomeckeliano. Las otras abreviaciones al igual que en Fig. 4.

brous tissue that allows mobility. The articular-angular is a solid bone with a short anterior process inserted into the furrow of the posterior border of the dentary (Fig. 5). The thick ventral process leaves a broad depression in the ventral border of the jaw. Mesially and close to its ventral border is located a markedly reduced Meckel's cartilage and associated with it a small coronomeckelian bone (Fig. 5). The retroarticular forms the postero-ventral extreme of the jaw, closely joined to the articular-angular (Fig. 5). The retroarticular does not form part of the quadrate articulation. The articular-angular and dentary show a great capacity for relative movement between them, not only of rotation along the longitudinal axis of the jaw but also along the vertical and lateral planes. This freedom of movement is due to the ligamentous connection existing between both bones.

Upper Jaw

The ascending process of the premaxilla is slightly shorter than the alveolar process (Fig. 5) and is closely associated with the rostral cartilage which shows, on its ventral side, a deep middle antero-posterior groove for the fitting of the ethmoidal cartilaginous plate. The ascending and articular processes of the premaxilla are joined.

The anterior border of that bone is thick; like the dentary, it shows an anterior depression for lodging the teeth (Fig. 4). The ventral portion of the alveolar process has a broad laminar projection posteriorly directed which overlaps with the internal surface of the maxillary arm (Fig. 5), the two being connected by fibrous tissue. The joint between both premaxillae occurs on a broad surface and by ligamentous tissue which allows some mobility between them. The maxilla is long, almost twice as long as the alveolar process of the premaxilla (Fig. 4). The maxillary arm presents a prominence on its postero-proximal border and a concavity on the internal face of its distal end.

Teeth

The premaxilla as well as the dentary bear two types of teeth: the first ones are short and tricuspid, closely joined to the bone and are generally straight or weakly curved posteriorly. They are arranged in a line across the alveolar process of the premaxilla and the coronoid process of the dentary, and in many rows (about 7 or 8) on the internal surfaces of the thicker anterior border of both bones, thus forming broad dental plates (Fig. 4). The second type is very modified; they lie in cavities along the anterior border of both bones and are arranged in a variable number of rows. These teeth are long, laterally compressed at their bases, narrow in the middle zone and with spatulate and tipless distal extremes forming a right angle with the longitudinal axis of the teeth (Fig. 6c). They are continually replaced in an anterior to posterior rotation. Juvenile specimens show only tricuspid teeth (Fuentes 1981). The tooth attachment mode does not agree with that reported by Fink (1981) for Actinopterygian fishes. In *G. laevis* the teeth are attached to a cylindrical and partially ossified structure, that is not directly related to the bone but is immersed in a fibrous tissue matrix. A similar arrangement of loosely suspended teeth is seen as well in Blenniidae (Springer 1968). There is a complete separation between the tooth and this basal structure

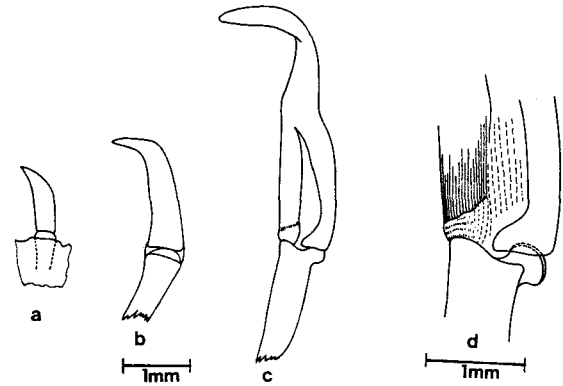


Fig. 6: Lateral view of an external mandibular tooth. (a) and (b) early teeth; (c) mature tooth; (d) tooth attachment.

Vista lateral de los dientes mandibulares externos. (a) y (b) dientes incipientes; (c) diente maduro; (d) inserción del diente.

which shows an articular condyle on its external border (Fig. 6d). The tooth can rotate in the sagittal plane due to the capacity of the internal border to be distorted. The configuration and replacement mode of these teeth have already been reported by Johnson & Fritzsche (1989) for *Girella*, who consider these features as autapomorphies, presumably associated with herbivory.

Hyoid Arch

This is short and wide, the anterior end of the ceratohyal being acute and joined to the ventral hypohyal by cartilage; the dorsal hypohyal has a cartilaginous posterior edge connected with the anterior dorsal inner surface of the ceratohyal forming a mobile articulation (Fig. 7). The ceratohyal shows near its dorsal border an oblong foramen like the one described by McAllister (1968) (known as the beryciform foramen). There are six broad and curved branchiostegal rays, the first and second being related to the ventral anterior border of the ceratohyal and the four posterior ones joined to the external face of the ceratohyal and epihyal. The interhyal is small (Fig. 7).

Branchial Arches

Three basibranchials are ossified while the fourth basibranchial is cartilaginous;

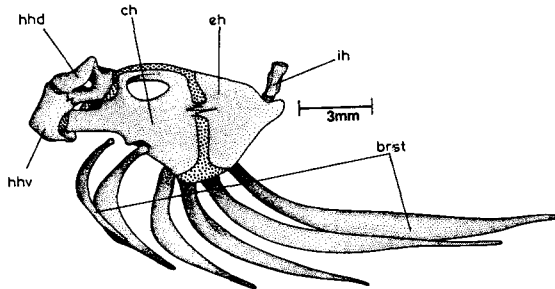


Fig. 7: Internal view of left hyoid arch. brst = branchiostegal rays; ch = ceratohyal; eh = epihyal; hhd = dorsal hypohyal; hhv = ventral hypohyal; ih = interhyal.

Vista interna del arco hioideo izquierdo. brst = radios branquiostegales; ch = ceratohial; eh = epihial; hhd = hipohial dorsal; hhv = hipohial ventral; ih = interhial.

the first hypobranchial has a laminar lateral projection and the third has an anterior tip that is acute and long. The fifth ceratobranchials are not fused (Fig. 8), and are long and thin with pointed and conical teeth. The fifth cartilaginous epibranchials are present. Three broad upper pharyngeal plates are related to pharyngobranchials 1, 2, 3 and a small tooth plate is fused to the internal face of the first epibranchial (Fig. 8). The gill-rakers of the first arch are well developed and bear numerous teeth-like structures on their inner edge. The gill-rakers of the second to fourth arch are short and thick, and are arranged transversally on both edges of each arch, their numbers and sizes increasing towards the posterior arches, all together forming wide dentated plates (Fig. 8).

Myology

Adductor Mandibulae

In *G. laevifrons* the configuration and interrelationships of the different sections of this muscle present some remarkable differences with regard to the basic plan suggested by Gosline (1986) for the Teleost group. It is possible to clearly identify four sections: A1, A2, A3, and Aw (Fig. 9). The A1 section is of large volume and occupies the upper section of the cheek (Fig. 9a). It originates from the hyomandibular and the metapterygoid and it is

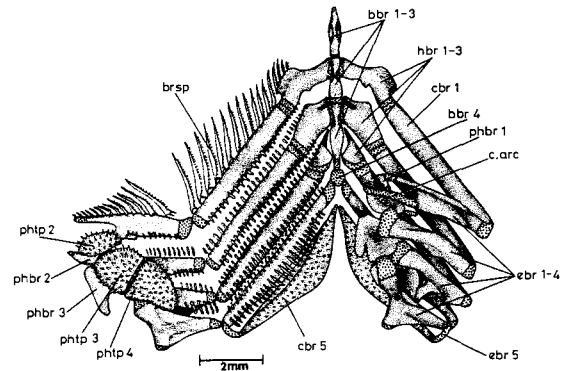


Fig. 8: Dorsal view of branchial basket. bbr = basibranchial (1-4); brsp = gill-rakers; c. arc = interarcual cartilage; cbr = ceratobranchial (1, 5); ebr = epibranchial (1-5); hbr = hypobranchial (1-3); phbr = pharyngobranchial (1, 3); phtp = pharyngeal tooth plate (2-4).

Vista dorsal de los arcos branquiales. bbr = basibranchial (1-4); brsp = branquispinas; c. arc = cartilago interarcual; cbr = ceratobranchial (1, 5); ebr = epibranchial (1-5); hbr = hipobranchial (1-3); phbr = faringobranchial (1, 3); phtp = placa dentada faringea (2-4).

inserted on the maxilla. From the anterior portion of A1, two fascicles emerge: the internal fascicle is extended through a thin and long tendon, reaching the internal face of the maxilla, close to the articular process for the premaxilla. The external fascicle, on the other hand, is inserted on the middle zone of the external face of the maxillary arm by means of a tendon. The most superficial fibres are directly inserted on the anterior margin of the bone (Fig. 9a). The A1 section is ventrally related to the lower jaw by means of a long and thin tendon to the internal face of the articular-angular bone (Fig. 9b and 9e). This double link to the two faces of the maxilla has been reported for *Diplodus sargus* (Sparidae) by Vandewalle *et al.* (1986), whereas in the case of *Scarus fasciatus*, the A1(α) and the A1(β) are also inserted on the maxilla by means of two tendons, but both to the internal face (Tedman 1980b).

The well developed A2 section originates from the preopercle and the hyomandibular. It is inserted, through a broad tendon, to the edge and external face of the ascending process of the articular-angular, and to the postero-lateral surface

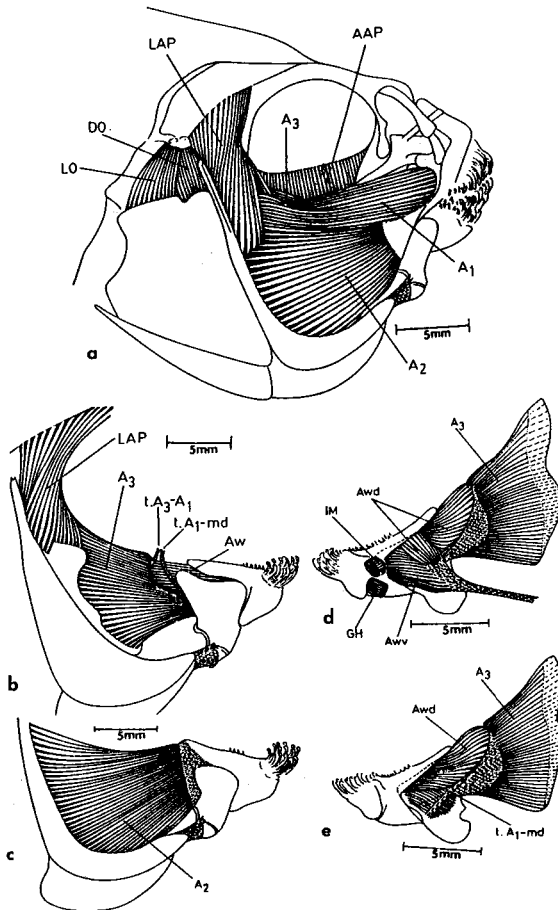


Fig. 9: View of muscles of the right side of the head. (a) general lateral view; (b) lateral view of A3 adductor mandibulae muscle, note the A3-Aw connection; (c) A2 attachment on dentary and articular-angular; lateral (d) and (e) internal views of A3 and Aw adductor mandibulae muscles. A = adductor 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.

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; t A3-A1 = tendón de los aductores mandibulares A1 y A3; tA1md = tendón del aductor mandibular A1 que se inserta en la mandíbula inferior.

of the dentary coronoid process (Fig. 9c). This singular condition of tendinous connection with the dentary has been described by Johnson & Fritzsche (1989) for *Graus* and *Girella* as a synapomorphy.

The laminar A3 section originates in the hyomandibular, metapterygoid and symplectic. The dorsal fibres of the anterior portion of the A3, are related with one fascicle of the Aw by aponeurotic tissue (Fig. 9b). With regard to the ventral fibres, they insert onto the coronomeckelian bone by a tendon. In the Aw section, it is possible to differentiate two fascicles. The ventral fascicle is superficial and its fibers originate on the posterior margin of the dentary, terminating in a long tendon inserted on the preopercle (Fig. 9d). The second dorsal fascicle, has fibers linking the dentary with the articular-angular; others between the dentary and the aponeurotic connection with A3 and, finally, there are other fibres fixed to the A1 tendon (Fig. 9e).

Levator Arcus Palatini

Its origin is found in the pterotic and sphenotic; the superficial fibres are inserted in the preopercle and run lateral to the fibers of the A1 and A2 sections of the adductor mandibulae muscle (Fig. 9a). The most internal fibres are inserted in the hyomandibular and in the inner face of the metapterygoid plate.

Adductor Arcus Palatini

It forms a wide plate all over the floor of the orbit and is continued posteriorly by the hyomandibular adductor muscle.

Buccal Ligaments

In general, the arrangement of the ligaments of *G. laevisfrons* agree with that reported by Stiassny (1986) for acanthomorphs. The ethmo-maxillary ligament underlies the palato-premaxillary ligament in the same way as in *Serranus scriba* (Serranidae) (Benmouna *et al.* 1984) instead of the inverse position of the ligaments as described by Stiassny (1986). *Girella laevisfrons* has the

same kind of strong ligament linking the anterior margin of the nasal with that of the maxilla and the same process of the mesethmoid where the ethmo-maxillary ligament is inserted. There is no well defined palato-maxillary ligament, and both bones are related to each other by means of a loose fibrous tissue that allows great mobility between them. At the distal end of the maxilla and the coronoid and primordial jaw processes is located a strong ligamentous bulk which, when the mouth is closed, folds and fits in the distal concavity of the maxilla.

Functional considerations of the feeding apparatus

The most conspicuous structural modifications observed in *G. laevisfrons* from a generalized percoid condition are those found at the level of the upper and lower jaws, both in design and proportions and in their relations with the other cephalic elements. In turn, these anatomical characteristics determine some very precise possibilities of movement related to buccal mechanisms for food acquisition.

Movements of the upper jaw

Although the configuration of the maxillae and premaxillae seem to be similar to that of species with a great capacity for protrusion, particularly regarding the development of the ascending processes (Gosline 1987), *G. laevisfrons* premaxillae are not protractile. Their movements are restricted to small vertical displacements and chiefly to an antero-posterior balancing of their dentate border. The direction of the movements is essentially determined by the almost vertical inclination of the anterior border of the ethmovomerine region.

The maxillae display a wide variety of movements, though of reduced amplitude: pendular movement in the sagittal plane, and a rotational movement about its longitudinal axis (Fig. 10). The pendular movement occurs because of its ligamentous attachments to the lower jaw (Fig. 10a).

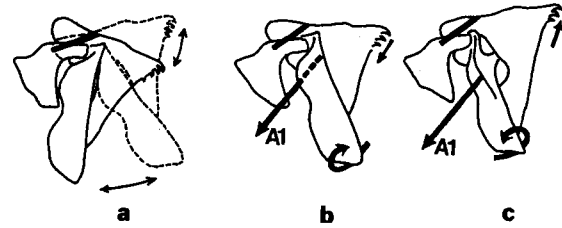


Fig. 10: Figure showing (a) the possible movement of the maxilla and premaxilla mediated by the lowering of the mandible; (b) and (c) the maxillary rotation mediated by internal (b) and external (c) fascicles of the A1, and its effect on the premaxilla. Esquema que muestra (a) posibles movimientos del maxilar y premaxilar mediados por la bajada de la mandíbula, rotación del maxilar mediado por los fascículos internos (b) y externos (c) del A1 y su efecto sobre el premaxilar.

Rotation about its longitudinal axis is possible by the action of the A1 adductor mandibulae muscle with points of insertion on both faces of its arm (Fig. 10b and 10c).

The great development of the A1 adductor mandibulae muscle, and its division into two anterior fascicles, both related with the maxilla, suggests a variety of movements of the maxilla which are possibly transmitted to the premaxilla (Fig. 10b, c). The above movements of the maxilla and premaxilla may be independent of the lower jaw movements. Despite the tendinous connection with the inner face of the articular-angular, the contraction of the A1 muscle does not seem to exert an important action upon that bone, since the direction of the tendon does not follow the line of action of muscle fibers. Probably the function of this connection would be to change the orientation of the line of action of the muscle on the maxilla, according to the degree of opening or closing of the mouth, while independence or decoupling between both jaws would be maintained.

Movements of the lower jaw

The most remarkable characteristic of the *G. laevisfrons* lower jaw is its capacity for intramandibular movements. The dentary displays a great mobility related to the articular-angular. The antagonistic action of the Aw adductor mandibulae and genio-

hyoideus muscles causes a vertical rotation of the dentary in the sagittal plane relative to the articular-angular, behaving like a mechanical unit independent of the rest of the jaw (Fig. 11a). The mandibular symphysis is very tall, large and vertical, and restricts the separation of the posterior ends of the dentaries; however, their freedom of movement relative to the posterior part of the jaw allows the abduction of the articular-angular following the movements of the suspensorium (Fig. 11b). The tendinous connection of the A2 adductor mandibulae muscle with the dentary and with the articular-angular, also would determine the possibility of alternative movements of the jaw allowing both bones to work in a combined fashion under the action of the muscle A2.

Movements of the suspensorium, opercular series and hyoid bar

The suspensorium is able to execute ample abduction and adduction movements owing to its tall vertical design and the development of its associates musculature. The flexibility of the connection between the palatine and the rest of the suspensorium implies that the movements of the latter may not affect the palatine, leading to a mechanical independence between the maxillo-premaxillar system and the suspensorium.

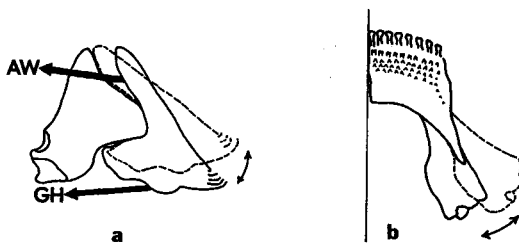


Fig. 11: Figures showing: (a) the dentary movements mediated by the antagonistic actions of the Aw and geniohyoideus (GH) muscles; (b) the relative movement of the articular-angular respect to the dentary.

Esquema que muestra: (a) movimientos del dentario mediados por la acción antagónica de los músculos Aw y geniohioideo (GH); (b) movimientos relativos del articular-angular respecto al dentario.

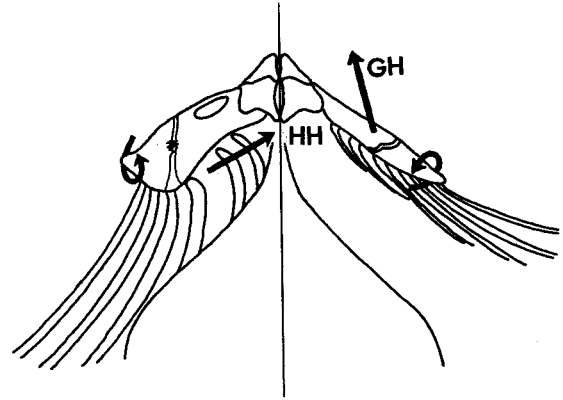


Fig. 12: Drawing showing the intrinsic movements of the hyoid arch and their effect on the mobility of the branchiostegal rays; GH = geniohyoideus muscle; HH = hyohyoideus muscle.

Esquema que muestra los movimientos intrínsecos del arco hioideo y sus efectos sobre la movilidad de los rayos branquiostegales; GH = músculo geniohioideo; HH = músculo hiohioideo.

The hyoid bars may execute simultaneously two types of movements when being propelled by the sternohyoideus muscle: in the sagittal plane, their anterior extremes rotate ventrally about the joint with the suspensorium; in the frontal plane, the posterior extremes abduce and produce a lateral action over the suspensorium. The mobile joint between ceratohyal and hypohyal allows the rotation of the ceratohyal along its longitudinal axis. This rotational movement can occur by contraction of the hyohyoideus muscles which approach the ventral edges of both bars and by contraction of the geniohyoideus muscle which causes the opposite movement (Fig. 12). This mobility of the hyoid bar might play an important role in the mechanical activity of the branchiostegal system, permitting the attachment of the rays to the body wall even when the bars are in a ventral position or abducted (Fig. 12).

The great development of the branchiostegal system, the large dimensions of the opercular bones, the very ventral location of the interhyal-suspensorium articulation, and the capability of intrinsic movements of the hyoid bar, make altogether possible the generation of a suction pump of great volume.

*Mechanical characteristics of
the mandibular teeth*

There is a great difference between the mechanical properties of both types of mandibular teeth. The small inner teeth are more directly related with the bones and slightly oriented forward, so that they may exert an action in their longitudinal axis. The outer teeth are long and very flexible, with their distal ends forming a right angle and being practically oriented in the same longitudinal axis of the jaw, and do not present mechanical properties allowing them to exert forces either in their longitudinal axis or directly over their distal border. The degree of flexibility is greater toward the inner face of the teeth, wherein their joint determines a top that makes a greater resistance to an outer flexion. The above features suggest a potential capability of the outer teeth to resist longitudinal or slightly tilted tractional forces, in such a way that their distal borders would act perpendicularly on food, be it by scraping or retaining it. But in no case do they have the possibility of biting or cutting.

DISCUSSION

From a functional viewpoint, the structural arrangement of the head of *Girella laevis* is characterized by the decoupling of the lower jaw and of the hyoid bar each into two independent mechanical units, and by the presence of independent kinematic systems for the maxillae, dentaries, and ceratohyals.

The mobility of the dentaries relative to the articular-angular, and the autonomy of the maxillary rotation movements which are transmitted to the premaxillae, make possible a wide array of food manipulations at the mandibular level. This manipulation capability allows seizing and squeezing of macroalgal tissue with small and controlled movements of both dentated surfaces.

The type and arrangement of the outer teeth suggest that their main function is related to a dragging action and not really to a cutting action. This is indicated both

by the direction of the mandibular movements (toward the inner part of the buccal cavity) and, the direction of teeth flexibility.

Although a short hyoid bar does affect the expansion efficiency of the buccal cavity in terms of both the volume and velocity, the tall arrangement of the suspensory and of the opercular bones, the development of the branchiostegal system and the intrinsic mobility of the hyoid bars, determine a considerable expansion capability of the buccal cavity, thus suggesting the existence of an important suction mechanism. The rotation of the ceratohyals may allow keeping the opercular valves closed, even during a great abduction of the suspensory, which suggests that in *G. laevis* the volume involved in the suction during feeding, would be of great importance.

It has been established that there are some constructional incompatibilities between systems that optimize suction and mechanisms that optimize biting and/or mandibular manipulation, and that accomplishment of suction in species of strong bite, although possible, would imply a greater energetic cost (Barel 1983). In *G. laevis*, the mandibular specializations affect the configuration of the suspensory and the hyoid system in the sense described by Barel (1983), and at the same time they restrict the possibility of a high speed suction. Notwithstanding, the construction of the posterior region of the buccal cavity associated with the decoupling of the lower jaw's dentary zone might allow the generation of a different sort of optimized suction.

The existence of this type of high volume suction with low velocity of expansion of the buccal cavity would render it possible the ingestion of an important volume of algae. The combined action of both jaw manipulation and suction is supported by the existence of thick lips and of fibrous connective tissue in which the teeth are embedded. These structures allow the regulation of the inflow according to the amount of algae being ingested, and to maintaining a closed mouth during the compression phase even when foods

is being held between the jaws. This effect may allow the consumption of long pieces of algae in a continuous fashion. On the other hand, food may be retained by the shape and arrangement of the mandibular teeth and also by the presence of vomerine and palatine teeth.

Gut contents analysis of the kyphosids *G. laevisfrons*, *Girella albobstriata* Steindachner 1898, *Medialuna ancietae* Chirichigno 1983, and *Scorpius chilensis* Guichenot 1848, and of the pomadacid *Isacia conceptionis* (Cuvier 1830), carried out by the authors (unpublished data) show that these fishes actually ingest long pieces of algae, mainly *Ulva* spp., which are usually found folded in small packages in the stomachs.

Given that macroalgae are poor quality food, in terms of energy and nutrients, for herbivorous fishes to meet their nitrogen and energy requirement, they must consume relatively large quantities of this material and assimilate it efficiently (Horn 1989). In this context, a continuous food capture system (as compared to a discontinuous one), an efficient force transmission system from the hyoid bars (because of the large angle between the hyoid rami) to the suspensorium, and the reduce magnitude of mandibular movements, may be interpreted as a feeding mechanism that minimizes the energetic cost of algal capture and maximizes the volumen of the ingested food.

Many of the structural and functional characters exhibited by *G. laevisfrons* are found in other groups of percoid fishes as well. In general, morphological adaptations related to optimized and specific functional demands, many of which can be seen in *G. laevisfrons*, especially those associated with a strong bite, have also been discussed in the literature. The shape of the premaxillae and their restricted protrusion capability, associated with a short and tall mandibular shape, are usually found in those species that have well developed biting mechanisms such as in Cichlidae (Barel 1983), Blenniidae (Vandewalle *et al.* 1982), Scaridae and Labridae (Tedman 1980b), and Odacidae (Clements & Bellwood 1988). In many other families, the

performance of intramandibular movements has also been related to short jaws and highly specialized teeth (Gosline 1987).

It is important to note that more than a similarity of isolated structures adequate to fulfill a certain functional demand, there is a structural organization which is recurrent in those groups having herbivorous representatives. Scaridae (Tedman 1980a; Clement & Bellwood 1988), Blenniidae (Vanderwalle *et al.* 1982), Acanthuridae (Gosline 1987), and Kyphosidae (this study) possess 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. This structural organization of the oral jaw apparatus suggests highly specialized mechanical possibilities involving the dentary and teeth as a mechanical unit independent from the remainder of the jaw (Gosline 1987).

The morphological evidence about great structural modifications existing in herbivorous fishes (mainly at the mandibular adductor muscles, mandibular structures and at the teeth level), suggests that in plant-eating fishes the mandibular manipulation imposes substantial functional demands on the head structures (*i.e.*, dominant demands *sensu* Dullemeijer 1974). These demand are likely related not only to food capturing but also to minimizing the energetic cost and to maximizing the volume of ingested food. Although future experimental studies are necessary to confirm the significance of the mandibular manipulation in herbivorous fishes as well as the validity of the feeding mechanism proposed for *G. laevisfrons*, recent comparative studies concerning mandibular structures of different representatives of Chilean Kyphosidae (Vial & Ojeda in prep) show differences with respect to *G. laevisfrons*. The modifications in these other kyphosid species respect to some or all structural aspects that we have interpreted as strictly related to herbivory in *Girella* (*i.e.*, intramandibular movements, mobile teeth, insertion mode of A1 and A2 muscles) determine omnivorous (*e.g.*, *Scorpius chilensis*) or carnivorous (*e.g.*, *Graus nigra*) diets.

From a constructional-morphology viewpoint, the different form-features of the structures involved in the performance of a function may impose constraints on the fish's head integration (Barel 1983). It is in this context that we suggest that structural and functional restrictions might hinder the development of efficient mechanisms for cropping and ingestion of algal material.

In conclusion, it seems that the most striking characteristics of a herbivore design in *G. laevis* correspond to structural modifications related to an increased number of biomechanical units and to kinematic paths which make possible the combined activity of modulating mechanisms associated with food apprehension and buccal expansion. The result of this operation is an optimization of the volumen of ingested food at low energetic cost.

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