Graus nigra, an Omnivorous Girellid, with a Comparative Osteology and Comments on Relationships of the Girellidae (Pisces: Perciformes)

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ABSTRACT.— *Graus nigra*, a common shore fish of Peru and Chile is redescribed and shown to be a senior synonym of *Pinguilabrum punctatum*. The osteology and the configuration of the adductor mandibulae of *Graus* are described and compared with those of the herbivorous genus *Girella*. Placements of *Graus* in the families *Labridae* and *Serranidae* are rejected because *Graus* is the sister group of *Girella*. For outgroup comparison scorpidids, kyphosids, and girellids are treated as a monophyletic clade within a larger monophyletic group including arripidids, kuhliids, microcanthids, oplegnathids, teraponids and stromateoids. *Graus* and *Girella* exhibit six synapomorphies, including distinctive configurations of the adductor mandibulae, distal radials of the spinous dorsal fin, orbito-pectoral branch of the ramus lateralis accessorius and pons moultoni. Comparison of feeding morphologies and habits of the two genera show an ontogenetic shift toward increased ingestion of algae. This shift is terminal for *Girella*, which morphologically is highly specialized for herbivory, whereas *Graus*, with no obvious specializations for gathering or assimilating plant material, eventually reverts to a carnivorous mode. We suggest that herbivory is primitive for girellids, that the more generalized feeding morphology of *Graus* is atavistic, and speculate that the retention of herbivorous behavior during one phase of its life history may have been possible because the ingested algae serves as a vehicle for ingestion of nonvegetative epiphytic organisms. [Girellidae, herbivory, Kyphosidae, morphology, myology, osteology, Perciformes, phylogeny]

A common shore fish of Peru and Chile, *Graus nigra*, was described by Philippi (1887) in the family Labridae, where it has remained in all subsequent classifications. In 1917, Evermann and Radcliffe described a new genus and species, *Epelytes punctatus*, which they placed in the Serranidae. Hildebrand (1946), redescribed the original Evermann and Radcliffe specimen and substituted the name *Pinguilabrum* for the preoccupied *Epelytes*. Comparisons of the descriptions given by Philippi, Evermann and Radcliffe, and Hildebrand and examination of the type specimen of *Pinguilabrum punctatum*, indicate that the latter name should be treated as a synonym of *Graus nigra*.

The systematic position of *Graus* has received very little attention. McCully (1961) erected a new serranid subfamily for *Graus*, Pinguilabrinae, based on distinctive scale morphology and a high number of dorsal-fin spines. Gosline (1966) left *Pinguilabrum* in the Serranidae, but was unable to

examine its osteology. The purposes of this paper are to describe major features of the skeleton and the cheek muscles of *Graus* and to present evidence that *Graus* is most closely related to *Girella* (Gray, 1985), an herbivorous genus of about 15 species in the Pacific and one in the Atlantic Ocean. *Graus nigra* is redescribed based on examination of several hundred specimens, including juveniles as small as 30 mm SL.

MATERIALS AND METHODS

Counts and measurements were made following the methods of Hubbs and Lagler (1958). Measurements are compared either to standard length (SL) or to head length (HL). Institutional abbreviations follow Leviton et al. (1985). Specimens examined for bone and cartilage were cleared and stained by a modified version of the method of Dingerkus and Uhler (1977). Prior to the initiation of this study, some of the specimens examined were stained for bone only, following the method of Taylor (1967). Some osteological information was determined from radiographs.

Osteological description of *Graus nigra* is based on the following cleared and stained specimens: SIO 65-670, 3 specimens; USNM 218732, 3: USNM 289502, 2.

Cleared and stained specimens examined for outgroup comparison include the following:

GIRELLIDAE: *Girella albostriata*, USNM 88727; *G. elevata*, USNM 269546; *G. laevifrons*, USNM 218733; *G. melanichthys*, USNM 233895; *G. mezina*, USNM 233894; *G. nigricans*, USNM 287441; *G. punctata*, USNM 71508; *G. simplicidens*, SIO H50-253; *G. tricuspidata*, USNM 218921, USNM 269547; *G. zebra*, USNM 269545.

ARRIPIDIDAE: *Arripis georgianus*, USNM 287442.

CORACINIDAE: *Coracinus multifasciatus*, USNM 274687.

KYPHOSIDAE: *Hermosilla azurea*, USNM 288877; *Kyphosus* sp., USNM 218888; *Neoscorpis lithophilus*, USNM 269544; *Sectator ocyurus*, USNM 288880.

MONODACTYLIDAE: *Monodactylus argenteus*, USNM 258894.

MICROCANTHIDAE: *Microcanthus strigatus*, SIO 61-146.

OPLEGNATHIDAE: *Oplegnathus fasciatus*, USNM 290489.

SCORPIDIDAE: *Labracoglossa argentiventris*, CAS (SU) 23217; *Medialuna californiensis*, USNM 288878; *Scorpis chilensis*, USNM 218922.

TERAPONIDAE: *Terapon jarbua*, USNM (297258); *Hephaestus transmontanus*, USNM (297276). Osteological data was taken from radiographs of *G. nebulosa* (USNM 65512) and *G. zonata* (USNM 42067, USNM 42076). Specimens dissected for examination of ramus lateralis accessorius and pons moultoni are not listed.

DESCRIPTION

Graus Philippi, 1887

Graus Philippi, 1887:572 [type by monotypy, *Graus nigra* Philippi]. Jordan, 1920:438 [listed]; Jordan, 1923:222 [included in Labridae].

Epelytes Evermann and Radcliffe, 1917:71 [type by original designation *Epelytes punctatus* Evermann and Radcliffe = *Graus nigra* Philippi]; Jordan, 1920:562 [listed]; Jordan, 1923:193 [included in Epinephelidae].

Pinguilabrum Hildebrand, 1946:168 [*Epelytes* Evermann and Radcliffe considered preoccupied by genus of insect].

Diagnosis.— A girellid with relatively large mouth, thick papillose lips, and simple, conical jaw teeth arranged in broad band, those in outer row enlarged, replaced from bone-enclosed trough; teeth firmly attached in adults, moveable, curved and somewhat flattened toward tips in young; vomerine teeth present; palatine teeth absent; gill rakers on arches 2-4 club-like, with tuft of teeth distally, each arch with mid-longitudinal band of large, sensory papillae similar to those on lips. Vertebrae 14 + 20 or 15 + 19; pleural ribs 12-13; epipleural ribs 14-16. Predorsal bones two. Gut simple, short, with single coil. Other characters are those of the single included species.
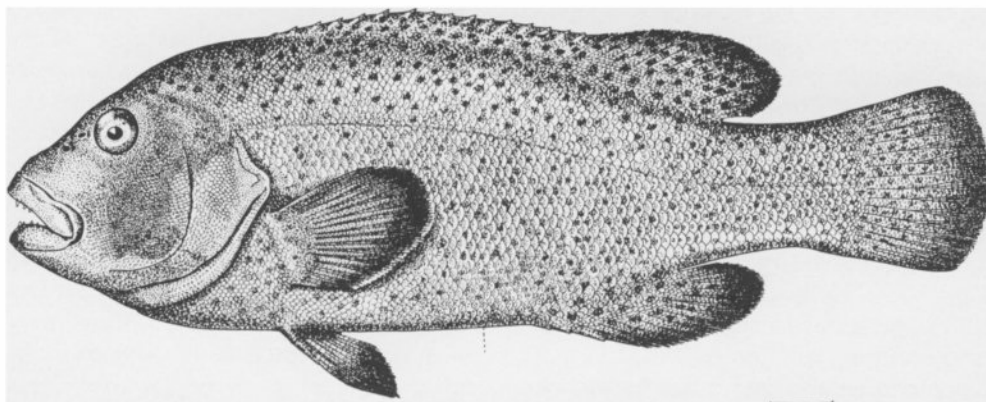
Fig. 1. *Graus nigra* Philippi, from the original drawing of the holotype of *Epelytes punctatus* Evermann and Radcliffe, USNM 77688, 317 mm SL.

Graus nigra Philippi, *1887*

Figure 1

Graus nigra Philippi, 1887: 572 [type locality: Navidad, Chile]; Jordan, 1887 (1891): 634 [compiled]; Delfin, 1889: 132 [listed]; Delfin, 1901: 75 [listed]; Fowler, 1926: 283 [description]; Fowler, 1944: 290 [listed, synonymy, range]; Mann, 1954: 258 [description, range]; Buen, 1959: 126-129 [synonymy, range, description]; Stuardo and Fagetti, 1961: [host for *Lepeophtheirus chilensis* Wilson]; Norman, 1966: 350 [included in labrid subfamily Bodianinae]; Moreno, 1972: 5 [range, diet]; Raymond, 1973: 60 [distribution and fishery]; Fuentes, 1982: 95-98 [diet]; Castro and Kuroki, 1984: 197 [host for *Lepeophtheirus frecuens* new species].

Epelytes punctatus Evermann and Radcliffe, 1917: 71, pl 6, Fig. 3 [type locality: Mollendo, Peru]. Fowler, 1945: 215 [listed]; Norman, 1966: 237 [included in serranid subfamily Serraninae].

Pinguilabrum punctatum, Hildebrand, 1946: 168 [description, range]; McCully, 1961: 127, 226 [description of scales, discussion of relationships]; Chirichigno, 1969: 47 [listed]; Chirichigno, 1974: 285, 345 [key, illustration, range].

Description.— Dorsal fin XV-XVI,16-17. Anal fin III,12-13. Pectoral fin 18-20; pelvic fin I,5. Caudal fin 9 + 8 principal, 12-14 + 11-12 procurrent rays. Branchiostegal rays 7. Gill rakers 7-8 + 14-16. Lateral-line scales 68-69.

Measurements as follows: Head 2.9-3.3, depth 2.6-3.5 in SL. Snout 2.6-4.3, maxilla 2.8-3.4, orbit 3.4-6.4, interorbital 3.7-5.0, depth of caudal peduncle 2.0-2.5, length of caudal peduncle 1.5-2.2 in HL.

Body elongate, laterally compressed. Caudal peduncle deep. Dorsal profile convex anteriorly. Mouth subterminal, large, maxilla reaching anterior rim of orbit. Teeth in both jaws in broad bands with outermost row enlarged, conical, curved, slightly flattened near tips; replacement teeth in bone-enclosed trough. Gill rakers short, club-like. Opercular margin with two flat spines, preopercular margin minutely serrate, serrae covered by skin. Posterior margin of anterior nostril with fimbriate flap, just reaching anterior margin of posterior nostril when depressed; posterior nostril almost completely surrounded by shorter fimbriate rim. Dorsal fin continuous, soft rays longer than spines, spines uniform in length, except for shorter first three. Pectoral-fin margin round. Scales ctenoid, relatively small on head and abdomen, above lateral line and along dorsal- and anal-fin base, larger below lateral line and on caudal peduncle.

Preserved specimens chocolate brown to dusky, smaller specimens covered with small dark spots that tend to coalesce into a reticulate network and to become obscure with increasing size.

Large dark spot below posterodorsal margin of caudal peduncle in small specimens, becoming obsolescent with growth. Two irregular light spots usually present between lateral line and dorsal-fin base, one under posterior part of spinous portion the other under middle of soft portion, becoming more obvious with growth. Pelvic fins uniformly dusky. Pectoral fins dark brown to light with dark distal edge.

Remarks.— Philippi's type of *Graus nigra* could not be located and has probably been destroyed (Prof. Nibaldo Bahamonde, pers. com.). Examination of the type of *Pinguilabrum. (=Epelytes) punctatum* (USNM 77688) confirmed that it is a specimen of *Graus nigra* as currently recognized. We are likewise convinced that Philippi's (1887) original description was based on a specimen of the species to which that name is currently applied, although there are discrepancies. Philippi's description of general body shape and relative proportions, jaw teeth configuration and number, relative size and distribution of scales on head and on body, and reticulate color pattern resulting from black skin covering the bases of many of the scales matches that of specimens we have examined, including the type of *Pinguilabrum*. Philippi stated that scales along the sides of the body were about twice the size of those above and below and that those on the operculum were extremely small; both conditions characterize our specimens and the type of *Pinguilabrum*. However, there is a discrepancy between the scales of those specimens, most of which are ctenoid, and Philippi's observation that the scales on his specimen were cycloid. We do not view this discrepancy as important; scales on the head and those on the upper and lower parts of the body anteriorly do not have free spine-like cteni, and those that do are covered with fairly thick epidermis to their margins, so that they appear cycloid without very close or microscopic examination. The other major discrepancy is Philippi's report of thirteen spines in the dorsal fin. The type of *Pinguilabrum* has sixteen, and we have examined no specimens with fewer than fifteen. However, the first two spines are very short and embedded in thick skin and could easily be overlooked.

Delfin (1901) listed *Graus fernandezianus* as a member of the Chilean fauna. This name was based on an unpublished manuscript by Phillippi, dated 1897. Without the inclusion of a description, definition, or indication, as required by the International Code of Zoological Nomenclature, this name must be considered a *nomen nudum*.

Distribution.— Casma, Peru (Chirichigno, 1974), 9°30'S, 78°18'W, south to Concepcion, Chile (Delfin, 1901), 36°42'S, 73°05'W.

Etymology.— From the Greek *Graus* for old woman and the Latin *nigra* for black, dark or dusky, aparently based on the common name "la vieja negra."

Material Examined.— PERU: Mollendo USNM 77688, holotype of *Epelytes punctatus* (317). CHILE: La Ventana SIO 65-670, 126 (54.5-168.5, 3 cleared and stained) and SIO 65-678, 4 (94.6-71.5). Valparaiso USNM 218732, 3 (34.6-85.5, 2 cleared and stained); USNM 289501, 18 (72.4-209.1); USNM 289502, 27 (30.4-185.5, 2 cleared and stained); USNM 289508, 27 (25.8-165.4). Bahia Inglesa USNM 202954, 4 (75.6- 130).

OSTEOLOGY

Supraoccipital crest low, extending short distance over frontals to about posterior margin of orbit. Parietal crests low. Cephalic sensory canals bone-enclosed with few pores; supraorbital commissure present, with pore on median line. Orbitosphenoid absent. Basiphenoid present, obscured in lateral view by anterior portion of prootic and ascending arm of parasphenoid; belophram portion without anterior projection. Mesethmoid saddle-shaped, anterior margin oriented obliquely, descending anteroventrally to vomer. Anterior margin of vomer vertically oriented; ventral surface with few small conical teeth. Lateral commissure of prootic with anterior and posterior openings, no additional bony strut dividing posterior opening; anterior to lateral commissure at anterior margin of prootic, a bony strut projecting dorsally to contact but not fuse with dorsolateral wall of prootic (prelateral commissure of Rognes, 1973); ventromedial flange of prootic joining that of opposite side in midline to form dorsal roof of posterior myodome. Pterosphenoids not meeting in midline.
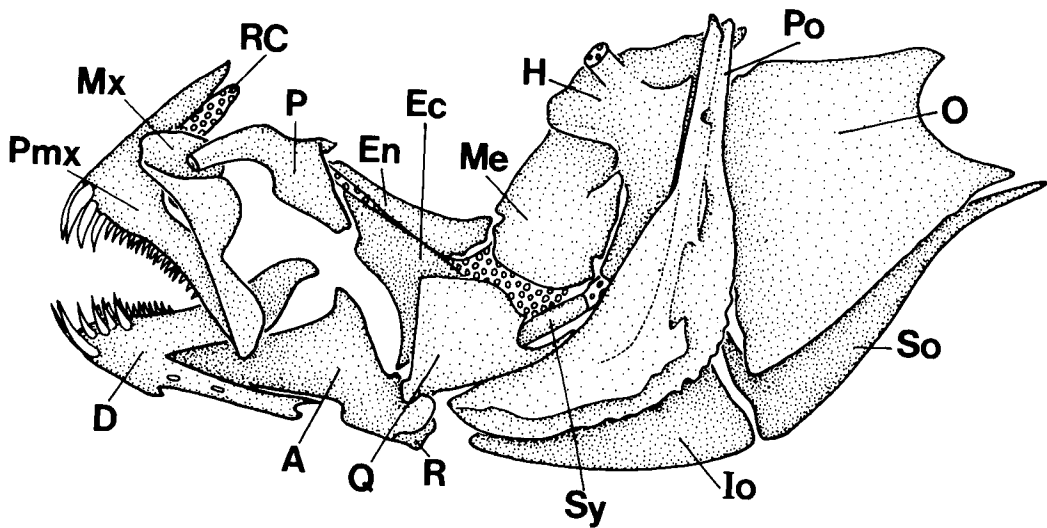
Fig. 2. Jaws, suspensorium and opercular series of *Graus nigra*; lateral view. A=angulo-articular; D=dentary; Ec=ectopterygoid; En=endopterygoid; H=hyomandibular; Io=interopercular; Me=metapterygoid; Mx=maxilla; O=opercle; P=palatine; Pmx=premaxilla; Po=preopercle; Q=quadrate; R=retroarticular; RC=rostral cartilage; So=subopercle; Sy=symplectic.

Parasphenoid with ventral median keel along midlength and dorsal median keel anteriorly; posterior myodome open ventrally at junction of parasphenoid and basioccipital. Basioccipital with small posterolaterally directed facet on each side for attachment of well-developed Baudelot's ligament, which passes around behind cleithrum to attach on medial side of supracleithrum. Exoccipital condyles meeting medially to form continuous articular surface for first vertebral centrum. Intercalar present.

Infraorbital bones six; lacrimal short, about as deep as long, remaining five bones tubular; third infraorbital about twice as long as second, fourth, fifth and sixth, and bearing large medially projecting subocular shelf; dermosphenotic (sixth infraorbital) resting loosely in sphenotic trough.

Opercle with two posterior projections, lower spine-like, upper slightly blunt. Subopercle and interopercle with smooth posterior margin. Preopercle with few relatively blunt serrations about midway along posterior margin.

Hyomandibular with broad laminar wing extending anteriorly from dorsal end of ventral shaft to a point below and anterior to anterior articular condyle, its ventral margin overlapping broad dorsal margin of rectangular metapterygoid

(Fig. 2). Metapterygoid with vertically oriented, posterolaterally directed shelf that posteriorly abuts ventral shaft of hyomandibular (metapterygoid lamina, Matsubara, 1943). Symplectic a simple strut, without flanges. Symplectic and ventral shaft of hyomandibular with cartilaginous tips that articulate to form dorsal portion of socket into which dorsal tip of interhyal inserts. Quadrate and metapterygoid separated by rectangular cartilaginous plate. Endopterygoid, ectopterygoid and palatine edentulous; palatine not directly contacting ectopterygoid and endopterygoid posteriorly, joined to them by connective tissue.

Jaw bones (Fig. 2) short. Ascending process of premaxilla rather long, about equal to length of alveolar ramus; articular process large, not fused to lateral margin of ascending process; rostral cartilage present, attached to posteromedial surface of ascending process. Maxilla with large, approximately rectangular, bladelike projection along dorsal margin extending from a point just distal to maxillary head to a point about halfway along maxillary shaft; small posterolateral projection for insertion of A_1 tendon of adductor mandibulae located on ventrolateral margin of maxillary shaft just distal to origin of the blade-

like projection. Supramaxilla absent. Dentary and premaxilla bearing simple, unjointed, curved, conical, firmly anchored teeth (Type 2 of Fink, 1981) in broad bands, outer row greatly enlarged anteriorly; replacement teeth completely enclosed in bone, except for tips of most fully developed, which apparently erode surfaces of dentary and premaxilla as they move into replacement position (two of these sockets can be seen in Fig. 8C, the replacement teeth having fallen out).

Nasal bone tube-like, nasal sensory canal extending forward from bone to margin of upper lip, not communicating with infraorbital sensory canal.

Pectoral rays 18-20; base of medial half of first pectoral ray extends laterally to form facet for articulation with scapular condyle. Pectoral actinosts (proximal radials) four, the dorsalmost with ventral spine-like process just distal to base (a ligament connects this process with a small posterolateral flange on scapula); upper two radials articulating with scapula, third articulating with scapula and cartilage between scapula and coracoid, fourth articulating with that cartilage and coracoid; distal radials cartilaginous, single free distal radial lying between the bases of each pectoral ray except first (dorsalmost). Medial and lateral extrascapular bones present; lateral extrascapular Y-shaped, with apex pointing ventrally; supratemporal commissure incomplete. Dorsal limb of posttemporal articulating with epiotic, ventral limb with intercalar; bone-enclosed canal at dorsal tip of supracleithrum connects posttemporal sensory canal with lateral-line canal. Dorsal postcleithrum broad and leaf-like, not attached to first pleural rib, ventral postcleithrum slender, rod like, somewhat expanded dorsally, where it articulates with medial side of dorsal postcleithrum.

Pelvic fin with one spine and five soft rays; a single oblong free cartilaginous distal radial present between bases of middle two or three rays. Pelvic girdle comprising two elongate triangular bones, slightly separated from one another along most of their length, tightly appressed at posterior ends; each bone with ventral median keel; accessory subpelvic keel (Katayama, 1943) absent; subpelvic process (Matsubara, 1943) absent; postpelvic process (Matsubara, 1943) present, short.

Anterior and posterior ceratohyals joined syn-chondrally, with some suturing medially and laterally; anterior ceratohyal perforated by oblong foramen dorsally (beryciform foramen of McAllister, 1968); posterior ceratohyal with strong, cord-like ligament from posterolateral surface to medial surface of interopercle; interhyal with cartilaginous tips, articulating ventrally with posterior ceratohyal and dorsally with cartilage between symplectic and hyomandibular. Branchiostegal rays six; anterior two inserting on ventromedial margin of anterior ceratohyal, small pointed projection between them; next two inserting on ventrolateral surface of anterior ceratohyal; fifth inserting ventrolaterally between anterior and posterior ceratohyals; sixth inserting on ventrolateral surface of posterior ceratohyal. Dorsal and ventral hypohyals present. Basihyal present, without teeth, its posterior end lying dorsal to first basibranchial.

Basibranchials 1-3 ossified, fourth cartilaginous, none bearing tooth plates; hypobranchials 1-3 present, without tooth plates, ceratobranchials 1-4 each bearing two rows of gill rakers which, on first three, extend onto serially corresponding hypobranchials and epibranchials; rakers (Fig. 10A) in lateral row of first arch long and blade-like with teeth along medial margins, remaining rakers short, club-like, rounded structures with tuft of teeth distally, fifth ceratobranchials separate, each with wide band of conical teeth dorsally, those of inner row considerably enlarged. All epibranchial and infrapharyngobranchial articulations (Fig. 3A) synchondral, unless otherwise noted; first epibranchial articulating distally with first infrapharyngobranchial; uncinate process of first epibranchial connected to anterior end of second infrapharyngobranchial by rod-shaped interarcual cartilage; second epibranchial articulating distally with posterior end of second infrapharyngo-branchial and condyle at midlength of dorsolateral surface of third infrapharyngobranchial; second epibranchial tooth plate present, autogenous, body of the plate thick, with cup-shaped facet at anterior end for articulation with cartilaginous posterior tip of the second infrapharyngobranchial; third epibranchial articulating distally with posterolateral corner of third infrapharyngobranchial; third epibranchial toothplate absent; fourth epibranchial
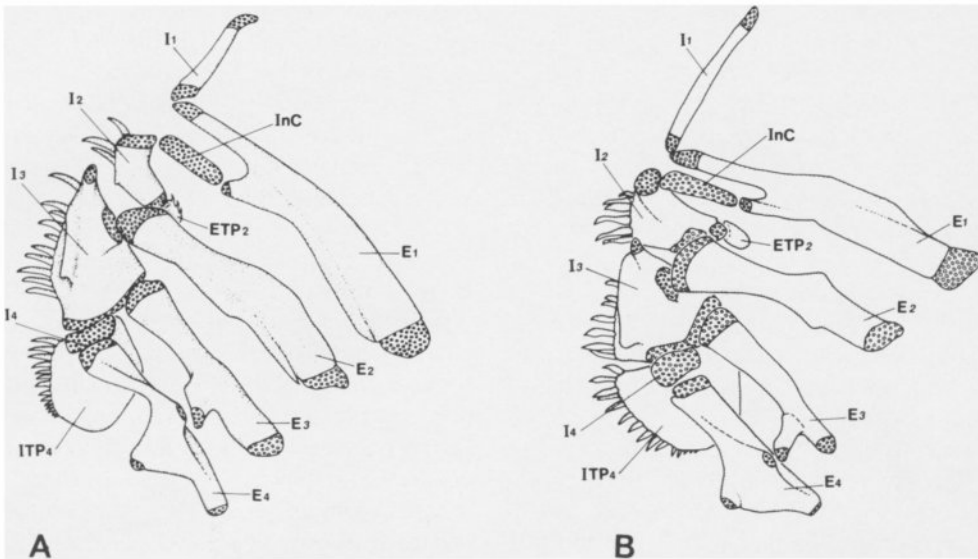
Fig. 3. Dorsal gill arches, right side in dorsal view. A, *Graus nigra*; B, *Girella zebra*. E 1-4= epibranchials 1-4; ETP2=second epibrancial toothplate; I 1-4=infrapharyngobranchials 1-4; InC=interarcual cartilage; ITP4=fourth infrapharyngobranchial toothplate.

articulating distally with small, block-shaped, cartilaginous fourth infrapharyngobranchial; third epibranchial with long dorsomedially directed process about midway along its length that articulates with shorter dorsal process about midway along length of the fourth epibranchial; medial side of fourth epibranchial with posteromedially directed flange that tapers to cartilaginous tip; first infrapharyngobranchial rod-shaped, edentulous, articulating dorsally with prootic; second infrapharyngobranchial lying along anterolateral margin of third infrapharyngobranchial, a dorsomedial bony flange at its anterior end articulating with anterior cartilaginous tip of latter; second infrapharyngobranchial toothplate fused; third infrapharyngobranchial largest, triangular in shape, with thin, triangular, vertical flange projecting dorsally from along medial edge; third infrapharyngobranchial toothplate fused; fourth infrapharyngobranchial a small rectangular cartilage articulating anteriorly with posteromedial end of third infrapharyngobranchial and ventrally with facet on dorsal surface of anterior end of fourth infrapharyngobranchial toothplate; fourth infrapharyngobranchial toothplate somewhat smaller than third and narrower anteriorly than

posterior portion of third, so that lateral margins of the two are not contiguous. All pharyngeal teeth simple, curved, conical (Fig. 9A), type 2 of Fink (1981).

Vertebrae 14 + 20 or 15 + 19; first neural arch autogenous; parapophyses beginning on fourth vertebra; pleural ribs 12 - 13, beginning on third vertebra; epipleural ribs 14 - 16 beginning on first vertebra, first two articulating at bases of first two neural spines, remainder articulating with pleural ribs or parapophyses.

Neural spine of second preural vertebra short broad crest; three epurals; anterior uroneural pair autogenous, expanded bases not resting directly on dorsal surface of urostylar centrum, but instead on two processes that project dorsally from anterior end of urostylar centrum, resulting in large space between uroneural bases and urostylar centrum; posterior uroneural absent; parhypural autogenous, with well-developed hypurapophysis; five autogenous hypurals. Principal caudal rays 9 + 8; procurrent caudal rays 12-14 + 11-12, all bilaterally divided, more anterior ones unsegmented; posteriormost ventral procurrent ray with very small ventral projection near base, the base of preceding ray not obviously shortened or modified.
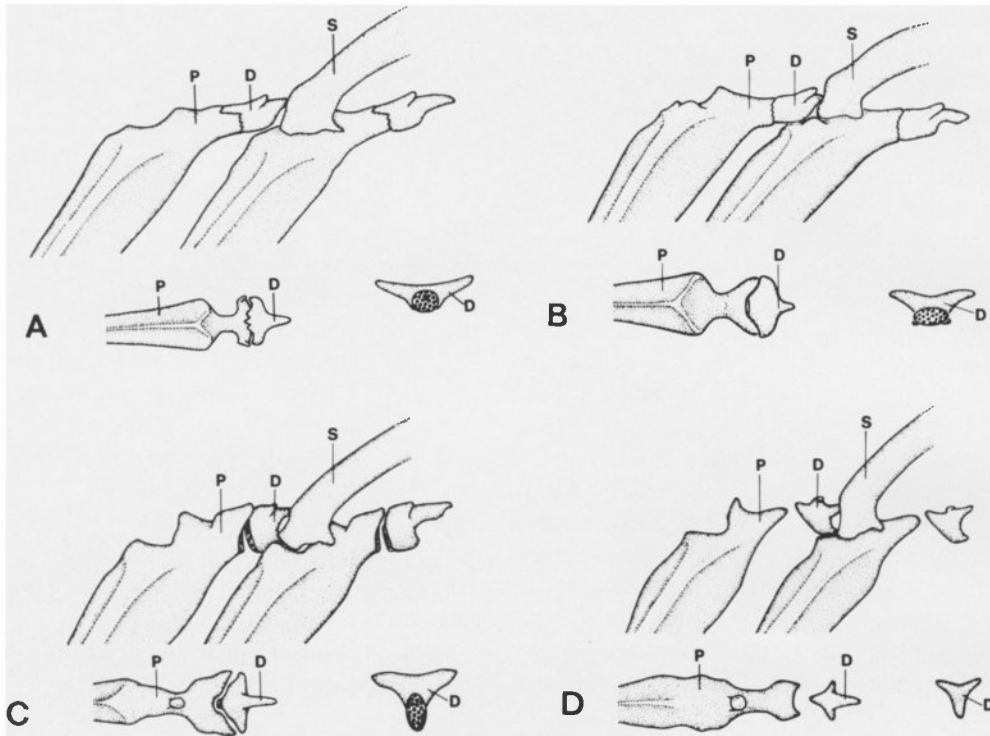
Fig. 4. Fifth and sixth spinous dorsal-fin pterygiophores; lateral (above), and dorsal (lower left) views, and isolated distal radial in anterior view (lower right). A, *Sectator ocyrus*; B, *Medialuna californiesis*; C, *Girella laevifrons*; D, *Graus nigra*. D= distal radial; P= proximal-middle radial; S= spine.

Dorsally, one or two small radial cartilages present below bases of anterior procurrent rays, anterior to third preural neural spines, and two or three small cartilages lying between ray bases near distal tips of posterior two epurals and fifth hypural; ventrally, one or two small radial cartilages above bases of anterior procurrent rays, anterior to third preural haemal spine, a larger cartilage projecting upward between distal ends of second and third preural haemal spines (associated with the two procurrent rays that articulate at this interspace), a small one just distal to tip of second preural haemal spine and an additional one lying between this one and ventral portion of tip of parhypural.

Two predorsal bones, neither notably expanded dorsally, first curved anteriorly, lying anterior to first neural spine, second curved posteriorly, lying between first and second neural spines. Dorsal fin with XV-XVI spines and 16-17 soft rays; first pterygiophore lying between second and third neural spines, bearing two supernumerary spines; proximal and middle radials of all dorsal pterygiophores (except frequently last one and occasionally last two) fused, distal radials all autogenous. Distal radials (Fig. 4D) of all spinous dorsal pterygiophores vertically elongate (depth equal to or greater than width), fully ossified and lacking cartilaginous condyles; each spinous distal radial separated from its serially corresponding elements, articulating only with next succeeding pterygiophore and with its serially corresponding spine (each distal radial rests on anterodorsal corner of succeeding pterygiophore and bears posteriorly directed process that projects through foramen in base of spine borne there). Distal radials of dorsal soft-ray pterygiophores median cartilaginous nodules with wing-like ossification on either side, lying between bases of ray halves and articulating anteriorly with their serially corresponding pterygiophore

(proximal-middle) and ventrally with anterodorsal corner of next succeeding pterygiophore; middle segment of last pterygiophore (whether autogenous or fused) embedded in cartilage that projects ventrally and expands longitudinally, with one and occasionally two additional ossifications occurring within it (more dorsal of two ossifications is stay typical of most percoids and variously present ventral ossification usually has form of a proximal radial).

Anal fin with three spines and 12-13 soft rays; first anal pterygiophore lying between haemal arches of 14th and 15th vertebrae, bearing two supernumerary spines; proximal and middle radials of all anal pterygiophores (except sometimes the last) fused, distal radials all autogenous; distal radial of first pterygiophore articulating anteriorly with first pterygiophore and posteriorly with anterodorsal corner of next succeeding pterygiophore (proximal-middle) and bearing anterior and posterior processes that project into foramina in bases of second (supernumerary) and third (serially corresponding) spines; pterygiophores supporting anal soft rays identical with those of dorsal fin.

ADDUCTOR MANDIBULAE

The adductor mandibulae comprises four primary sections: dorsal A_1, ventral A_2, medial A_3, and intramandibular A_ω (Figs. 5A & 6C). There are three distinct subdivisions of section A_1. The largest division (A_{1a}) is approximately rectangular with parallel fibers arising from the preopercle and hyomandibular and inserting broadly along the midlength of the maxillo-mandibular ligament, which extends in an arc from a ventrolateral process on the maxillary shaft to a small lateral prominence on the anguloarticular. On the medial side of A_{1a}, a partially separate bundle of fibers inserts on a strap-like aponeurosis that extends anteriorly as a cord-like tendon (tA_1) to insert on the posteromedial surface of the maxillary head. This aponeurosis is continuous with the medial side of the maxillo-mandibular ligament at the midlength of the latter. Ventrally, the aponeurosis extends as a flat tendon, passing lateral to and joining the flat tendon of A_3 (tA_3) which continues anteroventrally along the medial side of the

anguloarticular to insert on the coronomeckelian ossification. Along the lower portion of the anterior margin of tA_3 a triangular block of muscle originates and extends anteroventrally to insert along Meckel's cartilage.

A slightly smaller division of A_1 (A_{1b}) lies along the entire dorsal surface of A_{1a}, twisting and embracing A_{1a} in such a way that it is partially lateral to it anteriorly and partially medial to it posteriorly. Midway along its length A_{1b} is quite thin and flat, and the fibers are covered by a broad tendinous sheet. The ventral division of A_1 (A_{1c}) consists of a small oblong bundle of fibers lying along the anteroventral corner of A_2 and in some specimens, appearing to share a few fibers with that section. Section A_{1c} originates by a small tendinous strap on the lateral surface of the quadrate and inserts on the ventral portion of the maxillo-mandibular ligament near its insertion on the anguloarticular.

Section A_2 (Fig. 6C) is approximately hemispherical with its fibers converging anteriorly toward the area of insertion. It originates broadly along the lateral surface of the preopercle and inserts on a tendinous strap that continues forward lateral to the ascending process of the anguloarticular to insert on the posterolateral surface of the coronoid process of the dentary. The ramus mandibularis (rm) of the fifth cranial nerve passes medial to A_1 and A_2 and lateral to A_3. Section A_3 is a flat, triangular muscle whose fibers converge anteriorly toward the area of insertion. Ventrally, A_3 originates on the preopercle and hyomandibular and dorsally on the metapterygoid and hyomandibular, medial to the levator arcus palatini. Section A_3 inserts on a strap-like tendon (tA_3) that passes anteroventrally along the medial side of the anguloarticular, becoming cord-like distally to insert on the coronomeckelian. Section A_ω (cut in Fig. 6C) is a fan-shaped muscle that originates aponeurotically from the medial side of the quadrate and inserts along the posteromedial margin of the dentary.

Comparison with *Girella*.— For reasons discussed below, we believe *Graus* is most closely related to the genus *Girella*. In order to facilitate our discussion of relationships we first present a comparative description of the skeleton and adductor mandibulae. The following comparison
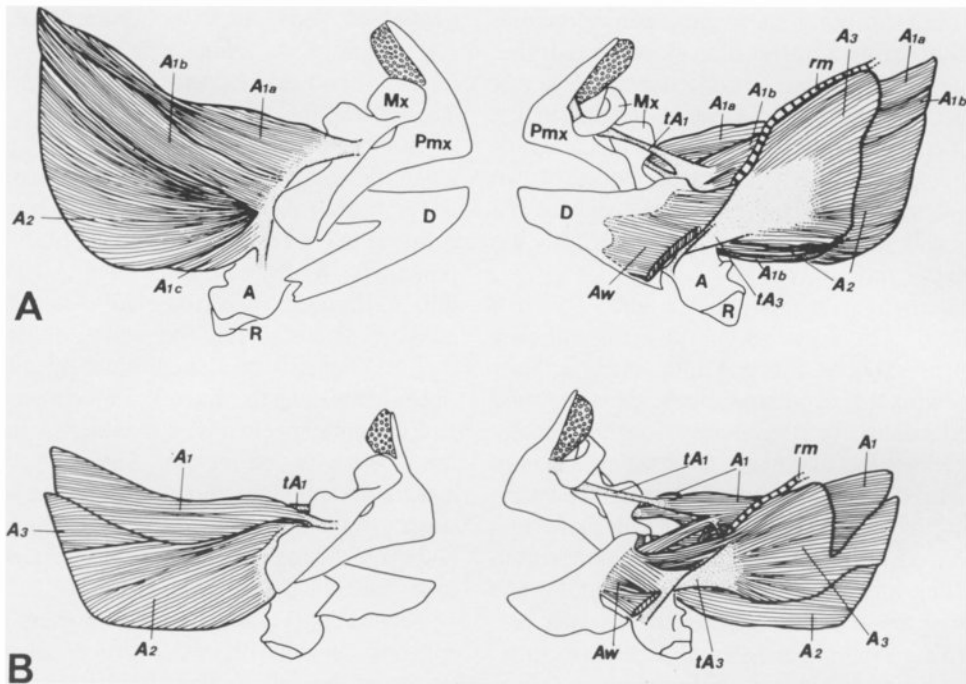
Fig. 5. Adductor mandibulae complex and jaws, lateral (left) and medial (right) views. A, *Graus nigra*. B, *Girella nigricans*. A_1, A_{1a}, A_{1b}, A_{1c}, A_2, A_3, A_ω, sections of the adductor mandibulae; A, angulo-articular; D, dentary; Mx, maxilla; Pmx, premaxilla; R, retroarticular; rm, ramus mandibularis of fifth cranial nerve; tA_1, tA_3, tendon associated with the insertion of respective sections of adductor mandibulae.

is based on the examination of cleared and stained specimens of 11 species of *Girella*.

The neurocranium of *Girella* is similar in general physiognomy to that of *Graus*. Only features that are consistent in all species examined and perceived by us to be substantially different from those present in *Graus* are discussed. The neurocranium is more truncated anteriorly, the anterior margin of the mesethmoid being vertically (or nearly so) rather than obliquely oriented; in most species, the vomer does not contact the mesethmoid dorsally, the ethmoid cartilage extends forward between the two bones so that it forms the anteriormost extent of the cranium. The bony interorbital region is much broader in *Girella* due to laminar extensions of the supraorbital portions of the frontals. In contrast to *Graus*, there is a variously developed process in *Girella* projecting anteriorly from the anterior margin of the basiphenoid. The prootic is not extended forward

in *Girella*, thus the basisphenoid is visible in lateral view. As in *Graus* there are anterior and posterior openings in the lateral commissure of the prootic. However, in *Girella*, the posterior opening is partially or completely divided by an additional flange-like bony strut that projects anteroventrally from just below the posteroventral corner of the anterior hyomandibular socket. This strut may be incomplete ventrally or may extend to the base of the lateral commissure, to which it is tightly appressed or fused. No such strut occurs in *Graus*. *Girella* has no prelateral commissure although in some specimens, there is a rudimentary dorsal projection at the anterior margin of the prootic.

There are typically six infraorbitals in *Girella*. Their configuration differs from that of *Graus* in that the sixth is usually about equal in length to the third, and the fifth is longer than the third. In *Graus* the third is always longest. In the speci-
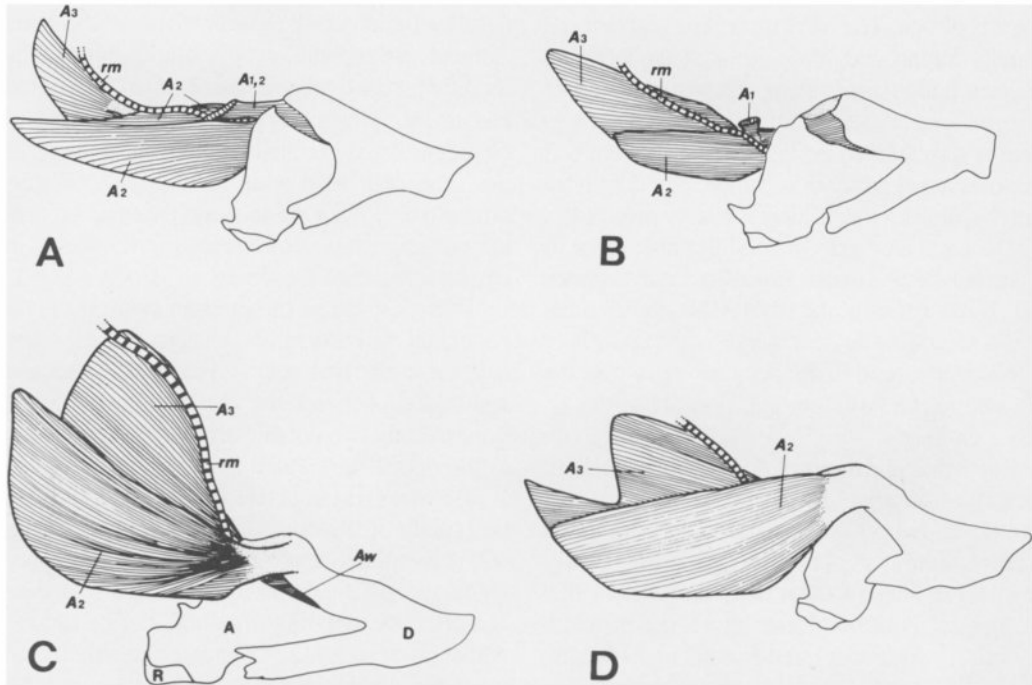
Fig. 6. Lateral view of right mandible, A1 section of adductor mandibulae removed to show insertion of A2. A, *Kyphosus cinerascens*; B, *Scorpis chilensis*; C, *Graus nigra*; D, *Girella nigricans*. Abbreviations as in Figure 5.

men of *Girella laevifrons* examined, there are seven infraorbitals, the third apparently represented by two segments, only the anterior of which bears the subocular shelf. Only five infraorbitals are present on the left side of the specimen of *Girella elevata* examined, the third and fourth apparently having fused. Infraorbital configuration may be intraspecifically variable in *Girella*; however, an insufficient number of specimens was examined to confirm this.

The opercular series of *Girella* differs from that of *Graus* only in that the dorsalmost of the two posterior projections of the opercle is more rounded. Preopercular serrations are well developed in all species examined except *Girella nigricans* and *G. punctata*.

In *Girella* the laminar portion of the hyomandibular does not extend as far forward from the ventral shaft as it does in *Graus*, and its junction with the metapterygoid ventrally is not a simple

overlapping of the two smooth bony margins, but is instead a suture-like interdigitation. In contrast to *Graus* the palatine directly contacts the endopterygoid and ectopterygoid in all *Girella* species examined and bears a few minute teeth in all except *G. mezina* and *G. albostriata*. No other significant differences are evident in the suspensorium.

The jaw bones are similar in configuration to those of *Graus*, except that the lower jaw is relatively shorter (about equal in length to upper jaw in *Girella* vs. 1.5 length of upper jaw in *Graus*) and the premaxilla is more robust anteriorly and has the articular process more consolidated with the ascending process. The teeth and tooth replacement mode are strikingly different (Fig. 8B). Each premaxilla and dentary has an open trough along its face from within which the primary row of functional teeth are replaced continually in an anterior to posterior rotation (progenic serial replacement,

Norris and Prescott, 1959). Each primary functional tooth consists of two segments, joined in a hinge-like articulation. The basal supporting segment is a laterally compressed, blade-like structure that rests between bony flanges along the posterior wall of the open trough. The proximal end of the distal segment is similar in shape to the basal segment and becomes anteroposteriorly compressed distally to form a spatulate structure that is usually tricuspid.

The nasal bones of *Girella* differ from those of *Graus* in having spatulate expansions at the anterior and posterior ends of the tubes. The sensory canal does not reach the anterior margin of the upper lip.

No pronounced differences are evident in the extrascapulars, posttemporal, pectoral girdle, or pelvic girdle.

The hyoid apparatus of *Girella* differs only in the lack of suturing laterally between the anterior ceratohyal and posterior ceratohyal. Suturing is present medially. The urohyal is essentially identical in shape to that of *Graus*, except that the ventral horizontal keel increases in width posteriorly for about three-fourths of its length, and then abruptly decreases and disappears.

The gill arches of *Girella* (Fig. 3B) are very similar to those of *Graus* in overall configuration. The second infrapharyngobranchial is broader in *Girella*. The fourth infrapharyngobranchial toothplate is also substantially larger than in *Graus*, being equal in size or larger than the third so that their lateral margins are contiguous. The most striking differences are in pharyngeal dentition and particularly gill raker morphology. The pharyngeal teeth of *Girella* are bicuspid (Fig. 9B), and in at least one species, *G. tricuspidata*, some of the upper pharyngeal teeth are tricuspid. Gill rakers in the lateral row of the first arch in most species are more numerous but similar in form to the club-like rakers of *Graus*. The remaining rakers (Fig. 10B) are substantially different from those of *Graus* (Fig. 10A), consisting of more closely-spaced, relatively flat plates with teeth along the dorsal margins, the general arrangement giving the appearance of an array of parallel combs along each arch.

There are fewer vertebrae (11+16), pleural ribs (8-9) and epipleural ribs (11-13) than in *Graus*, and well-developed parapophyses begin on the third, rather than the fourth vertebra.

The compostion and configuration of the caudal skeleton differs little from *Graus*. The same elements are present, and the relationships of the modified second preural neural spine, first epural and anterior uroneural pair are similar to those of *Graus*, as is the elevated articulation of the anterior uroneural bases with the urostyle. *Girella* differs only in lacking the small ventral spur on the posteriormost ventral procurrent ray and in having fewer total procurrent rays (9-11 + 8-10).

There are three rather than two predorsal bones, all with dorsal expansions; the first lies anterior to the first neural spine and the second and third lie between the first and second neural spines. Only two notable differences are evident in the dorsal fin. There are fewer spines (XII-XVI) and soft rays (11-16) in *Girella* and the distal radials of the spinous pterygiophores (Fig. 4C) are vertically elongate as in *Graus*, but they are larger and more closely associated with their serially corresponding proximal-middle radials. Although there is little or no interdigitation, each distal radial has direct bony articulation with the proximal-middle element at its anterodorsal corner; ventral to this point the opposing surfaces of the two radials bear vertically ovoid, cartilaginous condyles (lacking in *Graus*), that directly abut in larger specimens.

In the anal fin there are three spines and 10-13 soft rays. Pterygiophores are basically like those of *Graus*.

In *Girella*, as in *Graus*, the adductor mandibulae comprises four primary sections, A_1, A_2, A_3 and A_ω (Figs. 5B, 6D). Section A_1 is a rectangular muscle with parallel fibers originating on the vertical limb of the preopercle. The ventral surface of A_1 is closely contoured to the dorsal surface of A_2, essentially forming a pocket into which A_2 fits. The configuration of this pocket is such that the ventromedial portion of A_1 lies medial to A_2. Unlike *Graus*, A_1 has no fully separate subdivisions; however it bifurcates anteriorly along its vertical midline, giving rise to distinct medial and lateral heads. The larger lateral head inserts along a strong cord-like tendon that inserts on a posterolateral projection on the ventrolateral margin of the maxillary shaft. (This tendon apparently corresponds to the dorsal portion of

the maxillomandibular ligament of *Graus*.) Posteriorly this tendon becomes sheet-like and joins the aponeurosis on the medial side of A_1. Laterally, in some species (*Girella zebra, G. zonata, G. nebulosa, G. tricuspidata*, and *G. elevata*) a weak ventral ligament (presumably corresponding to the ventral portion of the maxillomandibular ligament) extends from the ventral margin of A_1 and attaches weakly to the lateral surface of the anguloarticular. In most species, there is no ventral extension.

The medial side of A_1 is associated with an aponeurosis corresponding to that on the medial side of A_1 in *Graus*. As in *Graus*, a cord-like tendon (tA_1) extends anteriorly from this aponeurosis to insert on the ventromedial side of the maxillary shaft, near the base of the maxillary head. Anterior to the aponeurosis, muscle fibers encroach about halfway along the length of tA_1, forming the distinct medial head of A_1. As in *Graus*, a small flat tendon extends ventrally from the A_1 aponeurosis to join the flat tendon of A_3 (tA_3). A strap-like bundle of muscle fibers extends anteroventrally from the A_1 aponeurosis, becoming confluent with the dorsal portion of section A_ω near its insertion in the Meckelian fossa.

Section A_2 (Fig. 6D) is essentially identical to that of *Graus* in origin, insertion and configuration. It is approximately hemispherical with its fibers converging anteriorly toward the area of insertion. It originates broadly along the lateral surface of the preopercle and converges anteriorly on a tendinous strap that continues forward lateral to the ascending process of the anguloarticular to insert on the posterolateral surface of the coronoid process of the dentary.

Aside from the prominent posterior extension of the ventral portion of A_3, configuration, origin and insertion of A_3 and A_ω (cut in Fig. 6D) are like those of *Graus*, as is the course of the ramus mandibularis (rm).

DISCUSSION OF RELATIONSHIPS

Philippi (1887) presented no evidence supporting his assignment of *Graus* to the Labridae, instead he discussed how it differed from other labrid genera and defended its status as a distinct

genus. It does, as he noted, bear some superficial resemblance to the "Peje perro," *Semicossyphus darwini* (Jenyns, 1842) (= *Trochocopus canis* Philippi, 1887), which has a similar body and fin configuration, thick fleshy lips and strong conical teeth, and this resemblance probably influenced Philippi's familial placement of *Graus*. In the original description of *Epelytes punctatus*, Evermann and Radcliffe (1917) noted independently that "this species bears a strong resemblance to some of the Labrids," and Hildebrand (1946: 169) reiterated "The shape of the body, the thick lips, the large teeth, and the long dorsal certainly are suggestive of the labrids."

Whatever superficial resemblance *Graus* may bear to the labrids, it is just that; there are no substantive characters that would suggest a close relationship between *Graus* and the Labridae or related families. In recent years a considerable body of evidence has accumulated supporting the monophyly of the suborder Labroidei, comprising the Cichlidae, Embiotocidae, Pomacentridae, and Labridae (including the Scaridae and Odacidae) (Liem and Greenwood, 1981; Stiassny, 1981; Kaufman and Liem, 1982; Stiassny and Jensen, 1987). This evidence primarily involves pharyngognathy in these fishes - coalescence of the fifth ceratobranchials into a single functional unit, true diarthrosis between the pharyngobranchials and the basicranium, and a suite of associated specializations involving pharyngeal muscles and bones. In the most recent treatment, Stiassny and Jensen (1987) identified seven specializations of the pharyngeal jaw apparatus that diagnose the Labroidei. All, including the most fundamental, union of the lower pharyngeals, are lacking in *Graus*. Additionally, *Graus* lacks the three synapomorphies that, in Stiassny and Jensen's scheme, unite the Embiotocidae, Pomacentridae, and Labridae, the four synapomorphies that unite the latter two families and all but one (two or fewer predorsals) of seven reductive specializations that labrids share variously with the other three families. Thus, although *Graus* has been retained in the Labridae since its original description, all available evidence conclusively refutes its relationship to this family.

Evermann and Radcliffe (1917) and

Hildebrand (1945) commented on the resemblance of *Pinguilabrum* to certain labrids. However, they apparently recognized the labrid similarities to be spurious and placed the genus in the Serranidae, without discussion of their reasons. The Serranidae at that time were a nebulously defined assemblage of generalized percoids, and it is undoubtedly the lack of obvious relationship to some other percoid group that led to the serranid placement. The Serranidae, as currently diagnosed (Gosline, 1966; Johnson, 1983), exhibit a unique innovative feature, three opercular spines, as well as three common reductive features, absence of the PU3 radial cartilages, procurrent spur and posterior uroneural pair. *Graus* has only two opercular spines, well-developed PU3 radial cartilages and a rudimentary procurrent spur. It shares with serranids the absence of the posterior uroneural pair, but this is a common specialization among percoids. There is, then little to suggest that *Graus* is closely related to the Serranidae.

In our study of *Graus*, two anatomical features stand out as particularly distinctive: 1) the insertion of adductor mandibulae section A_2 on the lateral side of the coronoid process of the dentary; and 2) the vertical elongation of the distal radials of the spinous dorsal fin and their complete separation from the serially corresponding proximal-middle radials. Among percoids, species of the genus *Girella* uniquely share the first condition with *Graus* and exhibit an arrangement of the spinous dorsal distal radials that appears intermediate between that of *Graus* and most other percoids. Recognition of these putative synapomorphies convinced us that *Graus* and *Girella* are sister taxa, and led us to investigate additional evidence to further corroborate or to refute this hypothesis.

The genus *Girella* comprises approximately fifteen species distributed antiequatorially in the Pacific with one in the eastern Atlantic. Recognition of generic status for certain of these species (e.g., *Doydixodon laevifrons, Melambaphaes zebra*) based on minor differences in dentition and scale size is not followed here. All species of *Girella* are primarily herbivorous and have dentition specialized for scraping or grazing and a long, highly coiled gut. The anatomy and

relationships of *Girella* have never been thoroughly investigated. Some early authors (e.g., Günther 1859) placed *Girella* in the family Sparidae; however since Jordan and Evermann (1898), *Girella* (Girellidae) has consistently been placed close to the families Scorpididae and Kyphosidae. *Girella* lacks the diagnostic characters of both the Sparidae and Sparoidea (Akazaki 1962; Johnson 1980), and we reject that relationship, as have subsequent authors. Most classifications have either recognized three distinct but closely related families, Scorpididae, Kyphosidae and Girellidae (Norman 1966; Johnson 1984), or have treated them as subfamilies under the family name Kyphosidae (Jordan and Evermann 1898) or Girellidae (Greenwood, et al. 1966; Nelson 1984). Evidence supporting this close relationship has never been explicitly presented, and the historical association of these three groups is apparently founded primarily in their general external resemblance and small, nibbling-type mouth. Our investigations have identified no convincing synapomorphies that would unite these three families unequivocally as a monophyletic group. Although they share a number of osteological features, those we have investigated are either widespread percoid symplesiomorphies or, if less common and possibly derived within percoids, are not unique to these three groups. Progenic serial replacement of primary jaw teeth (Norris and Prescott, 1959) may be synapomorphic for them, but a similar mechanism is known to have arisen independently within blennioids and labroids and its distribution has not been adequately surveyed among percoids. Perhaps the most substantive evidence in support of a close relationship among them is found in the striking resemblance of their larvae. Stevens, et al. (in press) note that larvae of genera representing the three families (*Girella* - Girellidae, *Medialuna* - Scorpididae, and *Hermosilla* - Kyphosidae) are frequently confused in sorted plankton samples. Those authors' descriptions of complete developmental series of each demonstrate the strong similarities in body form, opercular series spination, fin development and, most notably, distinctive pigment pattern, consisting of prominent midlateral, middorsal and midventral pigment. Johnson (1984) also noted these similarities for larvae of

scorpidids and girellids and suggested that this similar larval form might indicate a close relationship, although none of these features by itself is unique among percoids. With that in mind, and because we have found no evidence to suggest that any one of these three groups is more closely related to some other percoid family we treat them here as closely related for purposes of the character analysis required to test the hypothesized sister-group relationship between *Graus* and *Girella*.

Further evidence of a close relationship among scorpidids, kyphosids, girellids and a few other families exists in a shared arrangement of one ramus of one of the facial nerves. Freihofer (1963) reported that these three families share his pattern 10 of the ramus lateralis accessorius (RLA), a distinctive, uncommon pattern shared by only a few other groups - oplegnathids (Freihofer, pers comm), microcanthids (included by some in the scorpidids), arripidids, kuhliids, teraponids, pomatomids, nemastistiids and the several families that constitute the Stromateoidei. Based on Freihofer's descriptions and illustrations, pattern 10 can be easily distinguished from the most common pattern among percoids, pattern 9, and the other, somewhat less common pattern 8, by a simple dissection on preserved specimens. Only in pattern 10 does the orbito-pectoral branch (RLA-OP) reach the pectoral girdle by passing directly posteriorly from the sphenotic to the posttemporal-supracleithral joint, without crossing medially beneath the pterotic, lateral tabular and posttemporal, so that it lies just beneath the skin overlying the levator arcus palatini and dilator and levator operculi muscles. We were able to verify the presence of the pattern 10 RLA-OP in all those groups for which Freihofer reported it with the exception of *Pomatomus*. Dissections on four specimens of *Pomatomus* convinced us that Freihofer's report of pattern 10 in that genus is incorrect. We were unable to find the RLA-OP in the pattern 10 configuration. This is reasonable if Johnson's (1986) placement of *Pomatomus* as the sister group of the Scombroidei is correct; neither scombroids nor the more distant hypothesized outgroups, *Scombrolabrax*, *Scombrops*, and acropomatids, exhibit pattern 10 (pers obs). Consequently, even

if a pattern 10 path for RLA-OP were found in *Pomatomus*, as reported by Freihoffer, we would postulate that it was acquired independently.

Our observations on *Graus* are also contrary to those of Freihofer (1963), who, reporting on it under the synonym *Pinguilabrum* (then classified as a serranid), found it to have pattern 9, which is characteristic of serranine and anthiine serranids. Dissections on three specimens show conclusively that the RLA of *Graus* displays pattern 10. Moreover, *Graus* shares with *Girella* a unique variation. Whereas in other pattern 10 fishes RLA-OP lies superficial to the levator arcus palatini immediately upon its exit from the sphenotic, it passes medial to that muscle in *Graus* and *Girella*, and then emerges laterally through the dilator operculi to continue its posterior course superficial to the latter and the levator operculi (character 3 below).

Freihofer's (1963) survey of percoid families was extensive though not complete. It included one to numerous representatives of over 50 families. We have expanded the survey to include the 92 families or *incertae sedis* genera listed in the Percoidei by Johnson (1984), with the exception of the Leptobramidae, Coracinidae and Giganthiidae, which were not available for dissection. We identified pattern 10 in only one additional taxon, *Neoscorpis*, listed by Johnson (1984) as *incertae sedis*, but referred to in his discussion of girellids, scorpidids and kyphosids, and we now provisionally include this genus in the latter family. The larvae of *Neoscorpis* are undescribed.

In light of this more complete information about the distribution of RLA pattern 10 in percoids, we concur with Freihofer's hypothesis that it characterizes a natural assemblage. Because RLA pattern 10 is uncommon, and does not occur in beryciforms nor in any other percoid families, we interpret it as a specialization within the Percoidei and treat it as a synapomorphy uniting the few groups that possess it: Girellidae, Scorpididae, Kyphosidae, Microcanthidae, Kuhliidae, Arripididae, Oplegnathidae, Teraponidae and the families of the Stromateoidei. We propose that the "reduced pattern 10" (Freihofer, 1963) was independently derived in the carangoid *Nematistius*, because other

carangoids have pattern 9. However, *Nematistius* is the sister group of all other carangoids (Smith-Vaniz, 1984) and it is equally parsimonious that pattern 9 was independently derived in the latter, in which case carangoids may belong in the monophyletic assemblage diagnosed by pattern 10.

Haedrich (1967) discussed the potential importance of pattern 10 in establishing relationships of the stromateoids with the other fishes possessing it and presented evidence that he believed corroborated the integrity of the pattern 10 assemblage. He noted that pattern 10 fishes share another uncommon feature, a small bony bridge across the inside of the passage for the anterior vertical canal of the ear, which he later (Haedrich 1971) named the pons moultoni. Among the fishes he examined, Haedrich (1967) found this anterior to be present in only one non-pattern 10 fish, *Parastromateus* (RLA pattern 9) and to be absent in only one pattern 10 family, Girellidae. Our own observations (including examination of four specimens from Haedrich's study) differ substantially. Among pattern 10 fishes we found no bridge (bony or otherwise) in arripidids, microcanthids, scorpidids and oplegnathids (the latter not considered by Haedrich), and only a non-bony strap of connective tissue in kyphosids and pomatomids. We found a solid, very narrow, bony bridge only in kuhliids, some teraponids and stromateoids (not all genera of the latter two groups examined), and, contrary to Haedrich (1967; 1971), a broad, robust, bony bridge in *Girella*. Haedrich's report that girellids lack the pons moultoni was based on examination of *Boops vulgaris*, which is actually a centracanthid, and also on *Girella nigricans*. His failure to observe a bony bridge in *Girella* is particularly puzzling; *Girella* and *Graus* are unique among fishes we examined in having an extensively developed, broad, robust, bony bridge over the ventral portion of the passage for the anterior vertical canal. We interpret this distinctive configuration as a synapomorphy of *Graus* and *Girella* (character 4 below), but find the pons moultoni in general to be of no value in corroborating the monophyly of pattern-10 fishes for at least three reasons.

First, it characterizes fewer than half of the pattern 10 families. Secondly, Haedrich (1971), concluded that it is probably a primitive condition that is present in some percoids due to retention through an ancestral lineage, citing its presence in the beryciform *Trachichthys* and a Carboniferous palaeoniscoid. He argued that this does not detract from its support of the coherence of the pattern 10 fishes, but we disagree, since it may then be a symplesiomorphy in that assemblage. Thirdly, and further supporting the hypothesis of symplesiomorphy, the pons moultoni is considerably more widespread among percomorphs than suggested by Haedrich (1967). Haedrich (1971) discussed its distribution further, noting its presence in *Polymixia* (RLA absent), Caristiidae, Bramidae and Leiognathidae (RLA patterns unknown, but not pattern 10, pers obs) and Lactariidae (RLA pattern said by Haedrich to be unknown but listed by Freihoffer as pattern 9). Our own cursory survey indicates that among 17 families not considered by Haedrich (1967; 1971) a bony bridge spans the passage for the anterior vertical canal in eight: Gerreidae and Anomalopidae (RLA not pattern 10, pers obs); Apogonidae (RLA absent); Moronidae, Haemu-lidae, Sciaenidae (pattern 8); and Centropomidae, Pomacentridae (pattern 9). Useful phylogenetic information may be gained from the pons moultoni, but it cannot be meaningfully interpreted until its homology and distribution have been much more thoroughly investigated.

In the character analysis that follows, our outgroup hypothesis is based on the conclusions discussed above. The ingroup comprises Girellidae, Scorpididae, and Kyphosidae. The outgroup comprises Microcanthidae, Kuhliidae, Arripididae, Oplegnathidae, Teraponidae and the families of the Stromateoidei. Selected characters are compared in Table 1. The following are synapomorphies of *Graus* and *Girella*:

1). Adductor mandibulae section A_2 is fully separate from A_3 and passes *lateral* to the anguloarticular to insert on the *lateral* surface of the coronoid process of the dentary (Figs. 5 & 6). In scorpidids, kyphosids, the outgroups and all other percoids A_2 is frequently consolidated with A_3 and always passes *medial* to the angu-
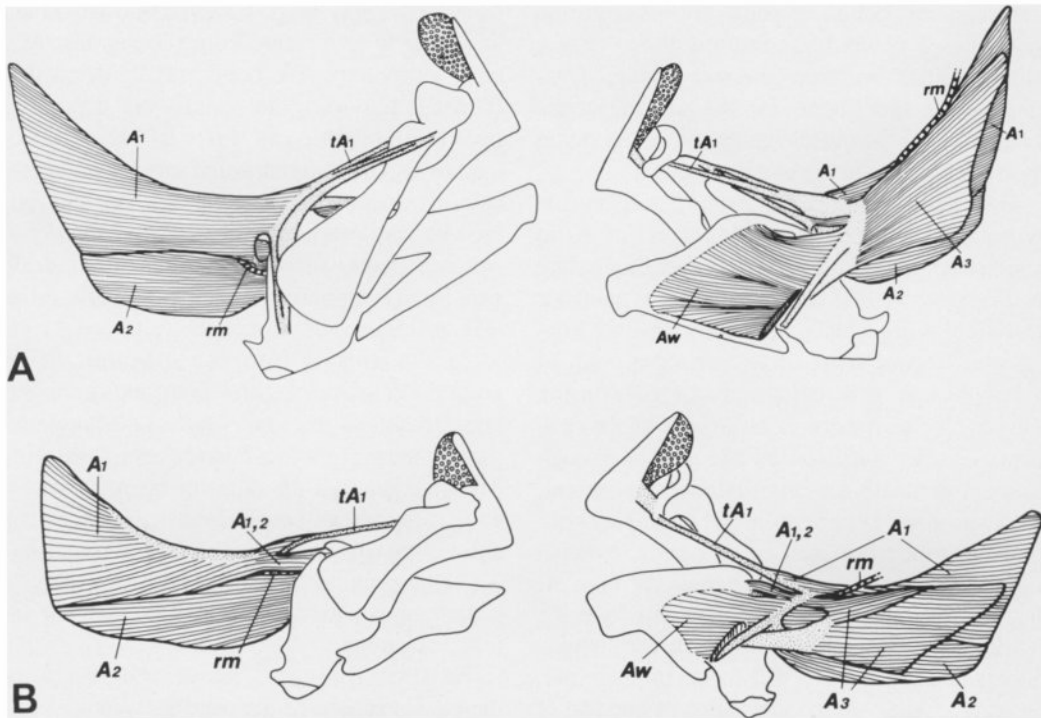
Fig. 7. Adductor mandibulae and jaws, lateral (left) and medial (right). A, *Scorpis chilensis;* B, *Kyphosus cinerascens.* Abbreviations as in Figure 5.

loarticular and inserts on the *medial* surface of the coronoid process or some other area of the dentary (Figs. 6 & 7). We are aware of only one other percomorph family, the Pomacentridae, in which the path and insertion of A_2 are like those found in *Graus* and *Girella.* As members of the Labroidei, pomacentrids have apparently acquired this condition independently of girellids. It warrants discussion nonetheless, because of its bearing on our assessment of homology. Stiassny (1981: Fig. 3) illustrated and described the adductor mandibulae of the Pomacentridae wherein a distinct subdivision lies lateral to the anguloarticular and inserts laterally on the coronoid process of the dentary. She identified that subdivision not as A_2 but as a ventral part of A_1 (A_{1b}), arguing that migration of the insertion site of A_2 from the medial to the lateral face of the mandible "seems to be improbable" and that the common presence in perciforms of a compound $A_{2,3}$ rather than an $A_{1,2}$ corroborated the proposed derivation from

A_1. Finally, she noted that in at least some labrids, a ventral portion of A_1 inserts on the ascending process of the anguloarticular, and she suggested a mechanism whereby a shift in the insertion of A_1 from the anguloarticular in labrids to the ascending process of the dentary could have produced the pomacentrid configuration. Relationships among labroid families remain unresolved (Stiassny and Jensen, 1987), and lacking an hypothesis of the ancestral configuration of the adductor mandibulae of pomacentrids we see no reason to view the A_1 scenario as more likely than one involving migration of the A_2 insertion, and, in fact, believe that the latter is better supported by the existing evidence. Stiassny's (1981) hypothesis would require the change in insertion of a specific muscle bundle (part of A_1) from one bone (anguloarticular) to another (dentary). In contrast, A_2 normally inserts on the dentary, medially, and at least some fibers usually attach to the coronoid process. Thus, the A_2 derivation of the

ventrolateral section in pomacentrids from the generalized percoid condition requires only a slight shift of insertion to a more lateral position on the same bone and the passage of the main body of the muscle along the lateral rather than medial side of the anguloarticular.

The latter hypothesis is even more plausible when one considers the arrangement of A_2 in another labroid family, the Cichlidae. According to Stiassny's (1981) description of the adductor mandibulae of cichlids, A_2 is fully separate from A_3 and is composed of two sections, one of which has, in part, the usual insertion on the medial face of the coronoid process of the dentary, but also inserts on its lateral face through association with the angulodentale ligament. Derivation of the ventrolateral subdivision of pomacentrids from such an arrangement would not require additional separation of A_2 from A_3 nor the migration of the A_2 insertion from the medial to the lateral face of the dentary, which Stiassny (1981) believed to be improbable. Instead, a shift only in the position of one part of A_2 relative to the anguloarticular could produce the pomacentrid configuration, and we believe this is more plausible than separation and shift in insertion of part of A_1 to a different bone. We conclude that the ventrolateral subdivision in pomacentrids is not part of A_1 but is the homologue of A_2.

For similar reasons, we interpret the ventrolateral section inserting on the lateral face of the coronoid process of the dentary in *Graus* and *Girella* to be A_2. In scorpidids (Figs. 6B, 7A) A_2 and A_3 are easily separable, although they are somewhat consolidated posteriorly. In kyphosids (Figs. 6A, 7B) A_2 and A_3 are fully separate, and the anterodorsal portion of A_2 (designated $A_{1,2}$ in Figs. 6 and 7 because it shares fibers with A_1 medially) inserts on the posterior or posterolateral margin of the coronoid process of the dentary. Thus, a hypothesis of derivation of the ventrolateral section in *Graus* and *Girella* from A_2 would be similar to that proposed above for pomacentrids. Whatever the origin and homology of this muscle section, its unique insertion is clearly a synapomorphy of the two genera.

2). The distal radials of the spinous dorsal fin

have a relatively deep, keel-like midsection and are either fully separate from (*Graus*, Fig. 4D), or lack any extensive bony interdigitation with (*Girella*, Fig. 4C), the serially corresponding proximal-middle radial. In scorpidids, kyphosids, the outgroups and most percoids the spinous dorsal distal radials are substantially broader than deep, lack the keel-like midsection and are usually strongly interdigitated with the serially corresponding proximal-middle radial (Fig. 4A, B).

3). On its path from the sphenotic to the postemporal-supracleithral joint, the orbitopectoral branch of the ramus lateralis accessorius passes medial to the levator arcus palatini, emerging through the dilatator operculi to continue a superficial course over the levator operculi. In scorpidids, kyphosids and the outgroups the orbitopectoral branch lies superficial to the levator arcus palatini as well as the dilatator and levator operculi.

4). There is a broad, robust, bony bridge on the medial surface of the pterotic covering about half of the anterior vertical canal of the ear. Kyphosids, scorpidids, the outgroups and most percoids lack a comparable structure. See the preceding discussion of Haedrich's (1971) pons moultoni for further details.

5). The procurrent spur (Johnson, 1975) is reduced (*Graus*) or absent (*Girella*), and the preceding procurrent ray is not foreshortened. In scorpidids, kyphosids and all outgroup taxa except some stromateoids there is a well-developed spur on the posteriormost ventral procurrent ray and the preceding ray is notably foreshortened.

6). The posterior uroneural pair is lacking. Scorpidids, kyphosids and all outgroups have two pairs of uroneurals.

Additional character states in which *Graus* and *Girella* differ from scorpidids and kyphosids include higher numbers of dorsal spines and vertebrae and lower numbers of branchiostegal rays and trisegmental pterygiophores. These may be synapomorphies, but polarity for them is equivocal (see Table 1).

Although we were not able to identify specific synapomorphies in the dorsal gill arch skeletons of *Graus* and *Girella*, the overall configura-

tions are very similar, the only notable differences being in the relative widths of the second and fourth infrapharyngobranchials (Fig. 3). The statement by Liem and Greenwood (1981), also mentioned by Kaufman and Liem (1982) and Stiassny and Jensen (1987) that the fifth ceratobranchials are united in *Girella* is erroneous; the exact source of this error has not been identified (K. Liem, pers comm). Interestingly, despite the similarity in the gill arch skeletons, there is a substantive difference in the musculature. In *Graus*, as in most other percoids, including scorpidids, kyphosids and the outgroup, there is a well-developed levator posterior muscle extending from the skull to the dorsal surface of the fourth epibranchial; the levator posterior is lacking in *Girella* (Liem and Greenwood, 1981; pers obs).

A few differences between *Graus* and *Girella*, numbers of vertebrae, dorsal spines, and procurrent caudal rays, cannot be unequivocally polarized. Others are clearly autapomorphic for one or the other genus. *Graus* exhibits several specializations with respect to *Girella*, sorpidids, kyphosids and the outgroups. Two of these have no obvious association with feeding. There are only two predorsal bones, and the distal radials of the spinous dorsal pterygiophores are completely separate from their serially corresponding proximal-middle radials. The higher number of vertebrae (34 vs. 27 in *Girella*) is probably derived as well; among scorpidids, kyphosids and the outgroups vertebral numbers greater than 30 occur only in some stromateoids. The other autapomorphic specializations of *Graus* are obviously feeding related. The jaws bear very large, robust, conical teeth anteriorly (Fig. 8C), the lips are thick and papillose, and gill arches 2-4 bear a mid-longitudinal band of large, prominent sensory papillae (Fig. 10A) similar to those on the lips.

All features of *Girella* that we were able to hypothesize as autapomorphies (lacking in *Graus*, scorpidids, kyphosids and out groups) appear to be feeding related, presumably specializations associated with herbivory. The most striking of these are the configuration and replacement mode of the primary jaw teeth (Fig. 8B). Each tooth is composed of two moveably articulated segments, the distal one with a spatu-

late, usually tricuspid tip, seemingly specialized for scraping. These teeth are continually replaced in an anterior to posterior rotation from within an open trough along the faces of the premaxilla and dentary. Norris and Prescott (1959) noted that kyphosids (they examined *Hermosilla*) have a similar "progenic serial replacement" mode, but with a closed rather than open trough, and we have observed the same condition in *Graus* and *Scorpis*. In this closed-trough condition, the tips of the replacement teeth erode the exterior walls of the troughs as they move into position (note resultant replacement teeth in sockets in Fig. 8A, C). Additional autapomorphies of *Girella*, presumably related to herbivory, are the bicuspid pharyngeal teeth (Fig. 9B), and modified gill raker configuration on arches 2-4 (Fig. 10). Absence of the levator posterior, also an autapomorphy, is presumably related to feeding as well.

Girella is further specialized with respect to *Graus* in having a long, extensively coiled gut and extremely numerous small pyloric caeca (100 or more), but these two features also characterize the phytophagous kyphosids; we hesitate to interpret them as autapomorphic for *Girella* until the exact relationships among girellids, kyphosids and scorpidids are resolved. If the Kyphosidae are the sister group of the Girellidae, as suggested by the arrangement of the adductor mandibulae discussed above, herbivory is primitive for girellids, and only those herbivory-associated specializations not present in kyphosids (noted in preceding paragraph) are autapomorphies of *Girella*.

When we began this study several years ago, we soon were convinced that *Graus* was a "primitive" girellid, that is a fish that was closer morphologically and ecologically to the common ancestor of the Girellidae than are the species of *Girella*. Here, we thought, was a classical example of what has often been called the "primitive sister group," a girellid that had diverged prior to the acquisition of herbivory and the concommitant morphological specialization of the jaw and pharyngeal teeth, gill rakers, branchial muscles and gut. Furthermore, because the passage of A_2 lateral to the posterior portion of the mandible appears ideally adapted
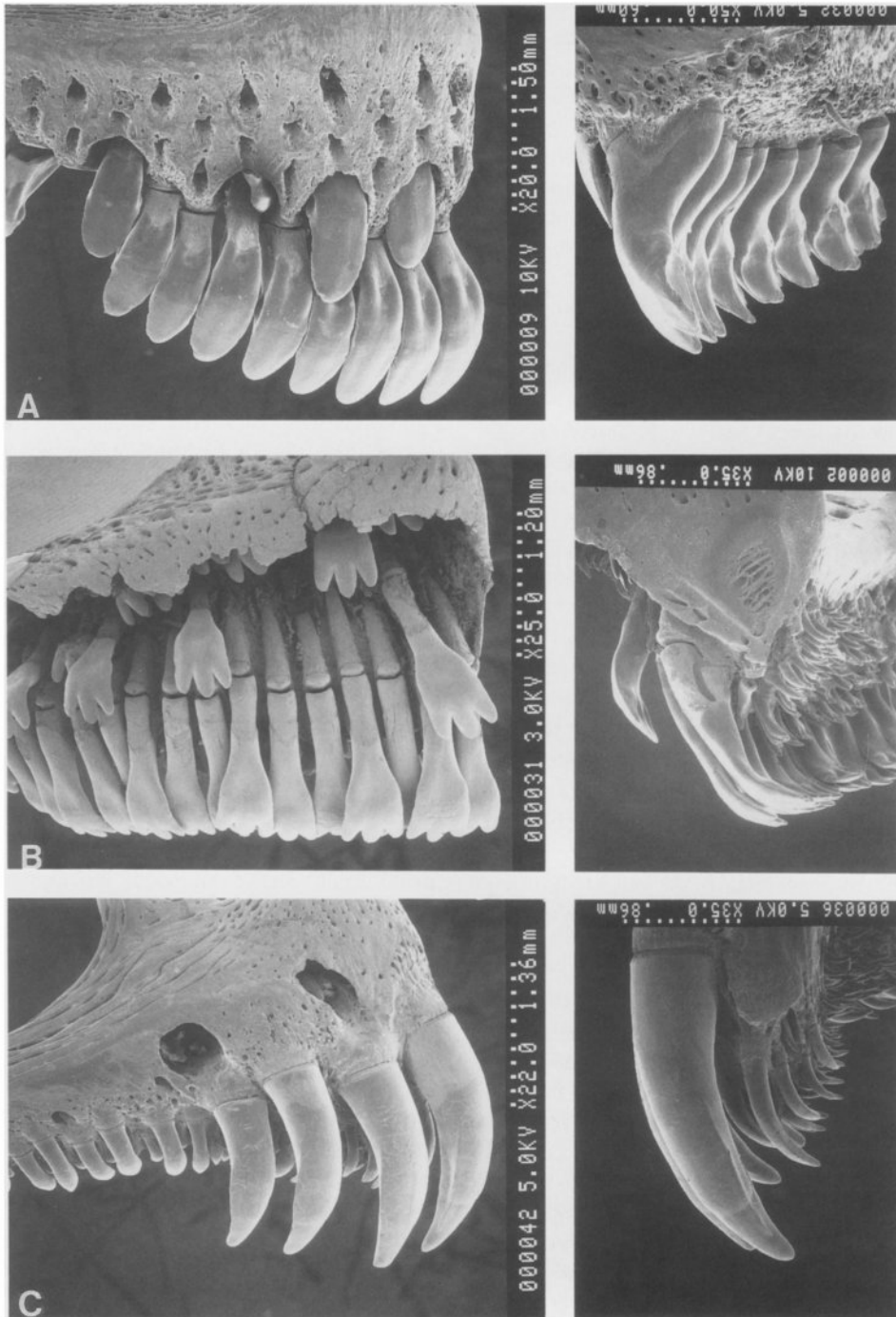
Fig. 8. Scanning electron micrographs of jaw teeth; lateral and medial views. A, *Kyphosus cinerascens*, 124.4 mm SL; B, *Girella nigricans*, 119.8 mm SL; C, *Graus nigra*, 112.7 mm SL.

to the horseshoe-shaped lower jaw characteristic of the small nibbling mouth of *Girella*, the presence of this lateral A_2 in *Graus* could be viewed as "preadapted" for the development of a herbivorous mode of feeding.

Our thinking at that time was admittedly constrained by the concept of the irreversability of extreme evolutionary specialization. The possibility that the generalized feeding habits and related morphology of *Graus* (seemingly identical to that of many lower percoids) might have developed from an ancestor highly specialized for herbivory seemed improbable. The senior author has since encountered numerous examples of reversals from highly specialized to more primitive morphologies that are irrefutable within the context of well-coroborated phylogenies (e.g., reversals in caudal fusion and vertebral number within scombroids, Johnson, 1986; reversals in jaw and gill arch configurations, predorsal number and scale type within acanthuroids, Tyler et al., 1989). Such reversions must have occurred repeatedly in the course of percomorph evolution. *Graus* may provide yet another example, although a parsimony-based resolution will have to await a more comprehensive analysis of family relationships. If kyphosids are the sister group of the Girellidae, herbivory may be primitive for girellids, having been lost in *Graus*; however the independent evolution of herbivory in kyphosids and *Girella* from a generalized ancestor would be equally likely.

Irrespective of the final outgroup hypothesis, *Graus* is clearly more specialized than *Girella* with respect to non-feeding related morphology, having one fewer predorsals, completely separate distal radials in the spinous dorsal fin and 34 vertebrae. Although irrelevant to the parsimony argument, this fact at least modifies our initial perception of *Graus* as a "primitive" girellid and thus lends some credence to the idea that the generalized feeding morphology is atavistic.

Finally, it is worth considering the available evidence on feeding habits of the two genera. Several studies have documented herbivory in adults of various species of *Girella* (e.g., Suyehiro 1942, *G. punctata;* Thomson 1959, Kilner and Akroyd 1978, *G. tricuspidata;* Norris 1963, *G. nigricans*). A few studies have exam-
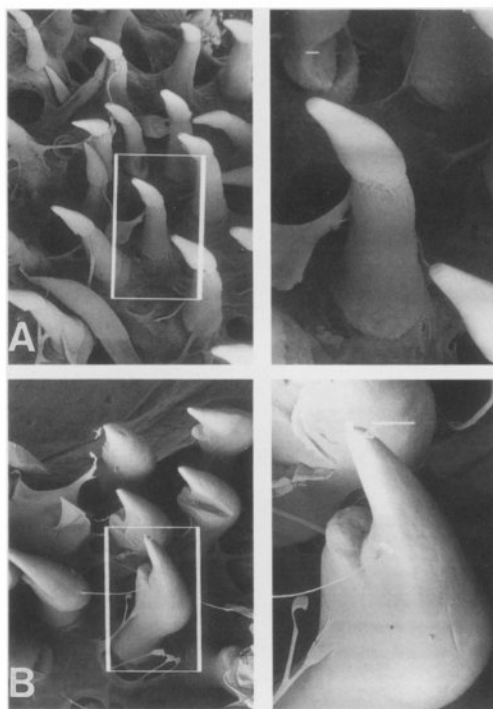

Fig. 9. Scanning electron micrographs of the upper pharyngeal teeth; box at left magnified at right. A, *Graus nigra,* horizontal bar 10μ; B, *Girella nigricans,* horizontal bar represents 100μ.

ined the ontogeny of feeding in *Girella* and have demonstrated a shift from carnivorous or omnivorous feeding in juveniles to largely or exclusively herbivorous feeding in adults. Mitchell (1953) found that individuals of *G. nigricans* were carnivorous below 50 mm, mostly herbivorous above 70 mm, and fed on a mixture of plant and animal matter between 50-70 mm. Williams and Williams (1955) reported a mixed diet only in newly settled *G. nigricans,* 23-32 mm SL, with a shift to mostly herbivorous diet above 32 mm SL. Bell et al. (1980) found that *G. elevata* is omnivorous at all sizes, but demonstrated a significant ontogenetic or size-related shift toward greater herbivory (13-55 mm SL, diet 40% algae; 73-144 mm SL, 74% algae; 240-490 mm SL, 77% algae) with a concomitant increase in relative length of the gut.

Two published accounts of the feeding habits of *Graus nigra* indicate that large adults are
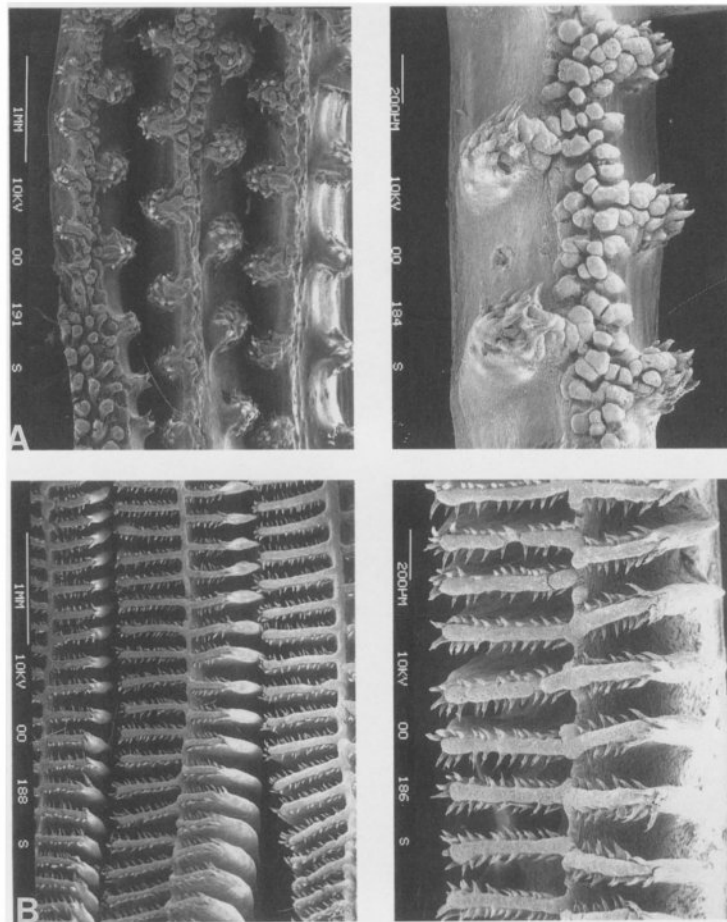
Fig. 10. Scanning electron micrographs of gill rakers on the second, third, and fourth cerato-branchials; right figures are higher magnifications of the third ceratobranchial in dorsomedial view. A, *Graus nigra;* B, *Girella nigricans.*

exclusively carnivorous. Fuentes (1982) examined the stomach contents of 37 large specimens (400-800 mm SL) from northern Chile and found that prey items consisted mainly of echinoderms, crustaceans and molluscs, with echinoderms constituting over 60% of the diet. Moreno (1972), based on ten specimens of unspecified size from central Chile, found the same three major prey categories, with crustaceans being more abundant than echinoderms. Neither study reported plant matter of any kind in the gut of *Graus;* however Fuentes examined no specimens smaller than 400 mm SL, and Moreno's specimens were also

apparently large ones from the fishery.

Our own examination of the stomach contents of 44 smaller specimens (32.4-237.7 mm SL) from central Chile indicates that *Graus* undergoes striking ontogenetic shifts in diet. All specimens below 80 mm SL appeared exclusively carnivorous, their guts containing mostly crustaceans and no algal material. However, in the majority of specimens above 80 mm, algae was present in the gut. Specimens 80-115 mm usually contained only a small amount of algae mixed with crustaceans, mollucs and/or fishes, but in most larger specimens the stomach and intestines

were tightly packed with algal material, and it frequently constituted as much as 75% or more of the total stomach contents by volume, the remainder comprising crustaceans, molluscs, polychaetes and bryozoans.

Thus it appears that *Graus* exhibits an early ontogenetic shift toward ingestion of large quantities of plant matter paralleling that documented for *Girella*. However, whereas the ontogentic trajectory of *Girella* (and kyphosids) culminates in herbivory, available data indicate *Graus* undergoes an additional shift in feeding behavior (apparently at some point above 240 mm SL, largest specimen vailable to us 238 mm SL), excluding algae entirely from its diet, and reverting to the carnivorous feeding of its early life, although concentrating on different types of prey, particularly echinoderms. The terminal shift to carnivory can be interpreted as a peramorphic addition (Alberch et al., 1979) to the *Girella* trajectory and as such represents an additional specialization of *Graus*, further corroborating the hypothesis that it is a derived girellid.

Graus exhibits no obvious ontogenetic changes in gross morphology or relative length of the gut, which remains short with a single loop and a few pyloric caeca. The absence of obvious specialized alimentary morphology raises questions about the nutritive value of the large amounts of algae ingested by *Graus* during one stage of its life history. It is conceivable that this algae passes through the gut undigested and that its ingestion serves only as a means of gathering nonvegetative epiphytic organisms that provide the actual source of nutrition. On the other hand, we cannot discount the possibility that *Graus* possesses other mechanisms, such as very low gastric pH or hind gut fermentation (Horn, in press), that facilitate digestion and assimilation of plant material.

Ontogenetic shifts from carnivory or omnivory to herbivory are common in fishes, but subsequent ontogenetic reversion to carnivory is not (Horn, in press). Thus *Graus* offers a particularly interesting and potentially important subject for the study of the evolution of herbivory. There is much to learn about the physiology and ecology of *Graus* if we are to understand its ontogenetically complex feeding behavior from an evolutionary perspective. However the historical component must also be considered. With the currently available evidence one viable hypothesis is that the transient herbivorous feeding behavior of *Graus* reflects its ancestry, and that this behavior has been retained even in the apparent absence of appropriate morphology for gathering and assimilating plant material only because the ingested algae serve as a vehicle for the ingestion of epiphytic prey items. A rigorous test of this and alternative hypotheses await a more complete knowledge of the biology of *Graus nigra* and a full resolution of the outgroup phylogeny.

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Table 1. States of selected characters in scorpidids, kyphosids, girellids and outgroups. Asterisks (*) designate synapomorphies of *Graus* and *Girella*.

CHARACTERS	OUTGROUPS		SCORPIDIDAE[2]	KYPHOSIDAE[3]	GIRELLIDAE	
	Stromateoidei	Others[1]			*Girella*	*Graus*
RLA Pattern	10	10	10	10	10	10
RLA-OP branch relative to LAP	lateral	lateral	lateral	lateral	medial*	medial*
Pons moultoni	weak or -	weak or -	-	weak	robust*	robust*
Insertion of A2 on dentary	medial	medial	medial	medial	lateral*	lateral*
Distal radials of spinous dorsal: Shape	broad	broad	broad	broad	deep*	deep*
Interdigitated with prox-mid.	yes	yes	yes	yes	no*	no*
Procurrent spur	+ or -	+	+	+	-*	vestige*
Preceding ray foreshortened	+ or -	+	+	+	-*	-*
Uroneurals	2	2	2	2	1*	1*
Dorsal spines	9 - 18	9 - 13	10	6 - 11	12 - 16	16
Vertebrae	24 - 61	25	25 - 26	25	27	34
Branchiostegals	5 - 7	6 - 7	7	7	6	6
Trisegmental pterygiophores	?	0 - 16	7 - 22	1 - 14	0 - 1	0 - 1

[1] Arripididae, Kuhliidae, Microcanthidae, Oplegnathidae and Teraponidae.
[2] *Labracoglossa, Medialuna* and *Scorpis*.
[3] *Hermosilla, Kyphosus, Neoscorpis* and *Sectator*.