

# Notes on the anatomy and classification of elopomorph fishes

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## Contents

Introduction . . . . .	65
Material examined . . . . .	66
Abbreviations used in the figures . . . . .	67
Jaw and associated muscles and ligaments . . . . .	68
I. Albulidae, Pterothrissidae and Halosauridae . . . . .	68
Pterothrissidae: <i>Pterothrissus bellocci</i> . . . . .	68
<i>Pterothrissus gissu</i> . . . . .	69
Albulidae: <i>Albula vulpes</i> . . . . .	70
Halosauridae: <i>Halosaurus guentheri</i> . . . . .	73
<i>Halosaurus carinicauda</i> . . . . .	75
<i>Halosauropsis macrochir</i> . . . . .	75
<i>Aldrovandia gracilis</i> . . . . .	75
<i>Aldrovandia affinis</i> . . . . .	76
Comments and comparisons . . . . .	76
II. Notacanthidae and Lipogenyidae . . . . .	77
Notacanthidae: <i>Polyacanthonotus rissoanus</i> . . . . .	77
<i>Polyacanthonotus africanus</i> . . . . .	79
<i>Notacanthus bonapartei</i> . . . . .	80
Comments and comparisons . . . . .	84
Lipogenyidae: <i>Lipogenys gilli</i> . . . . .	84
Comments and comparisons . . . . .	87
The sternohyoideus muscle in Elopomorpha . . . . .	87
The palatoquadrate arch in <i>Lipogenys gilli</i> . . . . .	89
The autopalatine problem in halosaurs and notacanthus . . . . .	90
Lateral line scales . . . . .	93
Interrelationships and classification . . . . .	94
Acknowledgements . . . . .	101
References . . . . .	101

## Introduction

Little detailed information is available on the cranial musculature of elopomorph fishes, a gap in our knowledge which was brought home when recently I was asked to comment on the possible significance of a bony bridge on the angulo-retroarticular of *Albula vulpes* (Nybelin, 1976).

From this initial involvement with *Albula* my interest turned to its supposed near relative, *Pterothrissus*. The nature of the similarities and differences I found in the musculature of these genera led me to consider the possible use of jaw muscles in testing some of the views expressed on the phylogeny and classification of the Elopomorpha (see Forey, 1973a & b; Nelson, 1973; McDowell, 1973; Gosline, 1971). This objective necessitated the investigation of jaw muscles in other elomorphs, especially the Notacanthiformes and Anguilliformes (both taxa *sensu* Greenwood, Rosen, Weitzman & Myers, 1966). McDowell's (1973) magnificent review of the Heteromi (= Notacanthiformes) includes some brief descriptions and comments on notacanth and halosaur jaw muscles. These I sometimes found in conflict with my own observations (and interpretations), thus highlighting the need for further detailed and illustrated descriptions of the musculature and

associated osteological features in these fishes as well as in the more basal members of the super-order. Amongst the osteological features may be mentioned the peculiarities of the palatopterygoid arch in notacanthiforms, in particular the specialization of the autopalatine suggested by McDowell (another area where an alternative explanation seems more probable).

The results of these comparative anatomical studies have provided new information which I believe can be used to throw light on the phyletic relationships and hence classification of the Elopomorpha.

Disappointing in this respect was the information obtained from the jaw musculature of the Anguilliformes. My preliminary investigations show that, although highly specialized in some details, the anguilliform 'bauplan' is essentially that of a basic elopomorpha such as *Elops*.

### Material examined

D = dissected; E = examined; SL = standard length; TL = total length.

BMNH (British Museum (Natural History)); JLBS (J. L. B. Smith Institute of Ichthyology); MCZ (Museum of Comparative Zoology, Harvard); VMS (Virginia Institute of Marine Science).

*Albula vulpes* (D), BMNH 1923.7.30: 47–51. Rio de Janeiro. 188 mm SL.

*Albula vulpes* (D), BMNH 1932.2.8: 5. Trinidad. 180 mm SL.

*Albula vulpes* (D), Gothenburg Museum. (Head only.)

*Aldrovandia affinis* (D), 'Discovery' Stn 7853, 25°51'7" N, 16°2'4" W, 1518–1503 m. 2 specimens, 290 mm SL; 223 mm (tail missing).

*Aldrovandia gracilis* (D), 'Discovery' Stn 7857, no. 5, 36°46'6" N, 14°31' W, 1356–1341 m. 1 specimen, 280 mm (tail broken).

*Aldrovandia phalacra* (D), 'Discovery' Stn 7853 (details above). 2 specimens, 320 mm & 365 mm TL.

*Amia calva* (D), BMNH unregistered specimen. Illinois, U.S.A. Head only, 50 mm.

*Anguilla anguilla* (D), BMNH 1962.6.29: 11–42. Isle of Man. 210 & 276 mm TL.

*Conger conger* (D), BMNH 1962.6.29: 45. Isle of Man. 425 mm TL.

*Elops saurus* (D), BMNH 1932.11.10: 3–4. Berbice, Guyana. 180 mm SL.

*Elops senegalensis* (D), Gothenburg Museum. Bathurst, Gambia. Head only, 74 mm from a specimen 325 mm SL.

*Halosaurus guentheri* (D), BMNH 1966.10.14: 1–2. 'Oregon' Stn 4375. 230 mm (tail missing) & 360 mm TL.

*Halosawopsis macrochir* (D), 'Discovery' Stn 8512, no. 4, 2281–2465 m. 1 specimen 556 mm TL.

*Lipogenys gilli* (D), MCZ 38322. 'Capt. Bill I' Stn 134, 38°05' N, 73°43' W. 337 mm SL.

*Lipogenys gilli* (D), MCZ 37612. 'Capt Bill II' Stn 95, 42°45' N, 63°47' W. 255 mm SL.

*Lipogenys gilli* (D), VMS 03465. 36°40'9"–41°6' N, 74°38'5"–35'2" W, 1111 m. 212 mm SL.

*Lipogenys gilli* (E), VMS 03467. 36°42'5"–44'0" N, 74°32'–30'9" W, 1190 m. 227 mm SL.

*Lipogenys gilli* (E), VMS 03466. 37°00'0"–00'2" N, 74°19'0"–17'6" W, 1698 m. 230 mm SL.

*Notacanthus sexspinis* (E), BMNH 1873.12.13: 27. Wellington. Skeleton in alcohol.

*Notacanthus sexspinis* (E), BMNH 1872.4.26: 14. Wellington. 375–420 mm SL.

*Notacanthus bonapartei* (D), BMNH 1972.1.26: 33–39. Off W. Ireland. 340 & 450 mm SL.

*Polyacanthonotus africanus* (E), 'Discovery' Stn 7853, 25°51'7" N, 16°2'4" W, 1518–1503 m. 123 mm TL.

*Polyacanthonotus africanus* (D), 'Discovery' Stn 8519, no. 7, 24°2'2" N, 16°59'2" W, 1037–997 m. 186 mm TL.

*Polyacanthonotus rissoanus* (D), 'Discovery' Stn 8512, no. 4, 2281–2465 m. 293 mm TL.

*Polyacanthonotus rissoanus* (E), BMNH 1904.3.4: 3. Off Cape Point. 297 mm TL.

*Pterothrissus bellocci* (D), JLBS 3677. No locality stated. 132 mm SL.

*Pterothrissus gissu* (E), BMNH 1879.5.14: 532 Mosina. (Holotype of *Bathythrissa dorsalis*.) 380 mm SL.

*Pterothrissus gissu* (E), BMNH 1903.5.14: 142. Japan. Skeleton

*Pterothrissus gissu* (D), BMNH 1977.1.22: 3. Japan. 315 mm SL.

In addition to all the above the following specimens were radiographed:

*Aldrovandia gracilis*, BMNH 1966.10.4:3.

*Aldrovandia affinis*, BMNH 1939.5.24: 662.

*Aldrovandia phalacra*, BMNH 1960.1.15:2

*Halosawopsis macrochir*, BMNH 1869.2.10:37.

*Halosaurus parvipinnis*, BMNH 1939.5.24: 660–661.

*Halosaurus oweni*, BMNH 1890.6.16: 55.

## Abbreviations used in the figures

A1 $\alpha$ :	A1 $\alpha$ division of the adductor mandibulae muscle
A1 $\alpha^1$ }	Superficial and deep subdivisions, respectively, of adductor mandibulae division A1 $\alpha$
A1 $\alpha^2$ }	
A1 $\beta$ :	Maxillary division (A1 $\beta$ ) of the adductor mandibulae muscle
A2:	A2 division (mandibular) of the adductor mandibulae muscle
A2 $^1$ :	Muscle slip from A2
A2 $\alpha$ }	Deep and superficial subdivisions, respectively, of adductor mandibulae A2 division
A2 $\beta$ }	
A3:	A3 division of the adductor mandibulae muscle
AbdM:	Abductor muscles of the pectoral fin
AdHy:	Adductor hyomandibulae muscle
Ad Mand:	Adductor mandibulae (undivided muscle mass)
Ad Op:	Adductor operculi muscle
Ant hyl:	Anterohyal (Anterior ceratohyal)
Ap Pmx:	Ascending process of premaxilla
A $\omega$ :	Intramandibular (A $\omega$ ) division of the adductor mandibulae muscle
? A $\omega$ :	Tendon thought to be remnant of A $\omega$ muscle
BBr:	Bony bridge of the angulo-retroarticular
C Emax-Pmx:	Combined ethmomaxillary and ethmopremaxillary ligaments
Ct:	Connective tissue
Ct nod:	Connective tissue nodule
D Ct nod:	Droque-shaped connective tissue nodule
D Emax:	Deep ethmomaxillary ligament
D Op:	Dilatator operculi muscle
D pal:	Dermopalatine
Ectp:	Ectopterygoid
E Max:	Ethmomaxillary ligament
End Pg:	Endochondral pectoral girdle
Entp:	Entopterygoid
Epal:	Ethmopalatine ligament
E Pmx:	Ethmopremaxillary ligament
Epx:	Epaxial body musculature
Fac:	Facet for articulation with the parasphenoid
Hyh:	Hyohyoideus muscle
Hyom:	Hyomandibula
Hypx:	Hypaxial body musculature
Ihy:	Interhyal
Lap:	Levator arcus palatini muscle
Lap D }	Deep and superficial parts, respectively, of the levator arcus palatini muscle
Lap S }	
LE Pmx:	Lateral ethmopremaxillary ligament
Lig Pri:	Ligamentum primordium
L Op:	Levator operculi muscle
Max:	Maxilla
Max-Pmx:	Maxillo-premaxillary ligament
Metp:	Metapterygoid
Nub:	Nubbin of cartilage
Op:	Operculum
Op ara:	Opercular-angulo-retroarticular ligament
Op met:	Opercular-metapterygoid ligament
P:	Autopalatine
? P:	Presumed autopalatine
PecF:	Pectoral fin
Phy:	Protractor hyoideus muscle
Phyc:	Pharyngoclavicularis muscle
P lig:	Posterior maxillo-mandibular ligament
P Max I:	Palatomaxillary ligament
Pmx:	Premaxilla

PPmx 1:	Palato-premaxillary ligament
Pthyl:	Posterohyal (Posterior ceratohyal)
Q:	Quadrate
SE Max 1:	Superior ethmoxillary ligament
So Lig P:	Suborbital branch of ligamentum primordium
Sthy M:	Sternohyoideus muscle
Symp:	Symplectic
T:	Tendon
TA1 $\alpha^2$ :	Tendon from adductor A1 $\alpha^2$ muscle
TA1 $\beta$ :	Tendon from adductor A1 $\beta$ muscle
TA $\beta$ +2:	Shared tendon of adductor A1 $\beta$ and A2 muscles
TA1 $\beta$ +A2 $\beta$ :	Shared tendon of adductor A1 $\beta$ and A2 $\beta$ muscles
TA2 $\beta$ :	Tendon from adductor A2 $\beta$ muscle
TD:	Ligament from dentary joining tendon from adductor A1 $\beta$ muscle
Ip:	Tooth plate on ectopterygoid
T Sthy:	Tendon from sternohyoideus muscle to hyoid arch
UE Pmx:	Upper ethmopremaxillary ligament
Vhyl:	Ventrohyal

## Jaw and associated muscles and ligaments

### I. ALBULIDAE, PTEROTHRISSIDAE and HALOSAURIDAE

#### PTEROTHRISSIDAE

##### *Pterothrissus belloei* Cadenat

Since the specimens available for dissection had suffered some damage to the snout region, only the jaw muscles will be described. The jaw ligaments are described from a specimen of *P. gissu* (p. 69).

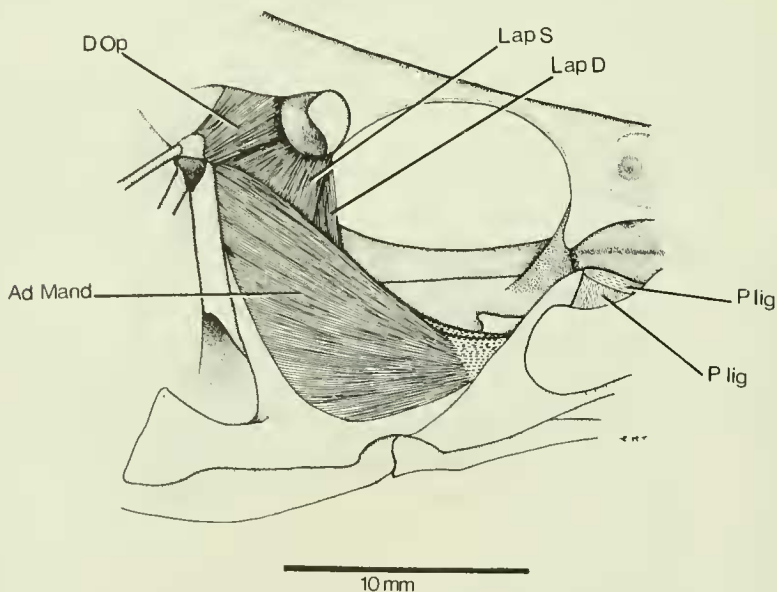


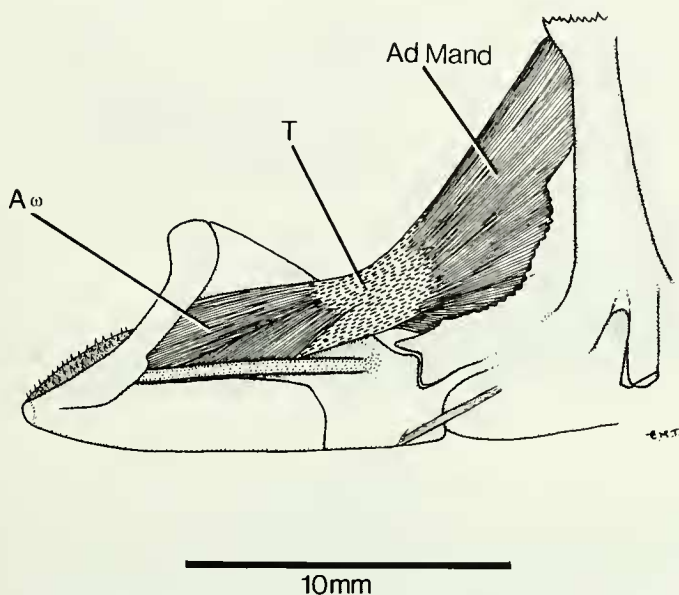
Fig. 1 *Pterothrissus belloei*. Jaw musculature in right lateral view. The supramaxilla has been removed to show the maxillo-mandibular ligaments. Drawn by Miss E. Tarr from specimen RUSI 3674, 13.8 cm standard length.



**ADDUCTOR MANDIBULAE MUSCLES** (Fig. 1). The adductor is a single muscle mass originating on the preoperculum and metapterygoid. Anteriorly it inserts through a fairly well-developed and deep tendon onto the posterior margin of the compound angulo-retroarticular bone at about its mid-point. Ventral to this point of insertion there appears to be another, effected through an area of much looser connective tissue.

On the medial face of the main adductor muscle mass the  $A\omega$  portion arises from an extensive tendinous aponeurosis (Fig. 2). Muscle  $A\omega$  deepens as it runs forward so that it comes to occupy almost the entire Meckelian fossa, in which it has its insertion.

Apart from the fact that no fibres of the adductor mandibulae are inserted onto the maxilla, this muscle in *Pterothrissus* closely resembles that of *Elops saurus* (see Vrba, 1968). The maxillo-mandibular ligaments of *Pterothrissus*, however, are quite different since there is no typical ligamentum primordium in this genus. In *Elops* there is what can be considered a typical lower teleostean ligamentum primordium (see Winterbottom, 1974: 232), as well as a posterior ligamentous connection between the maxilla and the lower jaw. I would interpret the latter as being homologous with the only ligaments present in *Pterothrissus*, which, therefore, does not have a true ligamentum primordium.



**Fig. 2** *Pterothrissus belloci*. Medial aspect of right lower jaw. Drawn by Miss E. Tarr; same specimen as in Fig. 1.

**LEVATOR ARCUS PALATINI MUSCLE.** This is a moderately large muscle originating from the pterotic and sphenotic regions of the skull (Fig. 1). Its main body is subdivided, one set of fibres running obliquely backwards and downwards to insert medially on the metapterygoid. The other part of the muscle runs almost vertically downwards to insert dorso-anteriorly on the lateral face of the metapterygoid.

**ADDUCTOR ARCUS PALATINI MUSCLE.** A few fibres representing this muscle are found in the connective tissue linking the pterygoid arch with the parasphenoid.

*Pterothrissus gissu* Hilgendorf

**MAXILLO-MANDIBULAR LIGAMENTS.** The *ligamentum primordium* is long and strap-like, and com-

posed of rather loose and thin connective tissue. It extends from a point at about the middle of the angulo-articulo-retroarticular near its ventral margin to the head of the maxilla; it inserts laterally on that bone near the base of the short ascending head. Since the ligament passes laterally over the dorso-posterior angle of the maxilla it binds that bone closely to the lower jaw. The origin of the ligament on the lower jaw is not marked by any noticeable protuberance.

There are two other ligamentous connections between the maxilla and the lower jaw. A broad, sub-triangular ligament runs from just below the coronoid process of the lower jaw to the inner aspect of the maxilla posteriorly. It attaches to that bone immediately below its line of articulation with the supramaxilla. A second, and narrower but denser, ligament extends from the crown of the coronoid process horizontally forward to the upper margin of the maxilla, inserting just anterior to the region of the supramaxillary articulation.

**OTHER JAW LIGAMENTS.** A long and stout *ethmopremaxillary* ligament runs from the dorso-lateral aspect of the dermethmoid to the premaxilla, attaching dorsally near the base of its ascending process. At its origin on the ethmoid the ligament is confluent with a similar *ethmomaxillary* one which is distinct from but closely applied to the ethmopremaxillary ligament over the posterior two-thirds of its length. The ethmomaxillary ligament attaches to the maxilla at a ventral point immediately below the ascending head of that bone.

A very short and small *maxillopremaxillary* ligament is present, linking the two bones at the point where the premaxilla passes medial to the maxilla.

From the inner aspect of the first infraorbital bone, a long and compact ligament runs down to the maxilla, attaching near the head of that bone and also attaching to the sesamoid cartilage lying between the palatine and the articulating surface of the maxilla.

An extensive sheet of tough connective tissue closely binds the dorsal dome of the sesamoid cartilage to the ascending head of the maxilla; it is probably homologous with the palatomaxillary ligament found in other elopoids (see Forey, 1973a: fig. 3).

According to Forey (1973a: 355) *Pterothrissus* has the same complement of jaw ligaments as do *Elops* and *Tarpon*, a statement with which I would agree, except that in the specimen I dissected no trace of a palatopremaxillary ligament could be found.

**JAW MUSCLES.** The arrangement and morphology of the jaw muscles in *P. gissu* are identical with those described above for *P. belloei* (see Fig. 1). However, in the specimen I dissected (315 mm SL) the adductor mass does show the incipient separation of a smaller, dorsomedial section.

## ALBULIDAE

### *Albula vulpes* (L.).

**MAXILLO-MANDIBULAR LIGAMENTS.** The *ligamentum primordium* is an inverted Y-shaped ligament (Fig. 3) with its stem attached anteriorly to a dorsally directed process of the maxilla lying above and lateral to the insertion point of a tendon from the adductor mandibulae muscle (see below, p. 71). The lower and broader of the Y's two arms is attached to the supramaxilla; the upper arm continues much further posteriorly, and attaches at the base of the bony bridge on the angulo-retroarticular (Fig. 3). This arm of the ligament also has a small area of attachment on the dorsal margin of the coronoid process.

In the smallest of the three specimens dissected (BMNH 1932.2.8: 5; 108 mm standard length), the *ligamentum primordium* is poorly differentiated from the other fibres of the connective tissue through which it runs. In the largest fish (Gothenburg Museum specimen) the ligament is thick, almost fleshy and readily distinguishable. In neither specimen is there any sign of muscle fibres from the adductor mandibulae complex inserting onto the *ligamentum primordium*.

**OTHER JAW LIGAMENTS.** A vertical *ethmopremaxillary* ligament runs from the dermal ethmoid to the head of the ascending premaxillary arm, and a broad, rather diffuse and horizontally aligned *ethmomaxillary* ligament connects the dermethmoid with the incurved part of the maxillary head. The maxilla is connected to the premaxilla through a short ligament (the *maxillopremaxillary*) running from the curve of the maxillary head to the premaxilla at a point slightly behind the base

of its ascending process. Another ligament, the *palatomaxillary*, runs from the head of the auto-palatine bone to the sesamoid cartilage interposed between the palatine and the maxilla; this ligament apparently continues around the posterior face of the cartilage (to which it is very closely applied) and inserts onto the maxilla itself.

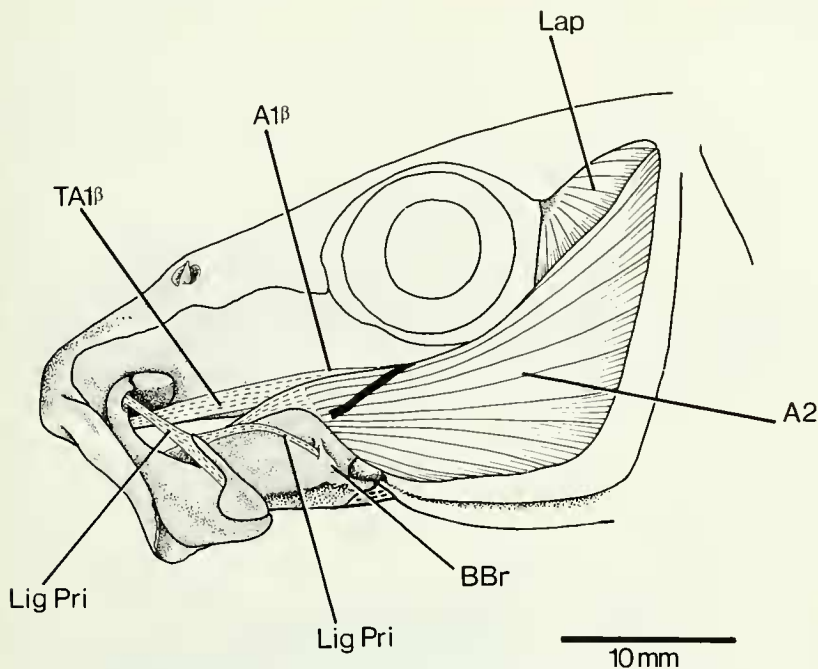


Fig. 3 *Albula vulpes*. Jaw musculature and ligaments in left lateral view. Specimen BMNH 1932.2.8 : 5.

**ADDUCTOR MANDIBULAE MUSCLES (Figs 3 & 4).** The adductor complex is a rather flat, not noticeably voluminous muscle mass. It shows no clear-cut subdivisions, except for a single tendinous slip which arises dorsomedially near the region of the muscle's insertion onto the dentary. From here it runs forward to insert, tendinously, onto the maxilla a little behind its palatine head (Figs 3 & 4). The few muscle fibres associated with the origin of the tendon are barely separable, as an elongate torpedo-shaped aggregate, from the main body of the muscle.

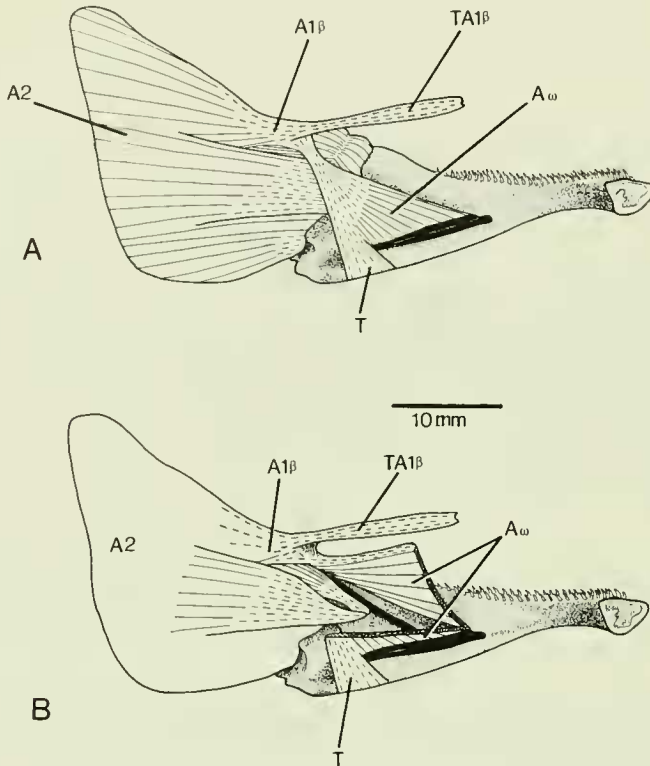
By definition (see Winterbottom, 1974 : 232) this ill-defined muscle should be identified as section A1 of the adductor complex. However, it must be stressed that the muscle in *Albula* does not appear to have '... developed from the dorsal enroachment of the fibres of A2 along the primordial ligament...' (Winterbottom, 1974 : 232) because an apparent ligamentum primordium, completely unconnected with any part of the adductores, is also present (see above).

This dorsal segment of the adductor in *Albula* seems to be homologous with the A1 $\beta$  division of that muscle in Halosauridae (and Notacanthidae); see below. Hence, it will be given the same designation in this species, viz. A1 $\beta$ .

The remaining and major part of the adductor mass in *Albula* is identified as an A2 muscle, principally because it has the same relationships with the lower jaw as does the A2 division in other fishes (see Winterbottom, 1974 : 233-234).

Almost at its origin the tendon of A1 $\beta$  bifurcates, the upper portion continuing forward to the maxilla, the lower portion running downwards at a steep angle. This division soon expands into a broad, deltoid sheet (Fig. 4). Some fibres of the main A2 muscle attach to this sheet dorsally,

whilst anteriorly it serves as an aponeurotic origin for a thin, triangular muscle which inserts into the Meckelian fossa. Because of its origin and insertion, this muscle is identified as the  $A\omega$  division of the adductor complex. The posterior part of the muscle-tendon sheet remains tendinous and inserts, rather narrowly, onto the ventral margin of the dentary, a little before its suture with the angulo-retroarticular bone (Fig. 4).



**Fig. 4** *Albula vulpes*. Musculature associated with the lower jaw; left side, medial aspect. (A) The muscles *in situ*. (B) Intramandibular muscle ( $A\omega$ ) cut near its insertion and reflected anterodorsally to show the insertion of the A2 adductor mandibulae muscle. Specimen BMNH 1923.7.30 : 47.

There appears to be some intraspecific variation in the shape and orientation of  $A\omega$ . The smaller fish dissected has the posterior margin of the muscle (and its associated tendinous area) sloping forward to lie in about the same line as the fibres of A2. The condition of the muscle in the larger BMNH specimen is illustrated in Fig. 4.

The main body of the A2 muscle inserts onto the medial and lateral aspects of the lower jaw (Figs 3 & 4). On the medial face it inserts chiefly through three stout tendons, two of which are contiguous and parallel with one another and lie lateral to the third tendon, the lowest and largest of the three, which inserts into a shallow, ill-defined recess on the dorso-posterior aspect of the coronomeckelian bone. A fourth, smaller, tendon runs parallel with the third tendon described above; it also attaches to the coronomeckelian bone, through a small eminence immediately dorsal to the other insertions. Finally, part of A2 has a more musculose insertion lateral to those already described, but also attaching onto the dorsal margin of the coronomeckelian bone.

On the lateral face of the lower jaw (Fig. 3), A2 attaches along the entire posterolateral margin of the angulo-retroarticular, and forward onto that small area of the dentary which contributes to the coronoid process. The lateral area of A2 insertion does not extend so far forward as does that of its medial part.

**LEVATOR ARCUS PALATINI MUSCLE.** As compared with the levator arcus palatini in halosaurs and notacanth, that of *Albula* is relatively very small (Fig. 3). Its origin is narrow and confined to the sphenotic; its insertion is mainly on the hyomandibula, but with a substantial part inserted on the metapterygoid (Fig. 3).

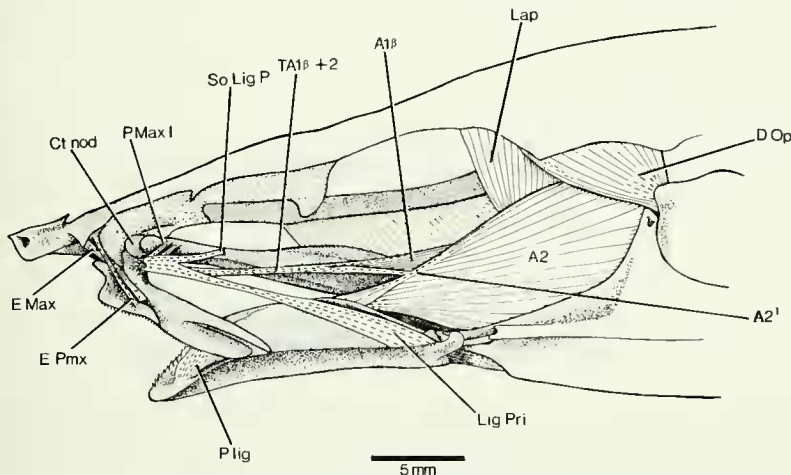
**ADDUCTOR ARCUS PALATINI MUSCLE.** No trace of this muscle can be found, presumably because of the close contact between the skull and the palatopterygoid arch (see Forey, 1973b : 159-160).

## HALOSAURIDAE

### *Halosaurus guentheri* Goode & Bean

**LIGAMENTUM PRIMORDIUM.** This well-developed ligament runs from the posterior part of the angulo-retroarticular to the head of the maxilla (Fig. 5). Here it attaches at a point slightly behind the maxillopalatine articulation and immediately posterior to the tendon from A1 $\beta$ .

There is also a posterior connection between the maxilla and the dentary effected through an ill-defined ligament lying in the connective tissue of that region.



**Fig. 5** *Halosaurus guentheri*. Jaw musculature and ligaments in left lateral view. Specimen BMNH 1966.10.14 : 1.

**ETHMOMAXILLARY AND ETHMOPREMAXILLARY LIGAMENTS** (Fig. 5). A strong ethmomaxillary ligament has its origin on the lateral cornua of the ethmoid, slopes steeply backwards and downwards, and inserts onto the maxilla along its anterolateral face below the palatine process. The ethmopremaxillary ligament is of almost the same size; since its origin on the ethmoid is much deeper than that of the maxillary ligament, it crosses over the latter near its origin. It inserts dorsally onto the premaxilla about two-thirds of the way along its length.

**PALATOMAXILLARY LIGAMENTS** (Fig. 5). On each side a pair of parallel and slender ligaments runs obliquely forward from the autopalatine (near its head) to insert on the maxilla at the same level as, but medial to, the ligamentum primordium.

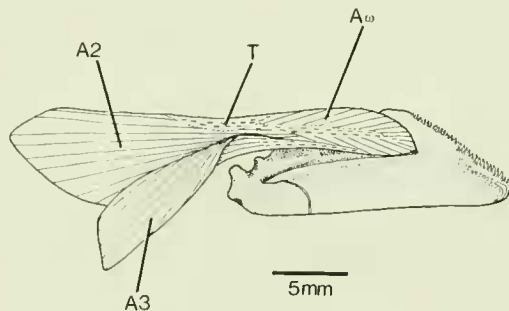
**PALATOPREMAXILLARY LIGAMENT.** A stout and strong ligament is present; it inserts medially onto the inner aspect of the premaxilla.



**SUBORBITAL MAXILLARY LIGAMENT (Fig. 5)** A long, thin ligament runs from the 3rd or 4th sub-orbital bone partly to the head of the maxilla, where it is either contiguous with or fuses onto the anterior part of the ligamentum primordium, and partly to the sesamoid bone (or cartilage) lying between the maxilla and the palatine. Slightly anterior to the midpoint of this ligament there is a smaller, inner division which runs rostrally to insert on the ethmoid.

**ADDUCTOR MANDIBULAE MUSCLES (Fig. 5).** The main body of this complex, the adductor A2, originates on the preoperculum, the hyomandibula and, to a lesser extent, on the metapterygoid. Its insertion is along the posterior margin of the angulo-retroarticular.

On its dorsal margin, at a point about one-quarter of the distance from the insertion, there is a small, ill-defined slip of muscle which soon becomes tendinous and joins the tendon running forward from the A1 $\beta$  muscle (see below). Since this muscle slip is so poorly differentiated from A2, and because I find difficulty in homologizing it with any jaw muscle in other teleosts, I have called it A2<sup>1</sup> (Fig. 5). With regard to its possible homology, it should be noted that A2<sup>1</sup> does seem to show some similarity with the muscle identified as A1 $\beta$  in *Albula vulpes* (see p. 71). The identity of A2<sup>1</sup> in *Halosaurus* is further complicated by the situation in *Aldrovandia* (see p. 77), where there is a ligament extending from the coronoid process to the anterior part of the tendon from A1 $\beta$ . In other words, the ligament in *Aldrovandia* could be the homologue of the A2<sup>1</sup> tendon in *Halosaurus*. The direction in which this change took place could be either the result of a maxillo-coronoid ligament (as in *Aldrovandia*) being taken over by a muscle slip from A2 (or its precursor), or through a tendon losing its muscular association and becoming attached to the coronoid.



**Fig. 6** *Halosaurus guentheri*. Inner aspect of left lower jaw. Specimen BMNH 1966.10.14 : 1.

Adductor A1 $\beta$  in *Halosaurus guentheri* (Fig. 5) is a long, slender, spindle-shaped muscle lying medial to A2 over the posterior half of its length, but dorsal to it anteriorly. The muscle has a long tendon which inserts onto the medial face of the maxilla immediately below the maxillo-palatine articulation. Posteriorly, A1 $\beta$  is mostly tendinous, lies lateral to the levator arcus palatini and has a flat, tendinous origin medial and slightly dorsal to that of A3 on the hyomandibula.

Adductor A3 lies medial to A1 $\beta$ , is a laterally compressed muscle and has an aponeurotic connection with the anterior part of A2 at about the level of the posterior margin of the angulo-retroarticular. From this aponeurosis there arises a fairly well-defined tendon which runs forward to insert on Meckel's cartilage below but touching that part of A2 which fills the entire Meckelian fossa. Within the fossa, the central part of A2 becomes tendinous, the fibres radiating out dorsally and ventrally in a distinct pinnate fashion (Fig. 6). Presumably this part of the muscle should be identified as the A $\omega$  portion of the adductor complex.

**LEVATOR ARCUS PALATINI MUSCLE (Fig. 5).** This large, top-shaped muscle has an extensive origin on the pterotic and sphenotic skull regions, and a much narrower insertion onto both the metapterygoid and the membrane spanning the gap between that bone and the hyomandibula. A small part also inserts onto the hyomandibula itself. The levator arcus palatini is not obviously subdivided, as it is in notacanthids, although the part inserting onto the hyomandibula is rather tendinous.

**ADDUCTOR ARCUS PALATINI.** No distinct muscle is present, but a certain amount of ligament-like thickening is visible in the posterior orbital part of the connective tissue joining the skull and palatopterygoid arch.

**DILATATOR AND LEVATOR OPERCULI MUSCLES** (Fig. 5) Both muscles are moderately well developed.

*Halosaurus carinicauda* (Alcock)

The cephalic muscles and ligaments of this species are virtually identical with those in *H. guentheri*.

*Halosauropsis macrochir* (Günther)

The *jaw ligaments* in this species are basically like those of *Halosaurus guentheri*, except that there does not seem to be a maxillo-suborbital ligament, and the *ligamentum primordium* has a double insertion, one part going to the maxillary head, the other to the sesamoid bone (see p. 91) intercalated between the maxilla and the articular facet on the palatine. The *ethmomaxillary* and *-premaxillary* ligaments both stem from the lateral end of the ethmoid cornua, and although the ligaments cross (near their origins), that to the premaxilla has the more lateral origin (that is, the reverse of the situation in *Halosaurus* and *Aldrovandia*). The paired *palatomaxillary* ligaments appear relatively stouter in this species than in the other halosaurids examined.

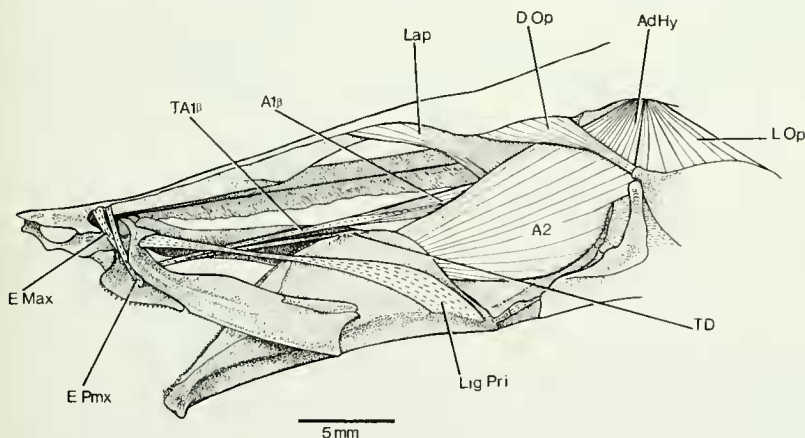
**JAW AND ASSOCIATED MUSCULATURE,** The jaw muscles are virtually identical in their gross morphology with those of the *Halosaurus* species examined. However, adductor A2<sup>1</sup> is greatly reduced so that its tendon joining that of A1 $\beta$  arises mainly from the tendinous sheet attaching A2 to the coronoid process of the lower jaw. Also, the union between the tendons of A2<sup>1</sup> and A1 $\beta$  occurs almost at the head of the maxilla and not about halfway along the tendon of A1 $\beta$  as in *Halosaurus*.

The *levator arcus palatini* muscle in *Halosauropsis macrochir* has a much larger area of origin than it does in *Halosaurus*. It extends forwards along the ventral face of the frontal to wrap around the posterodorsal half of the eyeball.

The *dilatator* and *levator operculi* muscles, however, are relatively no larger than those in *Halosaurus*.

*Aldrovandia gracilis* Goode & Bean

**JAW LIGAMENTS** (Fig. 7). The *ethmomaxillary* and *ethmopremaxillary* ligaments in this species are arranged as in the *Halosaurus* species examined, as is the posteriorly broadened *ligamentum*



**Fig. 7** *Aldrovandia gracilis*. Jaw musculature and ligaments in left lateral view. Specimen from 'Discovery' collections, station 7857, no. 5.

*primordium*. However, there is no maxillo-suborbital ligament; in this respect the species resembles *Halosaurusopsis macrochir*. The *palatopremaxillary* ligament of each side is stout and well developed, the paired *palatomaxillary* ligaments are finer and are closely applied to the sesamoid cartilage interposed between the maxillary and palatine heads.

**JAW MUSCULATURE** (Fig. 7). In its basic bauplan, the adductor musculature of *A. gracilis* closely resembles that in *Halosaurus* and *Halosaurusopsis*. The most noticeable differences are: (i) The absence of an A2<sup>1</sup> muscle slip from the dorsal margin of A2 (see p. 74 above). (ii) The virtual absence of a distinct A3 muscle except near its origin; distally, A3 is not readily separable from A2 and at that point the conjoined muscles are rather tendinous. The fairly extensive and muscose  $A\omega$  originates aponeurotically from this area.

The *levator arcus palatini* is a well-developed muscle and has a long origin extending into the orbit; in this respect it more closely resembles the muscle in *Halosaurusopsis macrochir* than that in *Halosaurus*.

As in other halosaurids, no obvious *adductor arcus palatini* is present, although a few muscle fibres are present in the connective tissue joining the palatopterygoid arch with the parasphenoid.

The *dilatator operculi* muscle in *Aldrovandia gracilis* is relatively smaller and weaker than that in the other halosaurids studied, but unlike these species *A. gracilis* does have a discrete *adductor hyomandibulae* muscle.

The *levator operculi* muscle is quite comparable with that in other halosaurids.

#### *Aldrovandia affinis* (Günther)

The jaw and palatine arch musculature, the jaw ligaments and the opercular musculature are identical with those of *Aldrovandia gracilis*, and include a separate adductor hyomandibulae muscle.

#### Comments and comparisons

*Pterotrissus belloei* has a primitive system of adductor mandibulae muscles in which only the  $A\omega$  (inframandibularis) muscle is differentiated from the main adductor mass.

There is no muscular control of the maxilla in this species, for although the ligamentum primordium is developed it is not associated with any muscle fibres. *Elops saurus*, whose adductor mandibulae muscles are almost as unspecialized as those of *Pterotrissus* (Vrba, 1968; Winterbottom, 1974), however, does have a few fibres from the adductor mass inserting onto the ligamentum primordium, thereby achieving some muscular control of the maxilla.

A ligamentum primordium occurs in *Amia* and is of widespread occurrence amongst teleosts. Generally, as in *Amia*, it is associated with part of the adductor muscle complex (see Winterbottom, 1974: 231–233). In some advanced teleosts this muscular encroachment results in the ligament losing its posterior connection with the lower jaw, thus becoming the tendon through which the A1 division of the adductor inserts onto the maxillary head. The absence of muscle fibres attaching to the ligament in *Pterotrissus* and *Albula* is probably a specialization and one correlated with the relative immobility of the upper jaw in those genera.

The subdivided levator arcus palatini muscle of *Pterotrissus* would also seem to be a specialized condition (and one repeated in notacanthids and lipogenyids; see pp. 79 & 83).

*Albula vulpes* has an undivided levator arcus palatini but like *Pterotrissus* it has no muscle fibres inserting on the ligamentum primordium (p. 71). As compared with *Pterotrissus*, its adductor muscles are more specialized. Of particular interest in this connection is the differentiation of a tendinous linkage between a dorsally located muscle slip on the main adductor and the maxillary head, quite independent of the ligamentum primordium. This connection seems to foreshadow the discrete A1 $\beta$  muscle found in halosaurids and can be considered a derived feature of *Albula*. It would also seem to be an actual manifestation of Dietz's (1912) hypothesized origin for A1 $\beta$  as a subdivision of the larger, more superficial division of the primitive adductor complex.

The adductor mass itself shows some incipient subdivision in *Albula*, at least with respect to its insertions on the lower jaw (see p. 72), although the body of the muscle remains undivided.

All the halosaurids examined share one specialized feature of the jaw musculature, a discrete A1 $\beta$  muscle (see pp. 73–76) lying lateral to the levator arcus palatini and inserting onto the head of the maxilla.

There is in these taxa, as compared with *Albula*, a greater differentiation of the main adductor mass, with the development of a distinct or almost completely distinct A3 division medial to A2.

In *Halosaurus* (and somewhat less obviously in *Halosauropsis*) there is a small slip of muscle originating from the main body of A2 (Fig. 5). It soon becomes tendinous and ultimately fuses with the tendon of A1 $\beta$ . This small muscle (A2<sup>1</sup>; see p. 74) appears to be a specialization found only in *Halosaurus* and *Halosauropsis*. *Aldrovandia* has no trace of the muscle slip, but there is a ligament running from the top of the coronoid process to join the tendon from A1 $\beta$  near the latter's insertion onto the maxilla (see Fig. 7). Presumably this ligament is homologous with the tendon from A2<sup>1</sup> in *Halosaurus* and *Halosauropsis*. Because it is impossible to determine the direction in which the evolution of these two conditions took place (see p. 74 above), one cannot say which is specialized relative to the other. However, if it be accepted that the two conditions are homologous, then it seems reasonable to consider both as derived features of the Halosauridae.

A well-developed ligamentum primordium, without any muscular associations, is present in the halosaurids (see pp. 73, 75 & 76).

The level of adductor subdivision and specialization in the Halosauridae, especially the evolution of an A1 $\beta$  control of the maxilla, closely parallels that seen in certain stomiatoids, as well as in at least some myctophids, and in certain cetomimoids amongst the neoteleostean Euteleostei (see Rosen, 1973 : 412–421 for details of these latter fishes). No halosaurid, it may be noted, shows a development of the adductor arcus palatini comparable with that found in these neoteleosteans. Indeed, an adductor arcus palatini could well be described as lacking in halosaurids. No described euteleostean shows a muscle slip comparable with the A2<sup>1</sup> of *Halosaurus* and *Halosauropsis* (or the morphologically equivalent tendon in *Aldrovandia*), and none has a ligamentum primordium like that in the halosaurids. What similarities there are in the jaw musculature of halosaurids and neoteleosts must therefore certainly be ranked as convergence.

McDowell (1973) does not give any direct account of the jaw muscles in the Halosauridae, although he does comment elsewhere in his monograph (1973 : 130) that the pattern in *Halosaurus* is essentially like that in the various notacanthids he had examined. This comment will be discussed on p. 84 below.

## II NOTACANTHIDAE and LIPOGENYIDAE

McDowell (1973 : 130) briefly describes and comments on the jaw musculature of notacanthids, his remarks being based on dissections of *Notacanthus chemnitzii*, *N. sexspinis*, *N. spinosus*, *N. abbotti* and *Polyacanthonotus africanus*, as well as on Trotti's (1945) account of *N. bonapartei*. There are several points where I would disagree with McDowell's generalizations, and these are discussed below (p. 84).

### NOTACANTHIDAE

#### *Polyacanthonotus rissoanus* (De Filippi & Vérany)

**MAXILLO-MANDIBULAR LIGAMENTS.** No discrete *ligamentum primordium* can be recognized; it seems unlikely that the ligament has been taken over by one of the adductor muscles (see below). Posteriorly there is a ligamentous connection between the hind margin of the angulo-retroarticular and the medial face of the maxilla near the base of its spine.

**ETHMOPREMAXILLARY AND ETHMOMAXILLARY LIGAMENTS** (Fig. 8). Both ligaments have a common origin almost at the tip of the ethmoid, the former ligament attaching to the premaxilla near its middle, the latter at the point where the lower limb of the maxilla curves ventrally and the spine is produced backwards.

A thick ligament runs from the ethmoid (above and posterior to the origin of the proximally united ethmomaxillary and ethmopremaxillary ligaments) both to the maxillo-palatine cartilage



and to the head of the maxilla (inserting mostly on the cartilage). This ligament would seem to be homologous with the *deep ethmomaxillary* ligament of *Notacanthus* (see p. 81).

**PALATOMAXILLARY LIGAMENTS.** I can find no trace of any palatomaxillary ligaments; their absence is probably to be correlated with the type of palato-ethmoid articulation found in this species; that is, indirectly through an interposed cartilaginous and connective tissue nodule and not directly between the palatine and ethmoid (see below, p. 90). A well-developed *palatopremaxillary* ligament, however, is present.

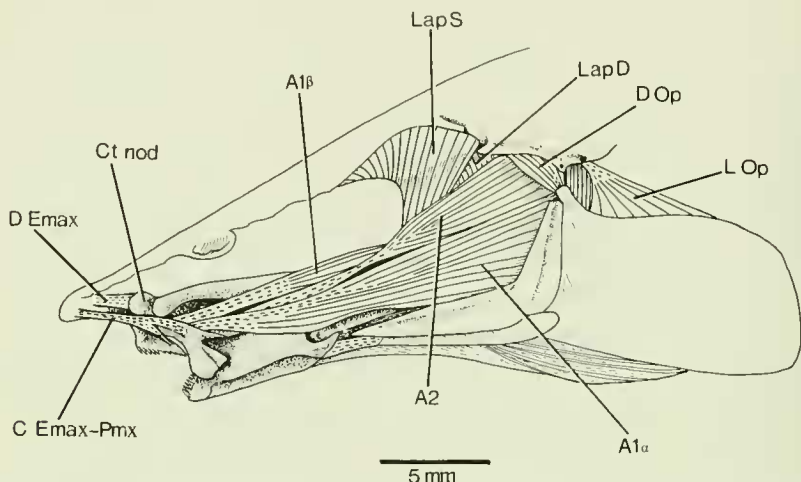


Fig. 8 *Polyacanthonotus rissoanus*. Jaw musculature and ligaments in left lateral view. The palatopremaxillary ligament has been removed to show the underlying ligaments. Specimen from 'Discovery' collections, station 8512, no. 4.

**ADDUCTOR MANDIBULAE MUSCLES** (Fig. 8). The largest element in this series is a ventral muscle which originates mainly on the preoperculum but with a few fibres also stemming from the pterotic. The muscle narrows anteriorly, and at about the level of the coronoid process becomes tendinous. In turn, the tendon narrows as it runs forward to insert medially on the head of the maxilla at the same level as does the ethmomaxillary ligament laterally. Posteriorly a few fibres from this muscle also insert onto the lower jaw, and there is an additional tendinous connection between the muscle and the coronoid process.

Since it inserts principally onto the maxilla the muscle should be identified as part of the A1 division of the adductor. Its lateral position in the series, and the fact that a medial A1 $\beta$  muscle is also developed suggests that it is a homologue of A1 $\alpha$  in other teleost groups (see Winterbottom, 1974: 232-233). The absence of a discrete ligamentum primordium, such as occurs in *Albula*, *Pterothrissus* and the Halosauridae, was noted above. Because in many taxa throughout the teleosts (including such primitive forms as the Elopidae) a lateral portion of the adductor musculature has encroached upon the ligament (thus gaining an insertion on the maxilla) it is possible that in *Polyacanthonotus* too the ligament has become incorporated with the adductor series. But if this is so, the ligament has lost its posterior contact with the lower jaw, which it has not done in the Elopidae (see Vrba, 1968) or in many other groups. For this reason I would argue that the maxillary insertion of A1 $\alpha$  in *Polyacanthonotus* is not *via* a former ligamentum primordium but is an insertion created *de novo* by the encroachment of the muscle onto the bone.

Dorsal to A1 $\alpha$  is a much smaller muscle (Fig. 8) with the outline of an isosceles triangle, and with a very elongate tendon (about twice the length of the muscle itself). It inserts onto the medial face of the dentary immediately below the last few teeth on that bone; its origin is entirely from



the pterotic region of the skull. From the tendon of this muscle there is a branch which runs medially to join the tendon from  $A1\beta$  (see below).

Since the principal insertion of this muscle is onto the lower jaw it would appear to be homologous with the A2 division of the adductor muscle in other teleosts, although in these fishes A2 generally lies ventral to A1 and not dorsally as it does here.

The  $A1\beta$  division is an elongate, rather tendinous muscle originating on the medial aspect of the hyomandibula (thus also medial to the levator arcus palatini). It inserts through a long tendon onto the medial face of the maxillary head; a few fibres also insert onto the pterygoid arch. There is a direct connection between the tendons of  $A1\beta$  and A2 (see above; Fig. 8); a branch from the tendon of  $A1\beta$  is attached to the posterior face of the dermopalatine, which is, of course, a separate and movable element of the palato-ptyergoid arch in notacanthids (see McDowell, 1973 : 129).

The deepest division of the adductor series (visible only after dissection), the A3 muscle, lies medial to  $A1\alpha$  and the ventral margin of A2 (Fig. 8). It is a narrow muscle originating from the hyomandibula, and has a long tendon running forward to insert onto the medial face of the dentary just below the insertion of the tendon from A2.

No definite  $A\omega$  division can be defined, the area it would otherwise occupy in the lower jaw being filled with the tendons from A2 and A3.

The *levator arcus palatini*, a large muscle whose origin extends anteriorly into the orbit (Fig. 8), is clearly subdivided into a major, vertically aligned and deep portion (inserting mainly on the hyomandibula but with a few fibres going to the pterygoid arch as well), and a smaller, more superficial and pyramidal part which inserts only on the pterygoid arch.

As in the halosaurs no trace of an *adductor arcus palatini* could be found in *Polyacanthonotus rissoanus*.

The *dilatator operculi* is a short and small muscle (Fig. 8), the *levator operculi* is comparable with that in the halosaurids dissected.

#### *Polyacanthonotus africanus* (Gilchrist & van Bonde)

Although the adductor musculature (and jaw ligaments) of the single specimen dissected are basically like those in *P. rissoanus*, there is one important difference, namely, A2 is divided into two discrete portions.

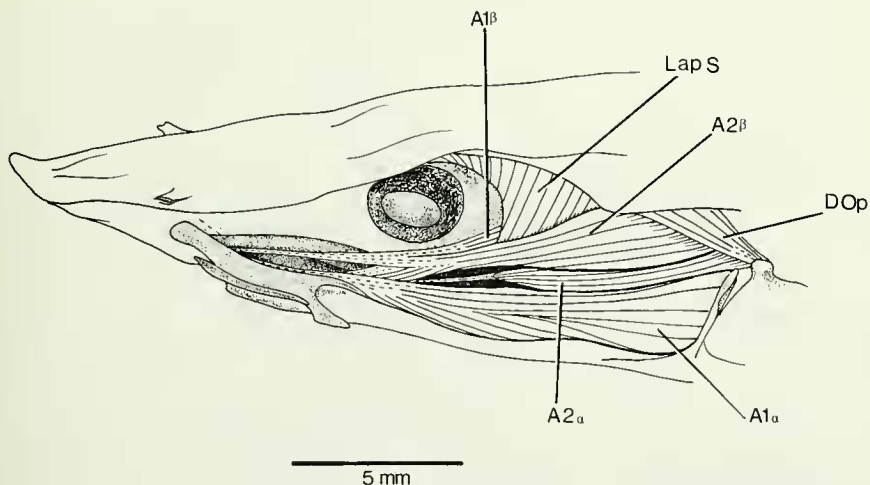


Fig. 9 *Polyacanthonotus africanus*. Jaw musculature of left side viewed obliquely from above. Specimen from 'Discovery' collections, station 8519, no. 2.

Adductors  $A1\alpha$  and  $A1\beta$  in *P. africanus* (Fig. 9) have a similar form and similar relationships with the maxilla (and in the case of  $A1\alpha$  with the dentary as well) as do these muscles in *P. rissoanus*. However, immediately dorsal to  $A1\alpha$  there is a relatively small and short muscle (Fig. 9) whose long and slender tendon inserts onto the coronoid process of the lower jaw. In this respect it resembles the  $A2$  division in *P. rissoanus*, although it has no tendinous linkage with  $A1\beta$  (see pp. 78–79). Above this muscle there is a longer and more voluminous one which, at about the level of the coronoid process, becomes partly tendinous. The upper part of the tendon fuses with the tendon of  $A1\beta$ ; the lower part, accompanied by a few muscle fibres, inserts onto the medial face of the dentary and the angulo-retroarticular.

Since together these two muscles in *P. africanus* have the same relationships with  $A1\alpha$  and  $A1\beta$  as does  $A2$  in *P. rissoanus*, it seems likely that they represent subdivisions of that muscle; they are accordingly designated as  $A2\alpha$  for the lower division and  $A2\beta$  for the upper one. In combination,  $A2\alpha$  and  $\beta$  of *P. africanus* have a relatively greater volume than does the single  $A2$  of *P. rissoanus*.

Adductor  $A3$  in *P. africanus* is like that in *P. rissoanus* and has a broad tendinous insertion in the Meckelian fossa. No  $A\omega$  division is discernible.

The *levator arcus palatini* is similarly subdivided in the two species, but the *dilatator operculi* of *P. africanus* is somewhat longer and slightly more voluminous than that in *P. rissoanus*.

#### *Notacanthus bonapartei* Risso

Trotti (1945) has given a detailed account of the jaw muscles, and their innervation, in this species. I am in substantial agreement with Trotti's description, but since he uses a different system of muscle nomenclature for the various divisions of the adductor complex his names will be given in parentheses and prefixed 'Trotti's'.

MAXILLO-MANDIBULAR LIGAMENTS. As in *Polyacanthonotus* there is no elongate and discrete *ligamentum primordium* of the halosaurid type. Also like *Polyacanthonotus* there is a dense con-

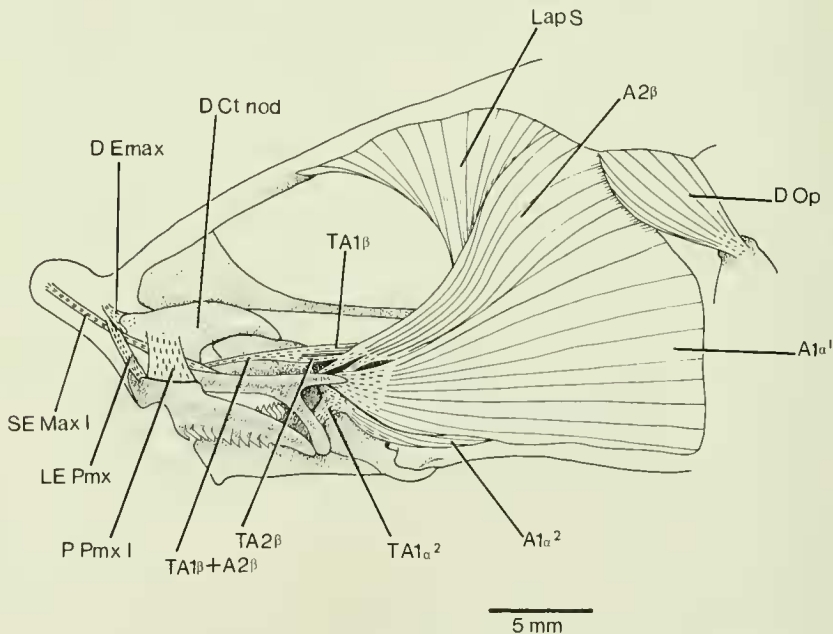


Fig. 10 *Notacanthus bonapartei*. Entire jaw musculature in left lateral view; maxillo-mandibular ligaments removed to show underlying structures. Specimen BMNH 1972.1.26 : 33.

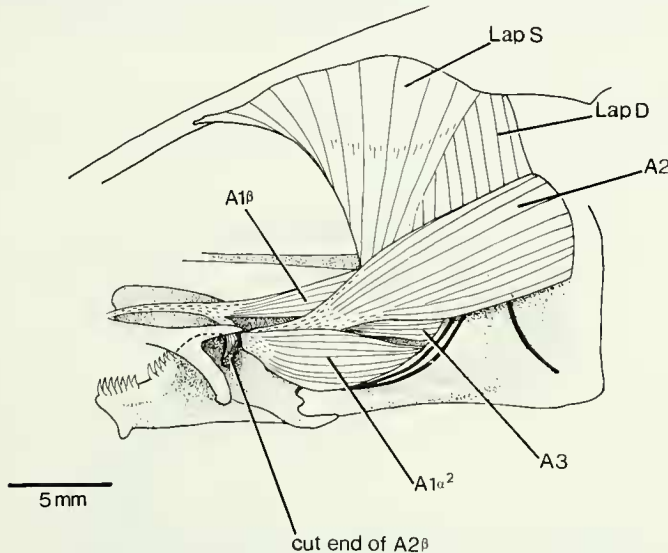
centration of connective tissue linking the inner aspect of the posteroventral maxillary tip with the lateral face of the angulo-retroarticular.

**ETHMOMAXILLARY AND ETHMOPREMAXILLARY LIGAMENTS (Fig. 10).** There are two distinct ethmomaxillary ligaments. The superficial one has its origin dorsally near the tip of the ethmoid, is long and slender, and inserts on the medial face of the maxilla at about its midpoint. The deep ligament is much stouter and shorter; it runs from the head of the maxilla (where its attachment to the bone is partly obscured by the drogue-shaped maxillo-palatine nodule) to the ethmoid. Here it is attached at about the same level as the superficial ligament, but posterior to it.

There are also two *ethmopremaxillary* ligaments. A single median element connects the ascending premaxillary process to the ethmoid, while a lateral ligament (one on each side) runs from the base of the premaxillary ascending process to a point on the ethmoid near the place where the deep ethmomaxillary ligament originates. This ethmopremaxillary ligament crosses over the superficial ethmomaxillary one at about the latter's midpoint (Fig. 10).

The *palatopremaxillary* ligament is represented by a broad band of tissue extending from the lateral face of the drogue-shaped maxillo-palatine nodule to the anterodorsal margin of the premaxilla (Fig. 10).

I can find no trace of any *palatomaxillary* ligament.



**Fig. 11** *Notacanthus bonapartei*. Jaw musculature of the same specimen as shown in Fig. 10 but with the superficial muscle layers removed. The tendon of adductor mandibulae  $A1\alpha^2$  to the lower part of the maxilla has been cut away.

**ADDUCTOR MANDIBULAE MUSCLES.** The largest superficial muscle in this series (Trotti's  $a1\beta$ ) occupies a ventral position on the cheek (Fig. 10). It originates on the preoperculum and inserts through a short, broad and well-defined tendon onto the medial face of the maxilla just behind the insertion of the superficial ethmomaxillary ligament.

Immediately below the large muscle, and almost entirely covered by it, is a much smaller element (Trotti's  $a1\alpha$ ) which originates on the quadrate and metapterygoid. It has a triple insertion, firstly through a weak tendon joining that of the large muscle and thus inserting on the upper posterior part of the maxilla, secondly through a much larger and stouter tendon (at right angles to the other) inserting low down on the ventrally decurved posterior part of the maxilla (Figs 10

& 11); the third insertion is through a weak tendon onto the lateral face of the angulo-retroarticular near its summit (Fig. 11).

Although in one of the three specimens dissected there is some fibre exchange between the two muscle masses, they should be looked upon as distinct entities, especially since in the other specimens there is no exchange of fibres between them. Taken together, these muscles have the same morphological and topographical relationships with the jaws as does  $A1\alpha$  in *Polyacanthonotus* (see above). Thus, I would identify the muscles in *Notacanthus* as subdivisions of that muscle, and would designate the larger and dorsal element as  $A1\alpha^1$  (Trotti's  $a1\beta$ ) and the small ventral part (Trotti's  $a1\alpha$ ) as  $A1\alpha^2$  (see Figs 10 & 11).

The large muscle dorsal to  $A1\alpha^1$  (Fig. 10) originates from the sphenotic and pterotic regions of the skull. It inserts through three tendons, the ventral and largest of which attaches to the dorso-posterior and medial aspect of the angulo-retroarticular. The second tendon also inserts onto the medial face of the angulo-retroarticular, but near its crown. The third and longest tendon from this muscle joins the maxillary tendon of the adductor  $A1\beta$  muscle at a point about halfway along its length, thus linking it, albeit indirectly, with the maxilla. At first sight this muscle would seem to be comparable with  $A2$  in *Polyacanthonotus* (and that designated as  $a2$  by Trotti). However, after the removal of  $A\alpha^1$  and this muscle, another large muscle (originating from the hyomandibula and inserting on the lower jaw) is exposed. When, in turn, that muscle is reflected, yet another and relatively large muscle is revealed. This last element originates on the hyomandibula and partly on the metapterygoid, and would seem to be the homologue of  $A3$  in *Polyacanthonotus rissoanus* (Figs 11 & 12). It inserts through a shared tendon onto the medial face of the angulo-retroarticular.

Thus, as compared with *P. rissoanus* there is an additional muscle in the adductor series; in other words, the situation here is like that found in *P. africanus*, namely, adductor  $A2$  is subdivided

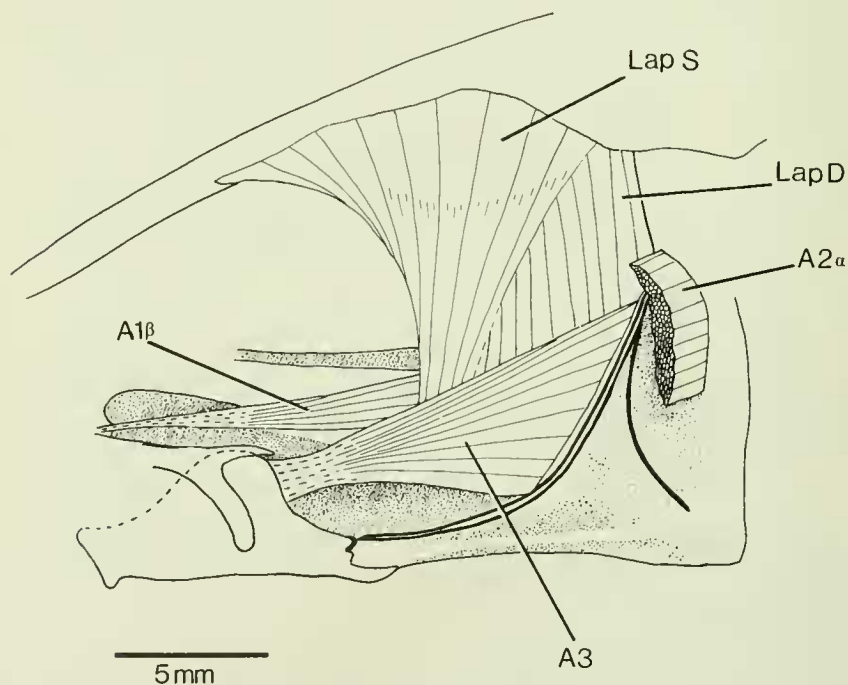


Fig. 12 *Notacanthus bonapartei*. Deep layers of the jaw musculature; same specimen as in Figs 10 & 11.

vided, its upper, and in *Notacanthus* topographically also its superficial part, having tendinous contact with the more medial  $A1\beta$  division as well as an insertion on the lower jaw, while its ventral and deeper division inserts only onto the lower jaw. Following the nomenclature used for *P. africanus*, the superficial muscle in *Notacanthus bonapartei* is designated  $A2\beta$  and the smaller, deeper division  $A2\alpha$ . These divisions of  $A2$  would seem to correspond respectively, with Trotti's  $a2$  and  $a3$  muscles (see Figs 11 & 12).

The deepest lying adductor muscle noted above (that originating on the hyomandibula and metapterygoid) should be identified as the  $A3$  division (=Trotti's  $a4$ ); see Fig. 12. It is comparable in all respects with the  $A3$  of *Polyacanthonotus* (and, indeed, of halosaurs as well).

The  $A1\beta$  division (Trotti's  $r$ ), like that in *Polyacanthonotus*, lies medial to the levator arcus palatini muscle and has a tendinous connection with the posterior face of the dermopalatine. It is an elongate, slender and rather tendinous muscle originating on the inner aspect of the posterior, horn-like projection on the metapterygoid, and inserting on the medial face of the maxilla near its head. According to McDowell (1973 : 130), this muscle (which he refers to as Trotti's 'Musculo R') originates on the entopterygoid, but I have not been able to confirm this in any of the specimens I have examined.

No distinct and muscose  $A\omega$  division is recognizable; a short rather narrow tendon, stemming from the already tendinous distal part of  $A2\beta$  and running obliquely forward and downwards along the line of the suture between the dentary and the angulo-retroarticular, may represent this division of the adductor series (Fig. 13).

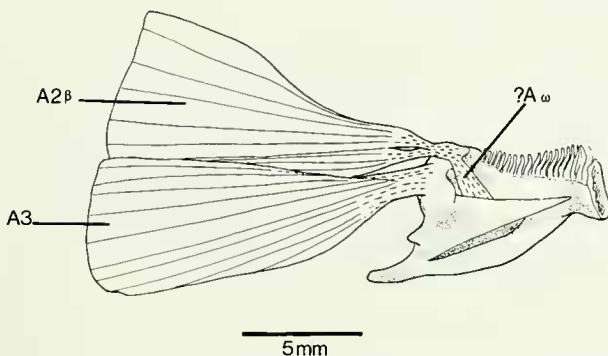


Fig. 13 *Notacanthus bonapartei*. Muscles of the lower jaw; left side, medial aspect.

McDowell (1973 : 131 footnote) describes a ligament extending from the middle of the dermopalatine to the coronoid process of the lower jaw. As far as I can tell, McDowell's ligament is the connection I have described above as the tendon stemming from the combined tendons of  $A2\beta$  and  $A1\beta$ . However, the latter attaches to the posterior face of the dermopalatine and not its middle. Despite this difference I believe that we are referring to the same element, especially since I cannot locate a ligament in addition to the tendon.

As in *Polyacanthonotus* the large and extensive *levator arcus palatini* muscle (Figs 10–12) is subdivided. The deeper part has vertically arranged fibres which insert mainly onto the hyomandibula, partly on its anterior margin but mostly onto the inner face. The smaller and superficial part is conical in shape, and has somewhat obliquely arranged fibres that insert onto the metapterygoid horn.

The *dilatator operculi* is a well-developed, deep-bellied muscle, but the *levator operculi* is thin and largely tendinous (a condition which stands in strong contrast to that in halosaurids).

No distinct *adductor arcus palatini* exists, but several groups of muscle fibres (more than in other notacanthids or in halosaurids) are present, especially anteriorly, in the connective tissue sheet spanning the gap between the skull and palatopterygoid arch.



### Comments and comparisons

All the notacanthid species dissected share a number of characters, or character states, not found in the Halosauridae. The combined  $A1\alpha$  and  $A1\beta$  muscular control of the maxilla is perhaps the most outstanding of these features. The absence in notacanthids of a discrete ligamentum primordium may be correlated with the development of the  $A1\alpha$  insertion onto the maxilla; in other words, the ligament may have been taken over by the muscle, although there are arguments against this interpretation (see p. 78).

Other peculiarities of notacanthids are the subdivision of the levator arcus palatini into distinct pterygoid and hyomandibular parts (as is also the case, of course, in *Pterothrissus belloci*; p. 69), the dorsal position of adductor A2 (the mandibular muscle) relative to A1 (the maxillary muscle), the origin of  $A1\beta$  medial to the levator arcus palatini, and the development of a tendinous connection between  $A1\beta$  and the highly mobile dermopalatine.

Of these various characters, it would seem that the addition of an  $A1\alpha$  muscular control to the maxilla, the inward shift in the origin of  $A1\beta$  and the development of a connection between that muscle and the dermopalatine can all be considered as derived (apomorphic) features.

Indeed, the development of a combined  $A1\alpha$ - $A1\beta$  control of the maxilla is otherwise reported only in neoteleostean fishes (Rosen, 1973), particularly from amongst the Acanthopterygii (some 'beryciform' families, the sciaenids and some cottoids; Rosen, 1973: 420). In none of these taxa, however, does the  $A1\alpha$  division lie ventral to A2. Rosen's statement (1973: 420) that '... only in Paracanthopterygii and Acanthopterygii do separate A1 and  $A1\beta$  occur together in the same individual ...', must now be modified to include notacanthid elopomorphs. This similarity can only be interpreted, with respect to elomorph relationships, as convergence.

In *Polyacanthonotus africanus*, but not in *P. rissoanus*, the A2 adductor muscle is subdivided into two parts (see p. 79), a state not found in any halosaurids. However, exactly the same subdivision of this muscle occurs in *Notacanthus bonapartei* and *N. spinosus*. I would interpret this apparent synapomorphy as being a case of parallelism since there are no other characters to suggest that *Polyacanthonotus africanus* is more closely related to *Notacanthus* than to the other species of its genus. (For detailed osteological and other descriptions of the taxa involved, see McDowell, 1973.)

The subdivided  $A1\alpha$  of *Notacanthus* (p. 82) is apparently a unique specialization; whether it occurs in all species of the genus still remains to be checked.

McDowell (1973: 130) gives a brief and very general account of jaw muscles in notacanthids. Using Trotti's (1945) description of *N. bonapartei* as a basis for comparison, he finds an identical pattern in *N. chemnitzii*, *N. sexspinis*, *N. spinosus*, *N. abbotti* and *Polyacanthonotus africanus*. It will be obvious from what I have described above and on p. 80 that I would agree, in broad terms, with McDowell's statement so far as it concerns *P. africanus*, but that *P. rissoanus* cannot be included in this generalization. I would also agree with McDowell's further generalization that the species he examined have essentially the same pattern as in *Halosaurus* (1973: 130), although I do not think that he has given enough prominence to the differences (mostly increased specializations in notacanthids) existing between the musculature in the two taxa. McDowell does emphasize one '... important and striking difference ...', namely the increased muscular control of the upper jaw in notacanthids, especially the development of an  $A1\alpha$  division inserting primarily on the upper jaw. In one place McDowell (1973: 130) refers to an increase in muscular attachment to the *premaxilla* (italics mine). From my dissections I can find no direct insertion of any muscle onto that bone in any notacanthid species; the insertion is only onto the maxilla, and I presume that McDowell's statement is a *lapsus*.

## LIPOGENYIDAE

### *Lipogenys gilli* Goode & Bean

McDowell (1973: 211-213) gives a detailed account of the jaw and associated musculature in this species, but unfortunately provides no illustrations of their complete layout. We are in general agreement in our interpretations of the rather peculiar jaw arrangement and myology of *Lipogenys*; any areas of disagreement will be obvious from the account given below.

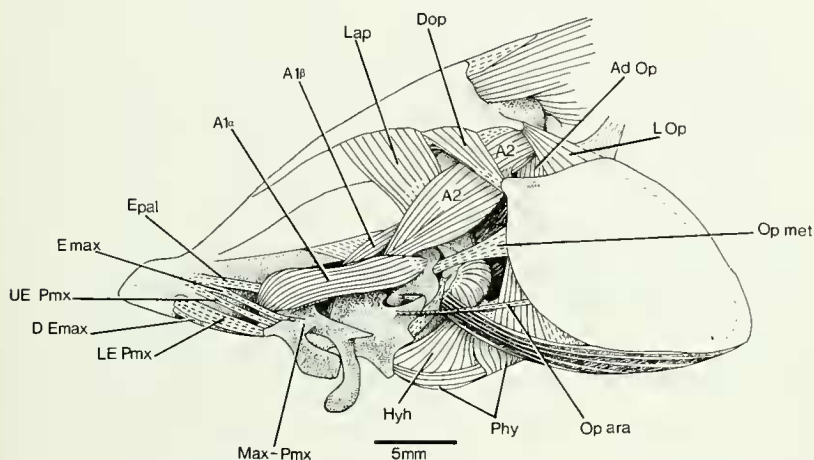
**JAW LIGAMENTS** (Fig. 14). These will be described in two groups, first the ones visible without more than superficial dissection, and secondly the deeper-lying group.

There are two *ethmopremaxillary* ligaments on each side; the lower and longer is broad and thick (in fact the largest ligament of the superficial series) and attaches to the median anterior projection of the premaxilla (Fig. 14). The second ethmopremaxillary ligament is thinner and originates a little above the lower ligament; it inserts slightly posterior to that ligament on the premaxilla.

A long, thin *ethmomaxillary* ligament originates slightly above the dorsal ethmopremaxillary ligament. It inserts conjointly with the broad maxillopremaxillary ligament at about the point where the premaxilla begins to curve downwards, the combined ligaments joining the maxilla at about the middle of its upper and horizontal arm.

There is a stout, moderately long *ethmopalatine* ligament originating immediately above the ethmomaxillary ligament; it inserts on the anterodorsal aspect of the dermopalatine.

The upper ethmopremaxillary, the ethmomaxillary and the ethmopalatine ligaments all originate from a common stem on the ethmoid, and all three run parallel with one another, sloping downwards and backwards.



**Fig. 14** *Lipogenys gilli*. Jaw muscles and ligaments in left lateral view. Specimen MCZ 38072.

There are two deep ligaments, a short, stout *ethmomaxillary* one, and a short, small and horizontally aligned ligament from the median face of the premaxilla to the dermopalatine. The deep ethmomaxillary ligament, unlike its superficial counterpart, runs upwards.

No discrete *ligamentum primordium* is present, but there is a rather diffuse condensation of ligament-like tissue in the connective tissue lying between the lower jaw and the maxilla.

In addition to those ligaments directly connected with the jaw elements there are a number of others which are involved in the mechanism of jaw movement. With two exceptions (the mandibular-opercular ligament and the posterior ceratohyal-quadrates ligament, see below), I have not been able to locate their counterparts in other notacanthoids. Presumably these neomorph structures have developed as a corollary of the profound changes in bone shape and position which characterize the jaws of *Lipogenys*.

A thin, stay-like ligament (Fig. 14) runs from the anterior border of the operculum to the angulo-retroarticular, its insertion being at a point immediately below the quadrates-articular joint. Another ligament, strong and dense, runs forward from the posteriorly directed horn of the angulo-retroarticular to insert on the quadrates immediately behind its articular head. A deep but thin ligament extends from the dorsal part of the anterior border of the operculum to the

posterodorsal margin of the metapterygoid; its insertion on that bone is at the same level as the origin of the  $A1\alpha$  muscle.

The angulo-retroarticular is also linked to the posterior ceratohyal through a strong, dense, ligament which runs from the retroarticular horn to the posterior ceratohyal, inserting on that bone below and a little anterior to the insertion of the protractor hyoideus muscle. Another ligament, broad and dense, runs upwards and forward from the posterior ceratohyal to the medial face of the quadrate. (In another specimen, however, this ligament links the anterior ceratohyal with the quadrate.) The ceratohyal-quadrate ligament is probably homologous with that ligament which, in halosaurs and notacanth, links the posterior ceratohyal with the dentary (see Gosline, 1969, who also lists the occurrence of this ligament in several other groups of primitive teleosts).

**ADDUCTOR MANDIBULAE MUSCLES.** The most superficial element in this series, the adductor  $A1\alpha$  (Fig. 14), is a moderately stout, elongate muscle originating from the metapterygoid, and inserting onto a distinct ledge near the head of the maxilla's lateral arm. (In *Lipogenys* the maxilla is bifurcate anteriorly; the median and shorter arm carries the articulatory head, the lateral arm is taken over almost entirely by muscle insertions and ligament attachments.)  $A1\alpha$  is slightly thinner at its origin than at its insertion, but both points are musculose. From about the middle of the muscle there is a slender tendon closely applied to its ventral outline (Fig. 14) and which runs forward to insert laterally and slightly below the main insertion of the muscle.

Adductor  $A1\beta$ , the most medial of the series (not visible without dissection), is a spindle-shaped muscle originating on the spur-like process developed from the postero-dorsal angle of the metapterygoid (a site shared with a small bundle of fibres from the levator arcus palatini muscle), immediately anterior to the main body of the levator arcus palatini. Thus, in *L. gilli*  $A1\beta$  lies ahead of, and not lateral or medial to the levator muscle as it does in halosaurs and notacanth respectively. From its origin  $A1\beta$  runs forward and outwards, narrows abruptly to a fine tendon and inserts on the medial face of the maxilla.

Adductor  $A2$ , the largest muscle of the series (Fig. 14), has a complicated origin from several but contiguous centres. It is a long deep-bellied muscle that inserts, tendinously, onto the dorso-posterior part of the dentary and the angulo-retroarticular, but with part of the tendon extending onto the dorsal outline of the coronoid process as well. Its main area of origin is from the epiotic and epioccipital regions of the skull (that is, further back than in any halosaurid or notacanthid). A small, virtually separate antero-dorsal part of  $A2$  stems from the pterotic. As the muscle runs forwards and downwards it is joined by fibres originating from the postero-dorsal part of the hyomandibula, and there is a tendinous union between  $A2$  and the operculum near the insertion of the dilatator operculi.

The deepest adductor muscle,  $A3$ , is small and spindle shaped; it originates on the hyomandibula immediately in front of, and slightly above, the foramen for the hyomandibular branch of the 7th cranial nerve. Its insertion is on the dorsal face of the angulo-retroarticular bone.

No  $A\omega$  division of the adductor series is developed.

As compared with *Notacanthus* and *Polyacanthonotus*, the levator arcus palatini muscle in *Lipogenys* is relatively small, though stout, and it is undivided (Fig. 14). It originates in part from the pterotic and in part from the pterosphenoid, and inserts only onto the hyomandibula.

The dilatator and levator operculi muscles, although small, are well developed and largely musculose.

There are distally distinct adductor operculi and hyomandibulae muscles in *Lipogenys*, but both share a common origin from the otic region of the skull somewhat anterior and medial to the origin of adductor  $A2$ . A few fibres from the adductor hyomandibulae insert onto the operculum.

Although not strictly part of the jaw musculature, the protractor hyoidei and the hyohyoideus muscles should be mentioned because of their prominence when the superficial musculature of the head is seen in lateral view (Fig. 14). The protractor hyoideus is in two parts, one of which originates from the posterior ceratohyal near its proximal head and runs, after curving ventrally and laterally, almost vertically to meet its fellow in the midline; the other part originates aponeurotically from that region where the two vertical divisions meet and runs horizontally to insert onto the medial face of the dentary (Fig. 14). The two divisions of the protractor embrace



the posterior and vertical aspects of the massive hyohyoideus muscle associated with the anterior and posterior ceratohyals. The two muscles bulge ventrally and ventrolaterally to produce the 'fat cheeks' which inspired the generic name *Lipogenys*. McDowell (1973 : 213) attributes the bulge to the hyohyoideus alone.

### Comments and comparisons

Basically, the arrangement of the adductor mandibulae muscles in *Lipogenys* is like that of the notacanthids, and includes  $A1\alpha$  and  $A1\beta$  muscular control of the maxilla. In particular, the muscle arrangement is nearest that found in *Polyacanthonotus rissoanus* since in this species there is no subdivision of the adductor  $A2$  as occurs in *P. africanus* and in *Notacanthus bonapartei*.

The most noticeable differences between *Lipogenys* and the notacanthids lie in the origins of the muscles, and in an increase in the number of ligamentous connections between the jaws and the skull, including the development of ligaments not found in either the notacanthids or the halosaurs. No adductor muscles originate from the preoperculum which in this genus is a flimsy ossification around the sensory canal. Instead, the muscles that should be associated with the preoperculum have all shifted their origins either to the skull (and far back on the skull too, see p. 86) or to elements of the palatopterygoid arch (see also McDowell, 1973 : 212–213). *Lipogenys* further differs from *Polyacanthonotus* in having no connection between  $A1\alpha$  and the lower jaw. In *Notacanthus* there is no connection between the upper division of  $A1\alpha$  and the lower jaw either, but there is one between the ventral division of the muscle and the lower jaw (see Fig. 11).

Unlike all notacanthids, *Lipogenys* has an undivided levator arcus palatini muscle (the condition found in halosaurids), and it also lacks a tendinous connection between  $A1\beta$  and the dermopalatine (undoubtedly a loss correlated with that bone's secondary fusion to the palatopterygoid arch, and its consequent immobility, in *Lipogenys*).

In brief, the jaw muscles of *Lipogenys gilli* (the monotypic representative of the Lipogenyidae) can be looked upon as a somewhat specialized form of those found in some *Polyacanthonotus* species (whose jaw musculature is most probably to be considered as basic for the notacanthid fishes). The muscular and ligamentous specializations of *Lipogenys gilli* are clearly correlated with the peculiar specializations of the jaws (see McDowell, 1973 : 208–214). The similarities would certainly suggest that notacanthids and lipogenyids have a shared common ancestry which is more recent than that which either family has with the halosaurs. Although the jaw musculature cannot be used to indicate a particular relationship between *Lipogenys* and *Polyacanthonotus* (because in this respect *Lipogenys* is autapomorphic and *Polyacanthonotus* is plesiomorphic for notacanthids as a whole) there are other anatomical features which do seem to suggest that these two taxa are more closely related to one another than either is to *Notacanthus* and that a shared common ancestor can be postulated for them (see below, p. 97).

### The sternohyoideus muscle in Elopomorpha

Both McDowell (1973 : 23) and Forey (1973a : 355) have commented on the relationships of the sternohyoideus muscle with the pectoral girdle in elopomorphs. Since I find myself in some disagreement with McDowell's account of the muscle in *Lipogenys* and with Forey's (1973a : 355) and McDowell's (1973) description of the situation in *Elops*, *Albula* and *Pterothrissus*, a short review of this muscle in elopomorphs would seem in order.

In *Elops saurus* much of the sternohyoideus arises aponeurotically from the hypaxial body musculature and thus lies lateral to the pectoral arch, which it covers; however, some fibres contributing to the sternohyoideus do originate from the anterior and ventral faces of the cleithrum. In contrast, the sternohyoid in *Albula vulpes* is clearly separated from the hypaxial musculature because the latter inserts onto the posterior face of the cleithrum but the sternohyoid originates mainly from its anterior and lateral faces, with a few fibres coming from the hypaxial muscles medially. The *Albula* condition is that found most commonly amongst teleosts.

In *Pterothrissus belloci* the muscle and girdle are exactly like those in *Albula vulpes*.

McDowell (1973 : 22), however, describes conditions in these two genera which are virtually the reverse of those I have found. According to McDowell (1973 : 22) for example, the situation

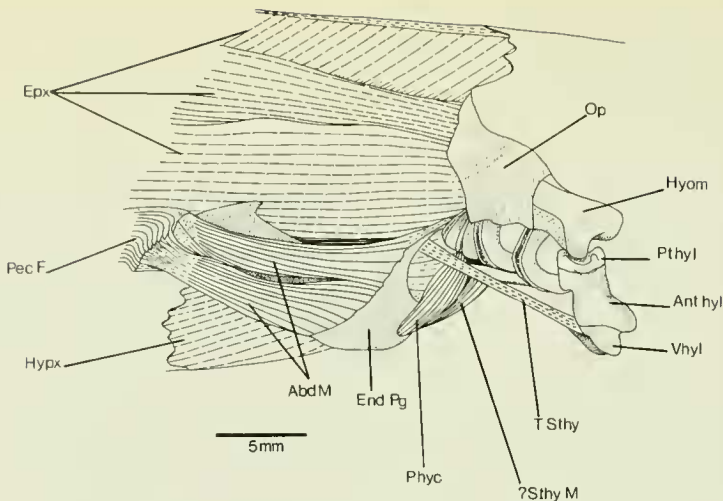


Fig. 15 *Lipogenys gilli*. Body and superficial pectoral fin muscles in the region of the sternohyoideus muscle (whose tendon, T Sthy, is visible), in right lateral view. Specimen MCZ 38072.

in *Elops* is like that I have described for *Pterothrissus* and *Albula*. Forey (1973a : 355) too describes *Pterothrissus* as having an *Elops*-like origin for the sternohyoideus.

In *Halosaurus guentheri* most of the sternohyoideus arises aponeurotically from the hypaxial muscles but a small part arises from fibres attached to the lateral face of the cleithrum's antero-ventral tip. In other words, the lateral aspect of the cleithrum is covered by muscle fibres, but none arises there (except for a few from the ventro-lateral tip). *Aldrovandia phalacra* resembles *H. guentheri* since most of the sternohyoideus originates from the hypaxial musculature, and although the lateral aspects of the cleithra are covered by the sternohyoideus, little of it originates on that bone. In other words, the condition in these fishes is like that in *Elops* and not that in *Albula* and *Pterothrissus*, a condition which I would consider derived rather than primitive.

The sternohyoideus in *Notacanthus bonapartei* is much like that in the halosaurids examined, but in *Polyacanthonotus rissoanus* and *P. africanus* the muscle is a much longer and more discrete

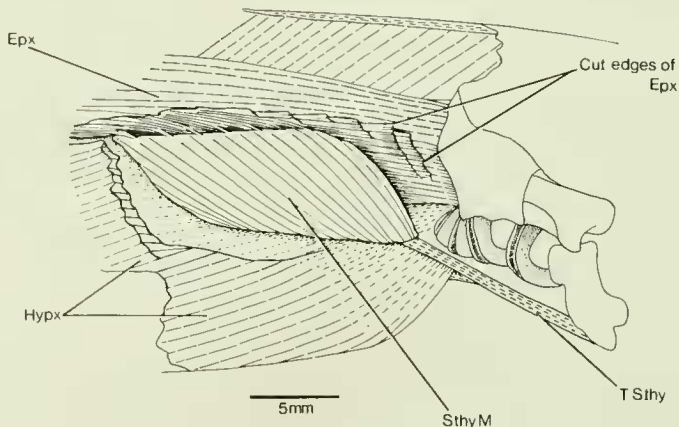


Fig. 16 *Lipogenys gilli*. Sternohyoideus muscle. The pectoral fin musculature and pectoral girdle removed, and the superficial body musculature dissected away. Specimen MCZ 38072.



entity. It still arises aponeurotically from the hypaxial muscles but in these species its origin lies further posteriorly and its dorsal margin, for the muscle's entire length, is free from the supradjacent epaxial muscles (in *Notacanthus* and the halosaurids only a short anterior portion has a free dorsal margin).

The trend seen in *Polyacanthonotus* is carried to its limit in *Lipogenys gilli* (Figs 15 & 16). Here the sternohyoid is completely separate from the body musculature and has shifted medially so that it is now covered by superficial sheets of the hypaxial musculature. It is, in fact, invisible until these muscle sheets are removed; this doubtless led McDowell into stating that the sternohyoideus (his *rectus cervicus*) is less well developed in *Lipogenys* than in the notacanthids and halosaurids (McDowell, 1973 : 220). I would agree with McDowell's correlation of the lower pectoral fin position in *Lipogenys* with the absence of a broad sternohyoideus muscle running across the lateral face of the pectoral girdle; but this is the result not, as he proposes, of sternohyoideus reduction but of its altered position. Indeed, the sternohyoid in *Lipogenys* is, relatively, a much larger muscle mass than it is in any other elopomorph fish.

The sternohyoideus of *Lipogenys* is an almond-shaped body (Fig. 16) clearly demarcated from the surrounding body musculature; it has an aponeurotic origin from the horizontal septum. From the narrow antero-ventral apex there is a stout tendon running forward to insert on the ventral face of the lower hypohyal. The tendon from the sternohyoid of each side fuses with its counterpart a little anterior to the endochondral girdle remnant; the single tendon so formed bifurcates just before the points of insertion are reached.

Two other muscles on each side are associated with the greatly reduced endochondral girdle and with the sternohyoid. A single *pharyngoclavicularis* muscle passes from the girdle to the branchial skeleton immediately behind the point where the sternohyoid tendons fuse. (As there is but one *pharyngoclavicularis* muscle on each side, the muscle must be considered undivided and therefore of the 'anguilliform' type; see Winterbottom, 1974 : 267.) The second muscle runs medially from the anterior face of the endochondral girdle and inserts onto the unpaired portion of the sternohyoid tendon. Since I cannot homologize this small element with any part of the musculature in this region of a more 'normal' teleost type, it is probably part of the sternohyoid. Possibly it represents the only remnant of the true sternohyoid, the larger deeper muscle then being a neomorphous feature.

Winterbottom (1974 : 266) has drawn attention to the difficulty of defining the posterior limits of the sternohyoideus when that muscle is continuous with the hypaxial musculature (as it is in most elopomorphs). He suggests that in such cases the first three myomeres of the muscle be considered as constituting the sternohyoideus. If such a definition be accepted, then virtually all of the 'sternohyoideus' in *Lipogenys* lies posterior to the third myomere and would have to be considered a neomorphous structure.

To summarize: amongst the 'herring-shaped' elopomorphs (McDowell, 1973 : 19), *Albula* and *Pterothrissus* have the usual teleost condition in which the sternohyoid originates mainly on the anterior and lateral aspects of the cleithrum, and the hypaxial muscles insert on to its posterior face. *Elops saurus*, in contrast, has much of the sternohyoideus arising aponeurotically from the body musculature and passing laterally over the cleithrum; a small part of the muscle does, however, still originate from the cleithrum. Halosaurids and notacanthids amongst the eel-shaped elopomorphs resemble *Elops*, with *Lipogenys* displaying an extreme development of the condition, in which the sternohyoid comes to lie below and free from the hypaxial body muscles.

In the few true eels (Anguilliformes) examined (*Anguilla* and *Conger*) the sternohyoid-pectoral girdle relationships are essentially of the *Elops*-halosaurid type.

### The palatoquadrate arch in *Lipogenys gilli*

The palatoquadrate arch in *Lipogenys gilli* differs markedly from that in other notacanthid fishes (and halosaurids too) because of its relative inflexibility and because the dermopalatine is firmly fixed to it. The position of the dermopalatine on the arch also differs in this genus since it lies on the medial side of the arch about halfway along its length (and not ventrally and near its anterior tip as in other genera); see Figs 17-19.

McDowell's (1973 : 211) description of the general features of the arch of *L. gilli* gives a good impression of the way in which it roofs the buccal cavity and of its relative rigidity. However, I disagree with McDowell's description of the spatial relationships existing between the ento- and metapterygoid, and those between the metapterygoid and quadrate. McDowell seems to have overlooked the fact that the two former bones have different relative extensions on the lateral and medial aspects of the arch (see Fig. 17) Medially, the metapterygoid expands so that it overlies the anterior and antero-superior third of the quadrate, thereby forming the dorsal and dorso-lateral roof to the posterior half of the cavity created by the left and right palatoquadrate arches. Each inner wall of this cavity is formed, posteriorly, by the quadrate, anteriorly by the ecto- pterygoid, and over its middle section by the ventrally directed tongue of the metapterygoid (see Fig. 17A).

On the lateral face of the arch, the metapterygoid does not extend ventrally over the quadrate; but the quadrate extends anteriorly on the *outside* of the ecto- pterygoid (which is just visible beneath and in front of the quadrate as a narrow keel). In other words, a greater area of ecto- pterygoid is visible on the medial than on the lateral aspect of the arch. The entopterygoid, on the other hand has its greater surface area exposed laterally (Fig. 17B), especially since medially the posterior part of the bone is covered by the dermopalatine (Fig. 17A).

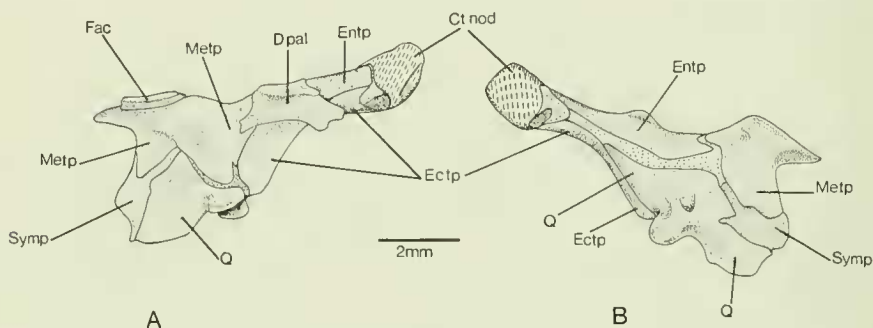


Fig. 17 *Lipogenys gilli*. Left palatoquadrate arch in (A) medial view, (B) lateral view.

Thus, I cannot agree with McDowell (1973 : 111) when he says that '... The largest dermal element, the entopterygoid, forms *most of the medial surface* of the palate, except at the anterior end, and is broadly spread out over the medial face of the metapterygoid and quadrate...' (italics mine). I would also disagree with his statement that '... There is a long, horizontal suture between the metapterygoid and quadrate...' In my interpretation the 'suture' is the ventral outline of the metapterygoid tongue overlapping the medial aspect of the quadrate, and its alignment is more obliquely upwards than horizontally (see Fig. 17A).

In all other respects (except for the interpretation of the autopalatine, see p. 92) I would endorse McDowell's (1973 : 211) description of the arch in *Lipogenys*.

A large, cartilage-capped articular surface on the metapterygoid provides, as McDowell notes in the caption to his text fig. 4, p. 13, an articulation facet between the arch and the parasphenoid, a unique feature not found in halosaurid and notacanthid fishes.

### The autopalatine problem in halosaurs and notacanth

When reviewing palatal structure and function in halosaurs, McDowell (1973 : 16) noted that '... the autopalatine cartilage is absent, unless it is represented by a small nubbin of cartilage between the anterior end of the pterygoid cartilage and the maxilla at the level of the maxillo-premaxillary articulation'. Again, when referring to the palate in notacanth he says (1973 : 131), '... The autopalatine is absent as a bone, but is probably represented by the "singular nodule of

cartilage” noted by Günther. This “cartilage” (only its core is cartilaginous, and most of its bulk is formed by a thick, connective tissue sheathing) lies between the anterior-dorsal edge of the maxilla, the ventral edge of the ethmoid region anterior to the olfactory sac, and the dorsal surface of the pterygoid-dermopalatine articulation.’

I would question both the idea that the autopalatine is absent and the idea that it might be represented by either the ‘singular nodule of cartilage’ in notacanthids or the nubbin of cartilage in halosaurs (see Figs 17–21).

The small nubbin of cartilage intercalated between the maxilla and the pterygoid arch in *Halosaurus* (Fig. 20), and its at least partially ossified counterpart in *Halosauropsis*, is present in such basal elopomorphs as *Albula*, *Elops* and *Pterothrissus*, species in which a clearly recognizable, albeit cartilaginous autopalatine is also present (Forey, 1973b). This nubbin also occurs in several non-elopomorph taxa as well (e.g. in clupeomorphs) where likewise there can be no doubt about the presence of an autopalatine element as well as the nubbin.

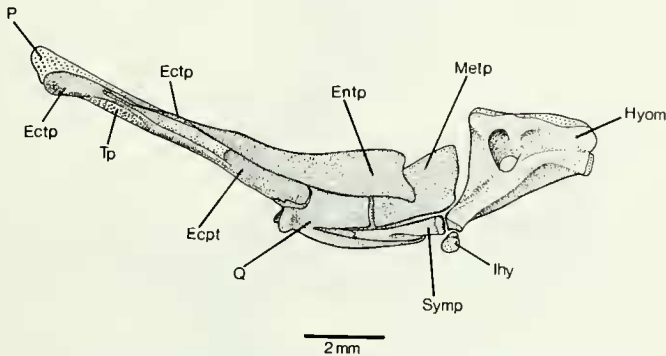


Fig. 18 *Halosaurus guentheri*. Right palatoquadrate arch, medial aspect.

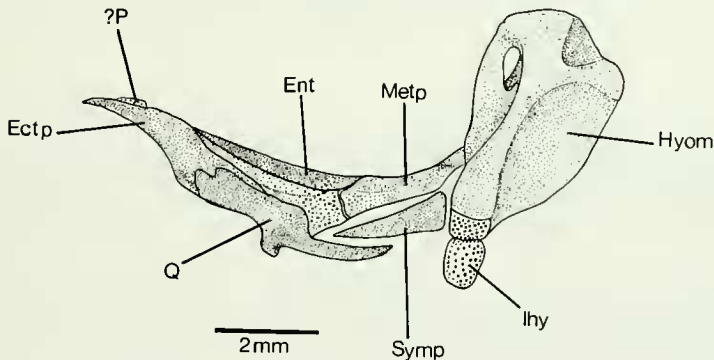


Fig. 19 *Notacanthus bonapartei*. Left palatoquadrate arch, lateral aspect.

Although I can find no trace of an ossified autopalatine in any halosaurid, I can see no reason why the cartilaginous anterior region of the palatopterygoid arch should not be identified as the autopalatine (see Fig. 18), nor why the nubbin of cartilage should not be the homologue of the similar body found in other fishes (including those elopomorphs in which an undoubted autopalatine is present; see above).

Before going on to consider the identity of Günther’s ‘singular nodule of cartilage’ in notacanthids (Günther, 1887 : 246) and its possible homology with the autopalatine as suggested by

McDowell, some attention must be given to what I take to be its homologue in halosaurs. McDowell (1973 : 16), incidentally, makes no mention of its presence in that group.

In *Halosaurus guentheri* (Fig. 20), *Halosauropsis macrochir* and *Aldrovandia gracilis* there is a moderately large, near pyramidal-shaped mass of very dense connective tissue occupying the space between the head of the maxilla (which it partly overlies when the jaws are *in situ*), the head of the pterygoid arch (i.e. the autopalatine) and the ethmoid (see Fig. 20). I can find no comparable structure in *Elops*, *Albula* or *Pterothrissus*, nor in non-elopomorph taxa.

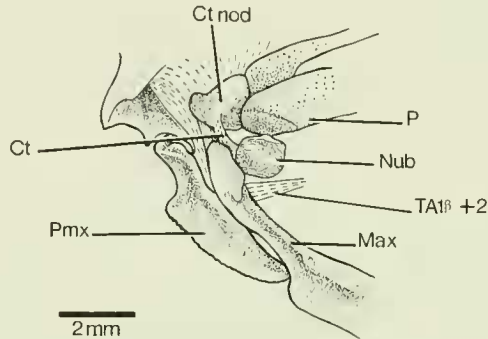


Fig. 20 *Halosaurus guentheri*. Figure to show interrelationships of ethmoid, palatine and maxillary bones (seen from left side). The maxilla and premaxilla have been displaced ventrally to show the connective tissue nodule (Ct nod) and the cartilaginous nubbin (Nub). Specimen BMNH 1966.10.14 : 1.

In *Notacanthus bonapartei*, however, there is a similar but larger structure occupying the same position between the ethmoid, maxilla and head of the pterygoid arch and actually linking the two latter elements (Fig. 21). The drogue-shaped body curves around the antero-medial surface of the pterygoid arch (which is cartilaginous at that point) and reaches to the spine-like tip of the maxillary head; a strong ligament connects the drogue with the tip of the premaxillary ascending process.

Unlike the pyramidal body in halosaurs, the drogue in *Notacanthus* has a cartilaginous centre but, as in halosaurs, its body is composed largely of dense connective tissue. I can find no cartilaginous or bony nubbin interposed between the pterygoid arch and the maxilla of *Notacanthus* and would thus suggest that it has been incorporated in the body of the drogue.

It is, I think, difficult to dispute the presumed homology of the pyramidal and drogue-shaped bodies in halosaurs and notacanthids respectively. Furthermore, judging from Günther's rather small figure and from his description (Günther, 1887 : 246 & plate 10), his 'singular nodule of cartilage' is the same body as that which I am calling the drogue-shaped one, and thus is the equivalent of the pyramidal body in halosaurs.

The autopalatine in *Notacanthus* would appear to be represented by a small conical area of cartilage near the tip of the pterygoid arch (Fig. 19).

*Polyacanthonotus rissoanus* and *P. africanus* are much like *Notacanthus bonapartei*, but with a narrower and more elongate drogue-shaped body.

In *Lipogenys gilli* (Fig. 17) the connective tissue mass is an elongate pyriform body, its apex directed anteromedially and its base closely applied to the cartilaginous head of the pterygoid arch (which, on my interpretation, is the autopalatine); a groove in the body provides an articular surface for the maxilla. Embedded within the pyriform body is a fairly substantial concavo-convex nubbin of what appears to be bone (or very hard cartilage); it is this nubbin of bone which provides an articular surface between the pyriform body and the autopalatine. (See also McDowell, 1973 : 210-211, under autopalatine.) The embedded bony nubbin in this species represents a condition in the relationships of the nubbin (bone or cartilage) and the larger con-



nective tissue body (the 'nodule') which is intermediate between the *Halosaurus* type and that of *Notacanthus* (see above, and Figs 20 & 21). The relationships of the maxilla with the pyriform body in *Lipogenys* can also be considered as intermediate between the other two types.

Thus, contrary to the view of McDowell (1973 : 6 & 131) cited on p. 90 above, I would consider that an autopalatine is present in halosaurids, notacanthids and lipogenyids, and that the nodule of connective tissue (or connective tissue and cartilage) present near the anterior tip of the autopalatine is a neomorphous structure (probably characteristic of these three families alone) which evolved as part of the peculiar jaw mechanisms found in these fishes. That the function of the connective tissue nodule differs in notacanthids (including lipogenyids) and halosaurs is perhaps indicated by its different relationships with the upper jaw and pterygoid arch in the two groups (cf. Figs 20 & 21).

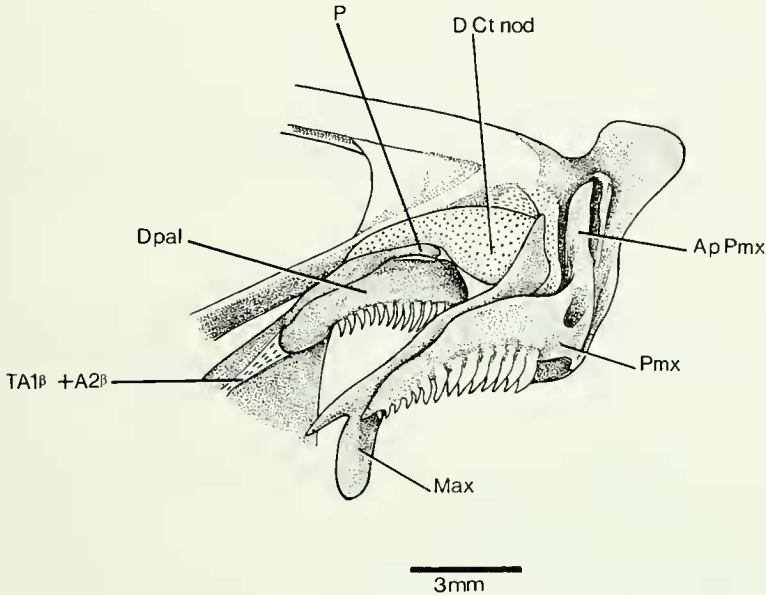


Fig. 21 *Notacanthus bonapartei*. Figure to show ethmo-palato-maxillary relationships, viewed obliquely from a ventro-anterior position (right side); the various elements are depicted *in situ*. Specimen BMNH 1972.1.26 : 33.

Since the primitive elopomorphs *Albula* and *Pterothrissus* have a double contact between the palatopterygoid arch and the skull (anteriorly with the ethmoid cartilage, and somewhat more posteriorly with the lateral ethmoid), the single contact in halosaurs and lipogenyids must be considered a derived condition, and the complete loss of direct contact in notacanthids (see above, p. 92) a further specialization.

### Lateral line scales

In all halosaurids, notacanthids and lipogenyids, the canal-bearing lateral line scales on the flanks are highly specialized. The sensory canal is a soft, membranous tube supported by a pair of flanges developed from the scale itself (see McDowell, 1973, for a detailed and illustrated account).

The notacanthid and lipogenyid types (McDowell, 1973 : 173 & 218 respectively) are very similar and seem to represent either a regressed or a basic state relative to those of the halosaurs.



In halosaurids (e.g. *Halosaurus guentheri*, *Aldrovandia affinis* and *Halosauropsis macrochir*) the canal scales are relatively enlarged (slightly to markedly so). But the overlap of the surrounding scales is such that the exposed area of each canal scale is not noticeably larger (and may even appear smaller) than that of its neighbours.

Notacanthids (e.g. *Notacanthus bonapartei*, *Polyacanthonotus rissoanus* and *P. africanus*) and lipogenyids, by contrast, have pore scales that are equal in size or even slightly smaller than the surrounding scales. The overlap of surrounding scales, however, is so extensive that no part of the canal scale, except for the canal, is visible; furthermore, the canal scale is very deeply embedded in the dermis. McDowell (1973 : 137) says that the canal scales are '... larger than the other scales of the flank ...' but this is certainly not the case in the species I have examined (see above).

Two different types of canal scale arrangement are found in the 'herring-shaped' elopomorphs, but the canal itself is of the usual teleost type. *Elops saurus* and *Albula vulpes* have canal scales that are the same size as their flanking neighbours, and a scale arrangement whereby equal, or almost equal, areas of the canal and neighbouring scales are exposed (*Albula* has the smaller area of canal scale visible). In *Pterothrissus*, however, the canal scales are almost completely covered by their neighbours so that the canal itself and a small sector of the scale's posterior margin are visible; the canal scales are also slightly smaller than the other scales.

In other words, the spatial relationships and the relative size of the lateral line canal scales in *Pterothrissus* are very similar to those in the notacanthids and lipogenyids, and should be considered specialized relative to the condition found in *Albula* and *Elops* (and in all other elopoids as well; personal observations). The condition in *Albula* is certainly unlike that in any halosaurid or notacanthid fish.

## Interrelationships and classification

In their provisional classification of teleost fishes, Greenwood *et al.* (1966) grouped in one superorder, the Elopomorpha, the albuloid, elopoid, anguilloid and halosauroid fishes. Their classification, which has formed the basis for all recent discussions, is as follows:

### Superorder ELOPOMORPHA

#### Order ELOPIFORMES

Suborder ELOPOIDEI (families Elopidae and Megalopidae)

Suborder ALBULOIDEI (family Albulidae including Pterothrissidae)

#### Order ANGUILLIFORMES

Suborder ANGUILLOIDEI (23 families)

Suborder SACCOPHARYNGOIDEI (3 families)

#### Order NOTACANTHIFORMES (families Halosauridae, Lipogenyidae and Notacanthidae).

Since 1966 there have been several important papers dealing with different aspects of elopomorph taxonomy and phylogeny, in particular with the phyletic integrity of the Elopomorpha as a whole (see Forey, 1973a, for a review; also Forey, 1973b; Nelson, 1973; McDowell, 1973 especially pp. 5-27). Intragroup relationships have been touched upon by McDowell (1973) and Nelson (1973), and have been discussed at length by Forey (1973b).

Apart from Nybelin (1971) and Gosline (1971), there seems to be a general agreement amongst those who have considered the question that the Elopomorpha do represent a monophyletic assemblage (see Forey, 1973a). None of the anatomical data discussed above would appear to contradict that conclusion, and some seem to provide new data for testing hypotheses already proposed on phyletic relationships within the superorder. Certain new hypotheses can also be generated.

Forey (1973a & b) maintains, as was inferred by Greenwood *et al.* (1966) that '... elopoids are more closely related to albuloids than to any other group'. However, the two synapomorphic characters which Forey (1973a) believes unite these suborders, the presence of rostral ossicles and a prenasal ossicle, are in fact features which characterize all the non-anguilliform Elopomorpha, and not just the elopoids and albuloids (see McDowell, 1973 : 5-12).

In the same paper, Forey (1973a : 358, Fig. 1) gives a cladogram in which the Notacanthiformes (*sensu* Greenwood *et al.*) have a common ancestry with the Pterothrissidae, both groups ultimately having a shared common ancestor with the Albulidae. This conclusion will be reviewed

later. Forey (1973b), in his monograph on fossil and living elopiforms, provides evidence, mostly osteological, for the proposed common ancestry of the albulids and pterothrissids. As far as I can see, his arguments for this latter relationship are sound. Unfortunately neither here nor in his other paper does he provide a really critical review of his proposal that the notacanthiforms may be pterothrissid derivatives (Forey, 1973b : 214). The main features on which Forey reaches this conclusion are seemingly the elongate snout and small, inferior mouth of notacanthiforms, coupled with the restricted mobility of the upper jaw elements and the slender, inturned head of the maxilla (Forey, 1973b : 211). Certainly these are derived features shared by the two groups, but I believe that other evidence argues against their use as indicators of ancestor-descendent relationship (although not against their relationships as sister groups). Again, I would have reservations about Forey's (1973a : 355) idea that '... the Pterothrissidae appear particularly important in the ancestry of the halosaurs'. Some of the characters he deals with are synapomorphic ones for the Elopomorpha as a whole (sensory canals, relationship of premaxilla and maxilla, reduction in ossification), while I would interpret the association of the sternohyoideus muscle with the pectoral girdle as being like that in *Albula* and not of the halosaur type as he suggests (see above, p. 87).

Nelson (1973) has proposed alternative views on intragroup phylogenies. Using the morphology of the lower jaw as a basis for his arguments, Nelson postulates the existence of three lineages within the Elopomorpha, viz. 'elopoids', 'albuloids' (i.e. albulids, pterothrissids, notacanthids and halosaurs) and 'anguilloids', the two latter groups being more closely related to one another than either is to the 'elopoids'. The characters used by Nelson provide no information on the inter-relationships of the taxa within his 'albuloid' lineage. The integrity of the 'albuloids', however, is supported by the nature of the specialized rostral commissure found in all its extant representatives (see McDowell, 1973 : 5-11).

The various characters and character suites which I have dealt with in this paper lead me to agree with Nelson's concept of an albuloid group that is but distantly related to the elopoids; unfortunately these same data do not provide any evidence either to support or to reject Nelson's idea of close relationship between albuloids and anguilloids.

Returning now to Forey's (1973a & b) contention that the Pterothrissidae and Albulidae, particularly the pterothrissids, are the taxa most closely related to the Notacanthiformes we find that some of the characters discussed previously in this paper appear to support this relationship; these must be reviewed critically before they are utilized as a basis for classification.

Although the pterothrissids show a predominance of unspecialized (i.e. plesiomorph) anatomical features, particularly in the jaw and buccal musculature (see p. 76), there is one character associated with the jaw mechanism which is shared with the Notacanthidae and Lipogenyidae but with no other elopomorph groups nor with any basal non-elopomorph teleosts, namely, a levator arcus palatini muscle which is clearly subdivided into two parts (see p. 69 & Fig. 1).

A second specialization shared by pterothrissids, notacanthids and lipogenyids lies in the almost complete overlap of the flank lateral line canal scales by neighbouring scales (see p. 93), with the result that only the canal and a very small sector of the scale's free margin is visible without dissection; in notacanthids and lipogenyids, this overlap is complete because the canal scale lies deep in the dermis (see McDowell 1973 : 136-137 & 221-222 for detailed descriptions).

In these two features the affinities of the Pterothrissidae would certainly seem to lie with the notacanthids and lipogenyids rather than with the Albulidae and Halosauridae. Are there then any features of the Albulidae which might suggest particular affinities within the Notacanthiformes, especially with the halosaurs?

The answer to that question would seem to be negative, both from the osteological and myological evidence available. The osteological evidence (see Forey, 1973b : 202-210; and below) shows only apomorph features shared by the Pterothrissidae and Albulidae, whilst the myological evidence provides only one derived feature (the development of an  $A1\alpha$  muscle) and that shared by albulids, halosaurids and notacanthids.

Thus, there might seem to be grounds for considering the pterothrissids to be more closely related to the notacanthids (and lipogenyids) than to the albulids or halosaurids.

However, the notacanthids, lipogenyids and halosaurids share five major derived characters

which are not present in either the Pterothrissidae or the Albulidae, viz. the presence of a spine posteriorly on the maxilla, extreme reduction of the caudal fin skeleton, the pelvic fins connected basally by a membrane, the pectoral fins set high on the body (see McDowell, 1973 : 2), and the presence of a large and characteristically shaped fibrous and sometimes partly cartilaginous nodule developed between the maxillary head and the palatine (see above, pp. 92-93).

Thus, if one were to link the Pterothrissidae with the Notacanthidae and Lipogenyidae because of their shared apomorph features of a divided levator arcus palatini muscle and the covered lateral line pore scales (see p. 95), how would the five halosaur-notacanth synapomorphies be explained?

One cannot argue that the halosaurs and notacanthids had a more recent common ancestry than that shared with the pterothrissids because the halosaurs do not share with the pterothrissids and notacanthids the two derived features of a divided levator arcus palatini and overlapped lateral line scales. Neither is it possible, as an alternative phylogeny, to ally as sister groups the albulids and halosaurs, on the one hand, and the pterothrissids and notacanthids, on the other, since this would demand that the five halosaur-notacanth synapomorphies were evolved in parallel (and, of even greater importance, there are no synapomorph features linking the albulids and halosaurids).

Finally, it must be noted that the pterothrissids and albulids share a number of derived features that do not occur amongst the halosaurids and notacanthids. These synapomorphies, according to Forey (1973b : 202-210) include a reduced intercalar bone, the nature of the ethmoid-palatine articulation, the morphology of the hypopalatine arch (including the foramen between the hyomandibula and metapterygoid bones), the spatial relationships of the hypohyals to one another and to the anterior ceratohyal, and various reductional trends in the caudal fin skeleton, including the loss of expanded bases to the inner caudal rays.

From all this evidence it would seem therefore that two sister groups can be recognized, an albulid-pterothrissid one and a halosaur-notacanthid one (the latter group including the lipogenyids, see below p. 97). Allowing for the various autapomorphic features present in each sister group, the pterothrissid-albulid pair would rank as the plesiomorph assemblage, the halosaur-notacanth-lipogenyid group as the apomorph one.

There is one difficulty in accepting this proposed phylogeny, namely the two synapomorph features shared only by the pterothrissids and notacanthids. For the moment this can only be explained as parallel evolution, probably the expression in one derived and one otherwise primitive lineage of features latent in their common ancestor. Certainly this degree of parallelism is far less extensive than that which would have to be invoked if the alternative phylogeny was proposed. In that case the albulid-pterothrissid synapomorphies as well as those shared only by notacanthids and halosaurs would all have to be attributed to parallel evolution, an altogether less probable and unparsimonious explanation.

The shared common ancestry of the pterothrissids, albulids, halosaurids notacanthids and lipogenyids (the five elements also of Nelson's 'albuloids') is reflected in the specializations of their lower jaw sensory canal system (see Nelson, 1973 : 346), in the rostral portion of the infra-orbital canal system (see McDowell, 1973 : 5-11), and probably also in the way in which the ligamentum primordium is either absent or is not associated with any part of the adductor mandibulae musculature. In the Elopidae, the adductor is inserted partly on this ligament; since a similar condition is found in *Amia*, this strongly suggests that the 'albuloid' condition is a derived one.

To these five taxa, all represented in the extant fauna, may be added a sixth, the extinct family Osmeroididae of Forey (1973b); various derived osteological features in that family suggest its close relationship with the Albulidae (see Forey, 1973b), and help better to define the relationship existing between the Albulidae and Pterothrissidae (see p. 35 below).

Before going on to propose a formal intragroup classification of the 'albuloids', and before considering Nelson's (1973) proposed relationships of the 'albuloids' with other elopomorph groups, one should review the inter- and intrarelations of the halosaurs, lipogenyids and notacanthids.

I can find no features which would indicate a close relationship between the Halosauridae and any particular lineage within the Notacanthidae or with the Lipogenyidae. The specialized



characters of the halosaurs are either autapomorphies, like the highly modified lateral line scales, or else merely indicative of a distant, shared ancestry with the notacanthids and lipogenyids.

McDowell's (1973 : 157) view that amongst the notacanthids *Polyacanthonotus* is '... the more halosaurid-like genus and presumably the more primitive ...' is deceptive. What, in effect, he is saying is that *Polyacanthonotus* retains some primitive features that are lost in *Notacanthus*. *Polyacanthonotus* shares several derived features with *Notacanthus* and *Lipogenys* alone (see below). I can detect none that would suggest closer relationship with the halosaurs.

Within the notacanth group (*Polyacanthonotus*, *Notacanthus* and *Lipogenys*), *Lipogenys* is outstanding for its obvious oro-buccal specializations (see McDowell, 1973 : 208–223); its phyletic relationships with the Notacanthidae are nevertheless clear-cut.

McDowell (1973 : 223) poses the cladistically somewhat imprecise question of whether *Lipogenys* is derived from the Notacanthidae or from some pre-notacanthid ancestor retaining resemblances to the Halosauridae. His answer is equivocal. However, if the question is rephrased in terms of identifying sister groups, then I think the new information available on lipogenyids and on notacanthids, combined with that already available from McDowell's work, points towards the recognition of *Polyacanthonotus* as the sister group of *Lipogenys*, the two taxa then becoming the sister group of *Notacanthus*.

Although most of the derived features seen in *Lipogenys* are autapomorphies (see McDowell, 1973 : 208–209), at least four specializations or trends in specialization are shared only with *Polyacanthonotus*, namely:

(i) There is a single lateral line scale for every three vertical scale rows on the trunk.

(ii) In *Polyacanthonotus* the endochondral shoulder girdle (scapula and coracoid) is clearly separated from the dermal girdle; in *Lipogenys* the endochondral girdle is also distinct, but in this case the entire dermal girdle has disappeared. I associate these characteristics on the grounds that the *Polyacanthonotus* condition represents a first stage in the evolution of the *Lipogenys* one. Furthermore, in both genera the scapula and coracoid ossifications of the primary girdle are well separated by a cartilaginous area; again, *Lipogenys* shows the more extreme condition.

(iii) The highly developed and well-differentiated sternohyoideus muscle in *Lipogenys* (see p. 89 and Figs 15 & 16) is foreshadowed by the large sternohyoideus of *Polyacanthonotus*, where the muscle is longer and more clearly demarcated from the body musculature than it is in *Notacanthus*.

(iv) In both genera the webbing between the pelvic fins is reduced. A fifth, and 'trend', character should probably be added to this list. In *Lipogenys* the frontal and parasphenoid are in broad contact through a deeply interdigitating suture anterior to the pterosphenoid; in *Polyacanthonotus* the frontal and parasphenoid are narrowly separated by a shallow tongue of the pterosphenoid, whereas in *Notacanthus* the bones are widely separated (see McDowell, 1973 : 12–13 & 223).

Of the five characters which McDowell (1973 : 223) lists as being shared by *Polyacanthonotus* and *Lipogenys*, three (the short ischial process of the pelvic girdle, the gradual transition between the spine-like and articulated anal rays, and the absence of scales anteroventrally on the snout) are plesiomorphic ones; the other two are derived features and were considered in the last paragraph.

McDowell (1973) also lists seven characters shared by *Lipogenys* and *Notacanthus*, which features he considers to be '... specializations ... that would suggest direct derivation ...' of *Lipogenys* from *Notacanthus*. These features are: (i) the loose attachment of the peritoneum to the body wall; (ii) the long and complexly folded intestine; (iii) A scaly branchiostegal membrane; (iv) the large number of spine-like pelvic rays; (v) the scaly sheath on all the sensory canals of the head; (vi) the very strong angulation of the maxilla; (vii) the shape of the scales.

I find it difficult to assess the significance of the peritoneal character, but since it does not occur elsewhere amongst the Elopomorpha it is presumably a derived one.

The intestine in *Polyacanthonotus africanus* and in *P. rissoanus* is elongate and folded, so the condition in *Lipogenys* could be interpreted as a further development of a trend already apparent in a common ancestor.

The question of whether or not a scaled branchiostegal membrane is an indicator of a *Lipogenys*–*Notacanthus* relationship is complicated by the fact that some individuals (or perhaps populations) of at least one *Polyacanthonotus* species do have scales on the branchiostegal mem-

brane. A specimen of *P. rissoanus* (BMNH 1904.3.4 : 3) from South Africa has numerous, but scattered, small and very superficial scales over the entire area of the branchiostegal membrane. No scales can be detected on another specimen of this species (N.I.O. 'Discovery' collection, Stn 8512) nor on two specimens of *P. africanus* (N.I.O. 'Discovery' collection, Stns 7853 & 8519) although in the larger of the two latter fishes there are marks on the membrane very similar to those left when scales are rubbed off from the scaled *P. rissoanus*. Whether the apparent nakedness of the branchiostegal membrane in many *Polyacanthonotus* is due to the abrasion of these small and superficial scales or whether scaled specimens are individual or population variants remains to be tested on larger samples than are available to me. Whatever the answer, it does seem that this feature cannot be used to indicate a closer relationship between *Lipogenys* and *Notacanthus* than between *Polyacanthonotus* and *Lipogenys*.

Two of the four other characters from McDowell's list, in my opinion, also fail to demonstrate any such relationships. Some species of *Polyacanthonotus* have two spine-like rays in the pelvic fin, that is the same number as occurs in *Lipogenys* and *Notacanthus*; the peculiar, apparently serrate second pelvic spine in *Lipogenys* (see McDowell, 1973 : 221) is certainly an autapomorphic character. In all specimens of *Polyacanthonotus* which I have examined the sensory canals of the head are scale-ensheathed except for the medial region of the rostral commissure; in having this canal region scaled *Lipogenys* does resemble *Notacanthus*, but again it is difficult to decide whether this is the primitive or derived condition (but see below). The maxilla in *Polyacanthonotus* is distinctly angled although not quite so strongly angled as in *Notacanthus*, but the difference between the three genera is one of only slight degree; the greater similarity existing between *Notacanthus* and *Lipogenys* in this feature could well be attributed to functional convergence. Finally, there is the question of scale shape. Again I must disagree with McDowell. As Fig. 22 shows, the scales of *Polyacanthonotus africanus* have a near vertical anterior margin, and clearly demarcated dorsal and ventral margins, in these respects differing from the scales of *Notacanthus bonapartei* but closely resembling those of *Lipogenys*. There is some topographically correlated variation in scale shape in any individual of *Polyacanthonotus*, but nowhere on the body could I find scales that were more like those of *Notacanthus* than those of *Lipogenys*.

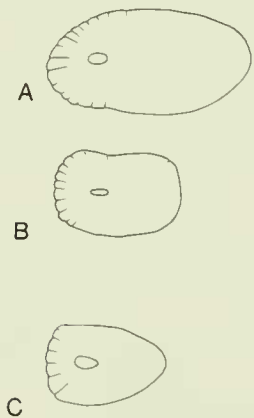


Fig. 22 Body scales from (A) *Notacanthus bonapartei*, (B) *Lipogenys gilli*, (C) *Polyacanthonotus africanus*.

In brief, only two of the supposedly *Notacanthus*-like features listed by McDowell (1973 : 223) seem to be shared uniquely by *Lipogenys* and *Notacanthus*, namely, the loose peritoneum and the absence of scales on the rostral commissure. The former is probably a derived feature since it does not occur in the primitive, that is elopoid, Elopomorpha, but the latter character may be primitive because this region of the snout is naked in halosaurs, pterothrissids and albulids, all taxa which are manifestly more primitive than the notacanthids.



If this analysis be accepted, then there is little to support the relationship implicit in McDowell's (1973 : 223) suggestion of *Lipogenys* having '... direct derivation ...' from *Notacanthus*. On the contrary, I would submit that the actual specializations as well as the trends of specialization shared by *Lipogenys* and *Polyacanthonotus* suggest a common ancestry for the two taxa and that *Notacanthus* represents their sister lineage.

The different lineages of Nelson's 'albuloid' group can now be brought together as shown in the accompanying cladogram (Fig. 23).

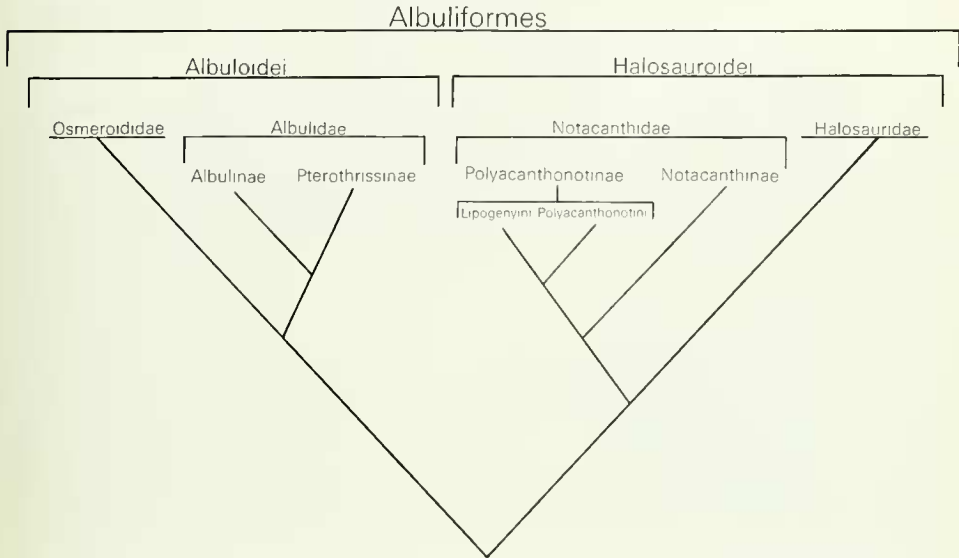


Fig. 23 Cladogram to show interrelationships of the various taxa comprising the order Albuliformes.

As this figure indicates, the overall classification agrees with Nelson's (1973) concept of an order Albuliformes; its two constituent sister lineages are given subordinal status as the suborders Albuloidei (plesiomorph) and Halosauroidae (apomorph). This arrangement differs substantially from that proposed by Greenwood *et al.* in 1966, where the Albuloidei were treated as the apomorph sister group of the Elopoidae (the two taxa constituting the order Elopiformes). In that classification the Halosauridae, Lipogenyidae and Notacanthidae were treated, without further grouping, as the constituent taxa of the order Notacanthiformes, whose relationships within the Elopomorpha could not be determined at that time.

The new arrangement also departs from Forey's (1973a) groupings which are essentially those of Greenwood *et al.* (1966). My reasons for rejecting that arrangement have been detailed above (p. 95).

McDowell's (1973) recognition of two suborders (Notacanthoidei and Halosauroidae) within a single order Heteromi (=Notacanthiformes of Greenwood *et al.*) is essentially a phenetic classification based on degrees of morphological difference, and would presumably have been the same had he taken into account the morphological differences existing between the Heteromi and the Albulidae and Pterothrissidae.

In other recent classifications (McAllister, 1968; Gosline, 1971) the albuloids have also been classified with the elopoids (*Elops* and *Megalops*) and not with the notacanthids and halosaurs, an arrangement which, as will be apparent from this paper and from Nelson's (1973) research on jaw structure, is not thought to reflect phyletic relationships.

My arrangement of taxa within the Albuloidei is based largely on Forey's (1973b) detailed and meticulous study of fossil Osmeroididae, Pterothrissidae and Albulidae, combined with personal observations on the soft anatomy of *Pterothrissus* and *Albula*. It differs from Forey's treatment of the Albuloidei only in ranking the species of *Albula* and *Pterothrissus* as members of two sub-families rather than representing two families, a change in status which I believe better represents their phyletic relationships.

Reasons for interrelating the constituent taxa of the Halosauroidae as shown in the cladogram (Fig. 23) are given on pp. 95-98 above. No further comment seems necessary if it be accepted that the categories in a classification should show propinquity of descent rather than emphasize phenetic dissimilarities, as does McDowell's (1973) recognition of the two suborders Halosauroidae and Notacanthoidei.

On the grounds of their shared specializations in swimbladder morphology (see Marshall, 1962; Greenwood *et al.*, 1966) and lower jaw structure (the angular fused with both the articular and retroarticular in *Pterothrissus* and all eels), Nelson (1973 : 348) suggested a sister group relationship between the Albuliformes (as here demarcated) and the Anguilliformes of Greenwood *et al.* (1966). As Nelson points out (1973 : 347), the fusion of the angular with both articular bones is '... at best a parallelism and a weak indicator of relationship.' The detailed similarities in swimbladder specializations (for which see Marshall, 1962), however, would seem to be a strong indicator of common ancestry. None of the characters dealt with in this paper weakens this hypothesis, and consequently Nelson's recognition of the Anguilliformes and Albuliformes as sister groups is accepted.

No information additional to that given by Nelson is available on the relationship between the elopiform fishes (that is, the Elopoidei of Greenwood *et al.* (1966) and Forey (1973b)) and the Albuliformes and Anguilliformes. Thus, I would also accept provisionally Nelson's (1973 : 346-348) suggestion that the Elopiformes be treated as the plesiomorph sister group of the Albuliformes and Anguilliformes combined. The plesiomorph status of the Elopiformes is clearly demonstrated by Forey's (1973b) work on both fossil and living representatives; Forey's conclusions about the intragroup relationships of these fishes are also accepted.

To summarize, I propose that the affinities of the various taxa discussed above be expressed in the following way:

Cohort: **TAENIOPAEDIA**

Superorder: **ELOPOMORPHA** (*sensu* Nelson, 1973)

Order: **ELOPIFORMES** (*sensu* Nelson 1973)

Suborder: **ELOPOIDEI**

Superorder: **ANGUILLOMORPHA** (Nelson, 1973)

Order: **ALBULIFORMES** (Nelson, 1973)

Suborder: **ALBULOIDEI**

Family: **Osmeroididae** (Forey, 1973b)

Family: **Albulidae**

Subfamily: **Albulinae**

Subfamily: **Pterothrissinae**

Suborder: **HALOSAUROIDEI**

Family: **Halosauridae**

Family: **Notacanthidae**

Subfamily: **Notacanthinae**

Subfamily: **Polyacanthonotinae**

Tribe: **Polyacanthonotini**

Tribe: **Lipogenyini**

Order: **ANGUILLIFORMES**

Suborder: **ANGUILLOIDEI** (*sensu* Greenwood *et al.*, 1966)

Suborder: **SACCOPHARYNGOIDEI** (*sensu* Greenwood *et al.*, 1966)

In an article published whilst this paper was in press, Patterson & Rosen (1977) put forward a revised interpretation of relationships within the neopterygian fishes. The section dealing with elomorph fishes in their new classification differs from that given above because Patterson & Rosen (1977 : 160, footnote) do not accept the validity of Nelson's (1973) dichotomy between

the Elopomorpha and Anguillomorpha. Instead, they treat the cohort Elopomorpha (= Taenio-  
paedia above) as an unresolved trichotomy comprising the orders Elopiformes, Megalopi-  
formes (new) and Anguilliformes, the latter with two suborders, the Anguilloidei and Albuloidei.  
(Patterson & Rosen do not discuss the interrelationships and ranking of taxa within the two  
suborders.)

Following the classification proposed by Patterson & Rosen (1973: 153 & 163) my suborders  
Albuloidei and Halosauroidae would have to be ranked as the superfamilies Albuloidea and  
Halosauroidae, but the other categories would remain unchanged (except, of course, for a down-  
grading to superfamilies of the Anguilloidei and Saccopharyngoidei).

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