CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES

PART VI

THE JAW MECHANISM AND FEEDING OF THE HOLOCEPHALAN, *CALLORHYNCHUS CAPENSIS* DUMERIL

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INTRODUCTION

Callorhynchus capensis Dumeril is a fairly common South African representative of the Chimaeroidei. According to Smith (1961) these holocephalans may be found from the surf-zone to a depth of 183 metres right around the South African coast.

The exact phylogeny of the chimaeroids is obscure due to difficulties encountered in obtaining embryological and fossil material. Stensio (1925) and Orvig (1960) believe that the ptyctodonts gave rise to the Holocephali, whereas Moy-Thomas (1939) and Patterson (1965) are of the opinion that the Holocephali and ptyctodonts diverged from a common pre-arthrodire ancestor. The reader is referred to Patterson (1965) who provides a comprehensive review and new ideas regarding chimaeroid phylogeny.

It appears as though the holocephalans have paralleled the teleosts in several respects, since they have an operculum which covers the gill slits, they are dorso-ventrally deepened, and they possess large eyes which constrict the interorbital region. Possibly vision and not olfaction is the dominant sense in the Holocephali.

Patterson (1965) maintains that the Holocephali contained the dominant durophagous fishes during the late Palaeozoic. The Holocephali replaced the arthrodires in this dominant durophagous role, and they were subsequently replaced by the rays and specialised actinopterygians. The few holocephalans which remain today are survivors of this once dominant group, which Smith (1961) considers to be moving towards extinction.

The extant Chimaeroidei are still well adapted for a durophagous existence. They have strong biting plates in the front of the upper jaw, and powerful cutting and crushing toothplates upon both the upper and lower jaw. The support for this powerful dentition is afforded by the holostylic jaw suspension. It appears as though this suspension limits jaw movements to a narrowly defined upwards and downwards movement. This restriction may probably be linked with the unparalleled development of labial cartilages found in the Holocephali. These cartilages support movable lips which appear to be responsible for the mechanism of food capture and manipulation.

The present paper deals with the movements of the lips and the jaw during feeding of these fish. The water movements through the buccal and branchial cavities have been dealt with only in so far as they affect feeding. The respiratory mechanism, the small branchial muscles, and the phylogenetic problems associated with the levatores arcuum branchialium (see Luther 1938) have not been considered.

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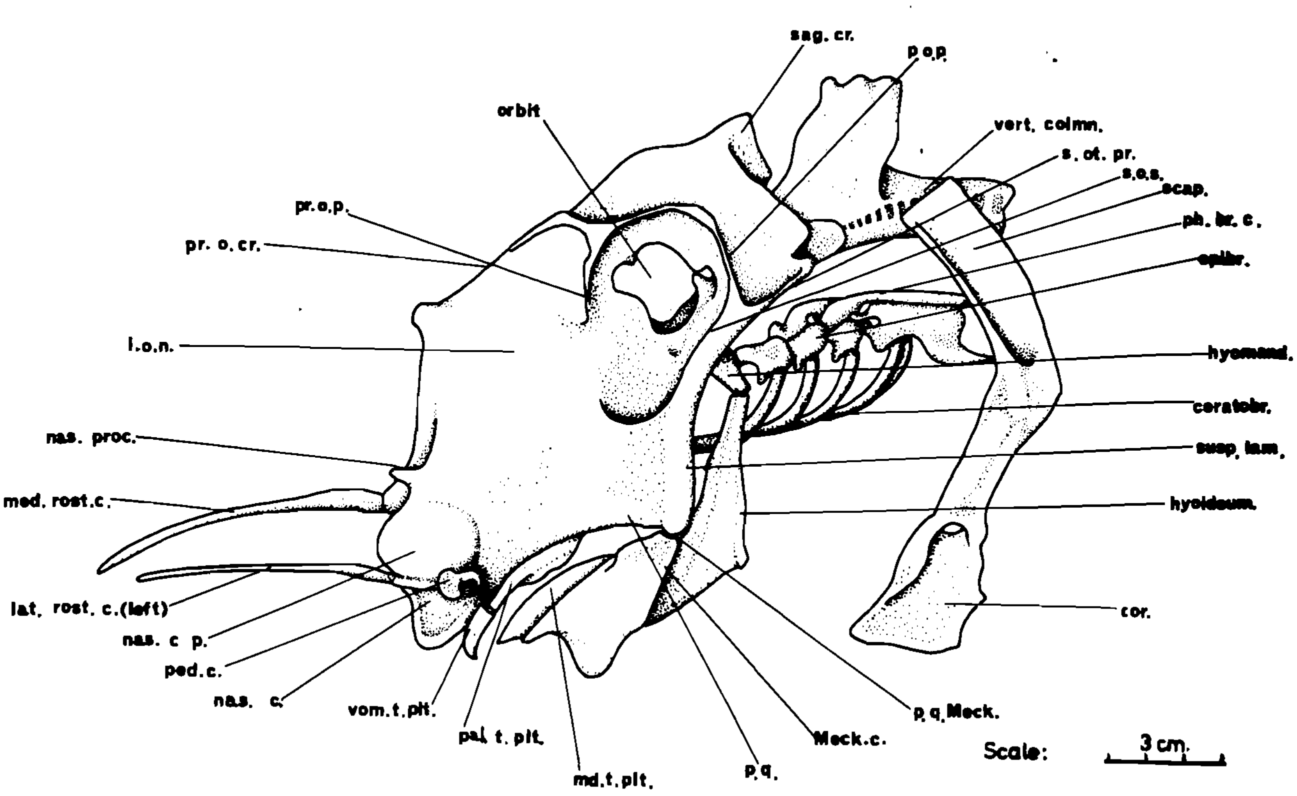

FIGURE 1
The chondrocranium, pectoral girdle, visceral and hyoid arches. With the exception of the pedicle cartilage the labial cartilages have been omitted. For abbreviations see p. 69.

The cranial musculature of several extant Chimaeroidei has been described previously. Vetter (1878) described *Chimaera monstrosa*, and Kesteven (1933) described *Callorhynchus antarcticus*. Other workers[1] have also made contributions to a description of the cranial musculature. Since the cranial anatomy of *Callorhynchus capensis* appears to be similar to that of *Callorhynchus antarcticus* the descriptive anatomy in the present paper will be brief.

The terminology used in this paper follows that of Edgeworth (1935) more closely than that of any other author. The nomenclature employed by various authors appears somewhat confused; a table of synonyms is therefore provided on page 72.

MATERIAL AND METHOD

The interpretation of the jaw mechanism is based on dissections of several fresh female *Callorhynchus*, whereas the gut contents of adults and juveniles of both sexes were examined.

THE SKELETON

It is not intended to give a complete nor detailed description of the skull and other skeletal structures as these are adequately described elsewhere.[2]

Figure 1 illustrates most of the relevant features of which a few will be briefly discussed below.

The Chondrocranium

The large orbit is situated posteriorly with the result that the palato-quadrate-meckelian articulation appears rather far forward. Anterior to the orbit the cranium is laterally compressed to form the lamina orbito-nasalis, the upper part of which forms the pre-orbital crest on which a number of the mandibular muscles originate.

Projecting anteriorly from the nasal region are three rostral cartilages. The single median rostral cartilage arises from a position antero-dorsal to the nasal capsule, and each of the two lateral rostral cartilages arises from a position ventro-lateral with respect to the nasal capsule of that side. The arrangement of the rostral cartilages in holocephalans is the reverse of that in the euselachians where the median cartilage is ventral to the paired cartilages.

The palato-quadrate is completely fused to the chondrocranium and the vomerine and palatine toothplates are joined to the ventral surface of the palato-quadrate. The lateral cutting edges of the palatine toothplates shave closely past those of the mandibular toothplates during jaw closure. The mandibular toothplates are joined to the upper surface of Meckel's cartilages. The tritorial areas of the toothplates are raised ridges of tubular dentine, surrounded by osteodentine. These prominent ridges of tubular dentine facilitate grinding and crushing (Patterson 1965).

Meckel's cartilages are strongly fused at their anterio-median symphysis to form a rather bulky lower jaw. The ventral edge of the suspensorial lamina furnishes the sole support and

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[1] See Cole (1896); Edgeworth (1935); Luther (1938).

[2] See Kesteven (1933); de Beer and Moy-Thomas (1934–5); Edgeworth (1935); Luther (1938); Holmgren (1942).

articulation for the lower jaw. This support is strengthened by fibrous connective tissue at the point of articulation.

The Hyoid Arch

A characteristic feature of the Holocephali is that the holostylic jaw suspension has left the hyoid arch complete, unmodified and in no way concerned with jaw suspension. Although somewhat larger than the branchial arches the hyoid arch has a similar shape. Articulating with the hyoid arch is the opercular plate to which are attached the opercular rays. Further opercular rays are attached to the hyoideum thereby completing the operculum. See Figure 11.

The Branchial Arches

In the Holocephali the branchial arches are crowded beneath the neurocranium. This is a feature which the holocephalans and arthrodires share, but which is sharply contrasted in the acanthodians and euselachians in which the branchial arches lie behind the neurocranium. Patterson (1965) is of the opinion that the presence of an operculum in Holocephali may be correlated with the anteriorly placed branchial arches.

The cartilaginous elements of the branchial arches are similar to those of selachians in both arrangement and structure.

The Pectoral Girdle

The pectoral girdle is similar to that of selachians except that it lies relatively far forward due to the anterior position of the branchial arches.

The Labial Cartilages

The cutaneous labial folds are supported by the labial cartilages and together they form movable lips. In the Callorhynchidae there are five pairs of upper labial cartilages and a single pair of lower cartilages. The nasal cartilages are not included as labial cartilages herein.

Holmgren (1942) found that the labial cartilages develop within ligamentous tissue. As chondrification proceeds, so the ligamentous tissue disappears.

The Cartilages of the Upper Lip (Figs. 3, 4, 5A, 7)

The entire upper labial complex articulates with the skull via the pedicle cartilage (Fig. 1). The pedicle cartilage carries the prelabial cartilage on its medio-dorsal border, the premaxillary cartilage on its antero ventral border, and the superior maxillary cartilage on its posterior border. The inferior maxillary cartilage is firmly attached to the posterior rim of the superior maxillary cartilage. It should thus be clear that the pedicle cartilage carries the entire upper labial complex. Rotation of the pedicle cartilage antero-laterally downwards moves the entire labial complex laterally away from the chondrocranium. Conversely the labial complex is brought medially inwards when the pedicle cartilage is rotated in the reverse direction.

The Cartilages of the Lower Lip (Figs. 3, 4, 5, 7)

On the outside of each Meckel's cartilage is a large flattened accessory premandibular cartilage which forms the support for the lower lip. The right and left cartilages are joined to one another

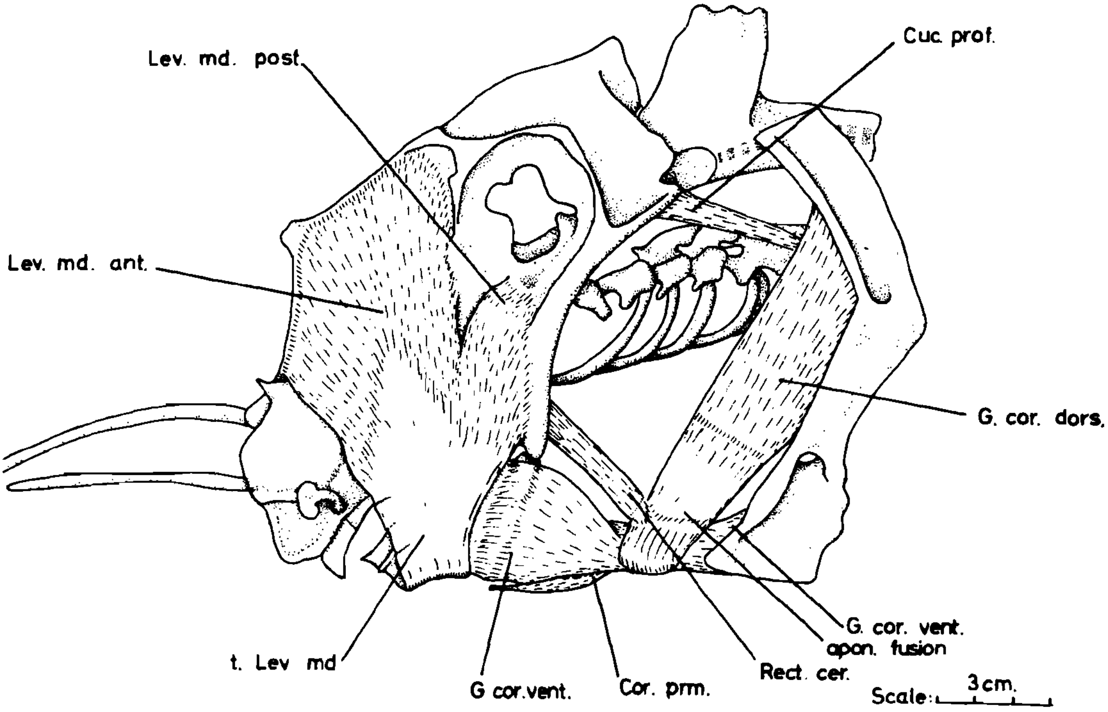

FIGURE 2
The levator mandibulae; the hypobranchial musculature and the cucullaris profundus. The insertions of the rectus cervicis and cucullaris are not shown. For abbreviations see p. 69.

anteriorly by a narrow, but strong band of connective tissue and overlying musculature.

The terminology is derived from Edgeworth (1935), who believes that the large premandibular cartilages of *Chimaera* have been reduced and lost in *Callorhynchus*, and the accessory premandibular cartilages retained and enlarged.

THE MANDIBULAR AND LABIAL MUSCULATURE

The Mandibular Muscles

According to Edgeworth (1935) the mandibular muscle plate in the early embryo is below the Gasserian ganglion and behind the eye. During development this muscle plate migrates forward to lie in front of the Gasserian ganglion, and below the eye. It then separates into the masticatory muscle plate and the intermandibularis. Apparently the muscles for the upper labial cartilages develop later.

The mandibular muscles are innervated by the Vth cranial nerve, some nerve fibres passing forwards and downwards via the ramus maxillaris (V2) and others via the ramus mandibulars (V3).

The Masticatory Muscle Plate (Fig. 2)

The levatores mandibulae* anterior and posterior are formed from the masticatory muscle plate. The anterior and posterior heads of the levator mandibulae are separated from one another by the ramus mandibularis of the trigeminal nerve which passes between their origins.

The levator mandibulae anterior arises broadly from the dorso-lateral surface of the cranium. Its origin extends from the nasal capsule, along the pre-orbital crest to the fascia of the pre-orbital process. The bulk of this muscle lies against the lamina orbito-nasalis. The posterior head is considerably smaller than the anterior, and it arises from the dorsal surface of the sub-ocular shelf and from the antero-dorsal aspect of the suspensorial lamina.

Both the anterior and posterior levatores mandibulae muscles insert upon Meckel's cartilage by means of broad tendons. These tendons become indistinguishable from one another as they pass ventrally to join the tendons from the opposite side. Together these tendons form a powerful sling around the lower jaw.

Contraction of the levator mandibulae results in a forceful closure of the jaw. The anterior head of the levator mandibulae provides the antero-vertical component, whereas the component of the posterior head would be slightly backward of vertical.

The anterior head of the levator mandibulae is innervated by a deep branch of the ramus maxillaris of the trigeminal nerve. In addition both the anterior and posterior levatores mandibulae are innervated by twigs of the ramus mandibularis of the trigeminal nerve which stem from the main nerve trunk as it passes between the two muscle components.

The Labial Complex (Figs. 3, 4, 5, 6 and 7)

In the closed position the skin linking and enveloping the three maxillary cartilages is thrown into folds (cutaneous labial folds), (Fig. 4a). When the premaxillary cartilage has been rotated forwards into the open position the skin between the cartilages becomes stretched to form a taut "skirt" around the mouth (Fig. 4b). This "skirt" is completed anteriorly by the premaxillary cartilage and the tough sub-rostral connective tissue. Posteriorly the cutaneous labial fold (a.prm.lab.fd) which links the accessory premandibular cartilage and the inferior maxillary cartilage closes the "skirt".

The Musculature of the Labial Complex

With the exception of the intermandibular muscle which develops from the embryonic mandibular muscle plate, all the muscles of the labial complex separate off from the external surface of the anterior levator mandibulae (Edgeworth 1935). In the adult the labial muscles are completely separate from the levator mandibulae, and they lie external to it.

The three muscles responsible for moving the labial cartilages into the closed position have

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* Kesteven (1933) named this muscle system the Adductor mandibulae, because he regards these muscles to be completely homologous with the adductor mandibulae of other fishes. Edgeworth (1935) considered that the muscle plate had closer homologies with the levator mandibulae of the Dipnoi. As Edgeworth is more generally accepted, and because Kesteven's nomenclature is considered rather unorthodox (Gregory 1959, p. 95) the name levator mandibulae is preferred.

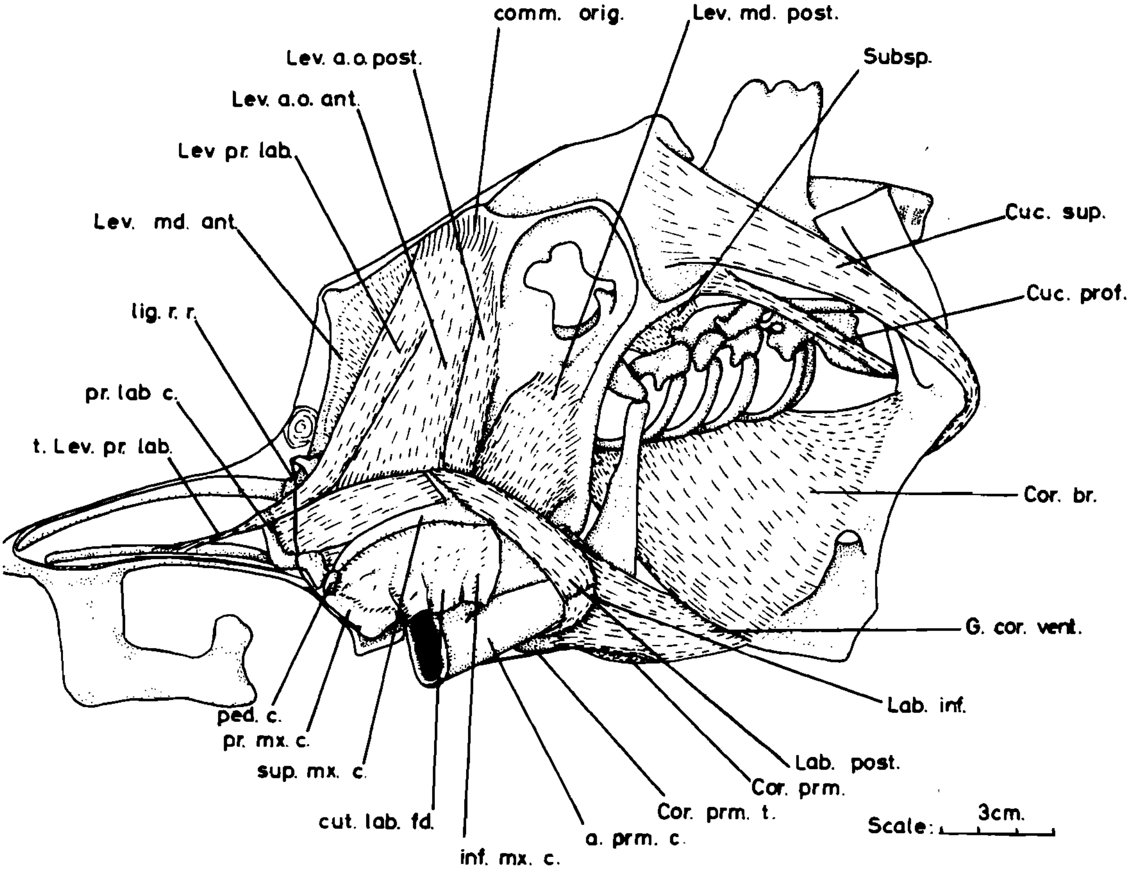

FIGURE 3
The labial musculature; the labial "skirt"; the coraco-branchiales; the cucullaris and sub-spinalis muscles. For abbreviations see p. 69.

a common tendinous origin,* which extends from the pre-orbital process to the pre-orbital crest. From their origin the three muscles pass ventro-rostrally to their respective insertions (Fig. 3).

The most anterior of the three muscles is the levator cartilaginis prelabialis which runs anteriorly downwards to the ligamentum radicis rostri (see below), beneath which it turns sharply forwards, then passes over the dorsal aspect of the prelabial cartilage to insert upon the lateral rostral cartilage. As the muscle passes over the prelabial cartilage several of its ventral fibres insert upon the cartilage. (Figs. 3 and 5a).

* Although in the majority of the specimens dissected the three muscles shared a common tendinous origin, a few specimens had separate origins.

Kesteven (1933) found that in *Callorhynchus antarcticus* the final insertion of the levator cartilaginis prelabialis was upon the "lateral ligament of the rostrum". In *C. capensis* the "lateral rostral ligament" is absent and the insertion is upon the lateral rostral cartilage.

Apparently the levator cartilaginis prelabialis inserts only upon the prelabial cartilage in *Chimaera*. (Vetter 1878; Edgeworth 1935; Luther 1938). In *Callorhynchus capensis* the muscle inserts upon both the prelabial cartilage and upon the lateral rostral cartilage.

The levator cartilaginis prelabialis is innervated by twigs of the ramus maxillaris of the trigeminal nerve (V2).

The ligamentum radicis rostri arises from the nasal process and runs ventrally to pass over the levator cartilaginis prelabialis and the prelabial cartilage, and then it dives into the subrostral connective tissue medially beneath the prelabial cartilage. In the subrostral tissue the ligament gives rise to two components. One component continues downwards to insert antero-laterally upon the premaxillary cartilage (premaxillary component). The other component passes medially beneath the rostrum as a broad band to join the ligament from the opposite side (subrostral band, Fig. 6).

The levator anguli oris anterior is the second muscle in this series. It runs parallel to the previous muscle, but it inserts upon the upper border of the superior maxillary cartilage and upon the premaxillary cartilage (Fig. 5a).

Holmgren (1942) found that part of this muscle in *Callorhynchus antarcticus* passed through a "canal" in the dorsal process of the superior maxillary cartilage. He found the insertions to be (*a*) upon the superior maxillary cartilage and (*b*) upon the inferior maxillary cartilage. His findings do not appear to hold true for all the *Callorhynchidae* as this "canal" is not present in *Callorhynchus capensis*, nor does the levator anguli oris anterior insert upon the inferior maxillary cartilage. Kesteven (1933) did not give the precise insertions of this muscle.

This muscle is innervated by twigs from the ramus maxillaris of the trigeminal nerve (V2).

The third muscle in this series is the levator anguli oris posterior which originates from the preorbital process, and inserts upon the fronto-dorsal edge of the accessory premandibular cartilage. A slip from this muscle inserts upon the inner aspect of the inferior maxillary cartilage (Fig. 5a).

The levator anguli oris posterior is innervated by twigs of the ramus maxillaris and also by twigs from the ramus mandibularis of the trigeminal nerve (V2 and V3).

External to the muscles which close the labial complex are the horizontally oriented muscles which open the labial "skirt" (Figs. 3 and 5b).

The musculus labialis anterior runs from the posterior edge of the upper arm of the prelabial cartilage to the dorsal edge of the superior maxillary cartilage. From Edgeworth's (1935) descriptions it appears as though this muscle developed from the external surface of the levator mandibulae anterior. This is of interest since the first three labial muscles described, which also arise from the levator mandibulae anterior, are concerned with closing the labial complex, whereas the labialis anterior opens the complex. Hence two sets of muscles which are derived from the same embryonic muscle-plate apparently close and open labia respectively, with no apparent alterations to the nervous system. As in the previous three muscles, the labialis anterior is also innervated by the trigeminal nerve.

The labialis posterior and the labialis inferior represent the intermandibularis which separated from the embryonic mandibular plate earlier than the other labial musculature (Edgeworth 1935).

The labialis posterior runs from the hind edge of the dorsal process of the superior maxillary cartilage to the caudal edge of the accessory premandibular cartilage. The labialis inferior runs from a midventral origin on the mandible in a latero-dorsal and caudal direction to the posterio-ventral edge of the accessory premandibular cartilage.

Both of the intermandibularis muscles are innervated by the trigeminal nerve (V3) and by the external mandibular branch of the ramus hyomandibularis of the facial nerve. The latter innervation suggests that the intermandibularis muscles have contributions from the hyoid musculature.

The mechanisms of the labial complex

From a consideration of the anatomy of the muscles and from manipulation in freshly killed animals the following deductions are made:

A. Opening

During the opening of the labial "skirt" the muscles responsible for the closing the labial complex would of necessity be relaxed, or in the process of relaxing.

Contraction of the labialis anterior muscle pulls the superior maxillary cartilage forwards and anteriorly downwards in such a manner as to transmit the force of its movement to the pedicle cartilage (Fig. 7). Consequently the pedicle cartilage pivots downwards and forwards, and as a result tends to push the premaxillary cartilage downwards. However, concurrent with the increased downward force of the pedicle cartilage upon the proximal end of the premaxillary cartilage, there is an increased upward force exerted by the ligamentum radicis rostri upon the antero-distal end of the premaxillary cartilage (Figs. 5a and b). The result of these two concurrent forces is a forward rotation of the distal end of the premaxillary cartilage (Figs. 5a, 5b and 7).

As the pedicle cartilage is pushed forwards it also moves laterally away from the cranium (Fig. 7). Since all the upper labial cartilages are carried by the pedicle cartilage, they too would be moved laterally away from the cranium. However the sub-rostral connective tissue and sub-rostral ligamentous band (Fig. 6) restrict the anterior proximal edge of the premaxillary cartilage from moving sideways. Consequently only the posterior distal border can be moved away from the cranium. The posterior edge is therefore swivelled forwards.

The premaxillary cartilage is thus rotated forwards and upwards and swivelled laterally outwards by the contraction of the labialis anterior, thereby extending the labial skirt (Fig. 4b).

The prelabial cartilage is relatively firmly held in position, however the labialis anterior does depress and rotate the prelabial cartilage to a certain extent. The dorsal "toe" of the prelabial cartilage is moved caudally while the ventral "heel" is rotated rostrally. The effect of this is twofold. Firstly, the toe is connected to the lateral rostral cartilage by means of the tendinous end of the levator cartilaginis prelabialis. Contraction of the labialis anterior therefore results in a slight elevation of the rostrum thus holding the rostral flap away from the mouth. The second function is a reinforcement of the pressure of the superior maxillary

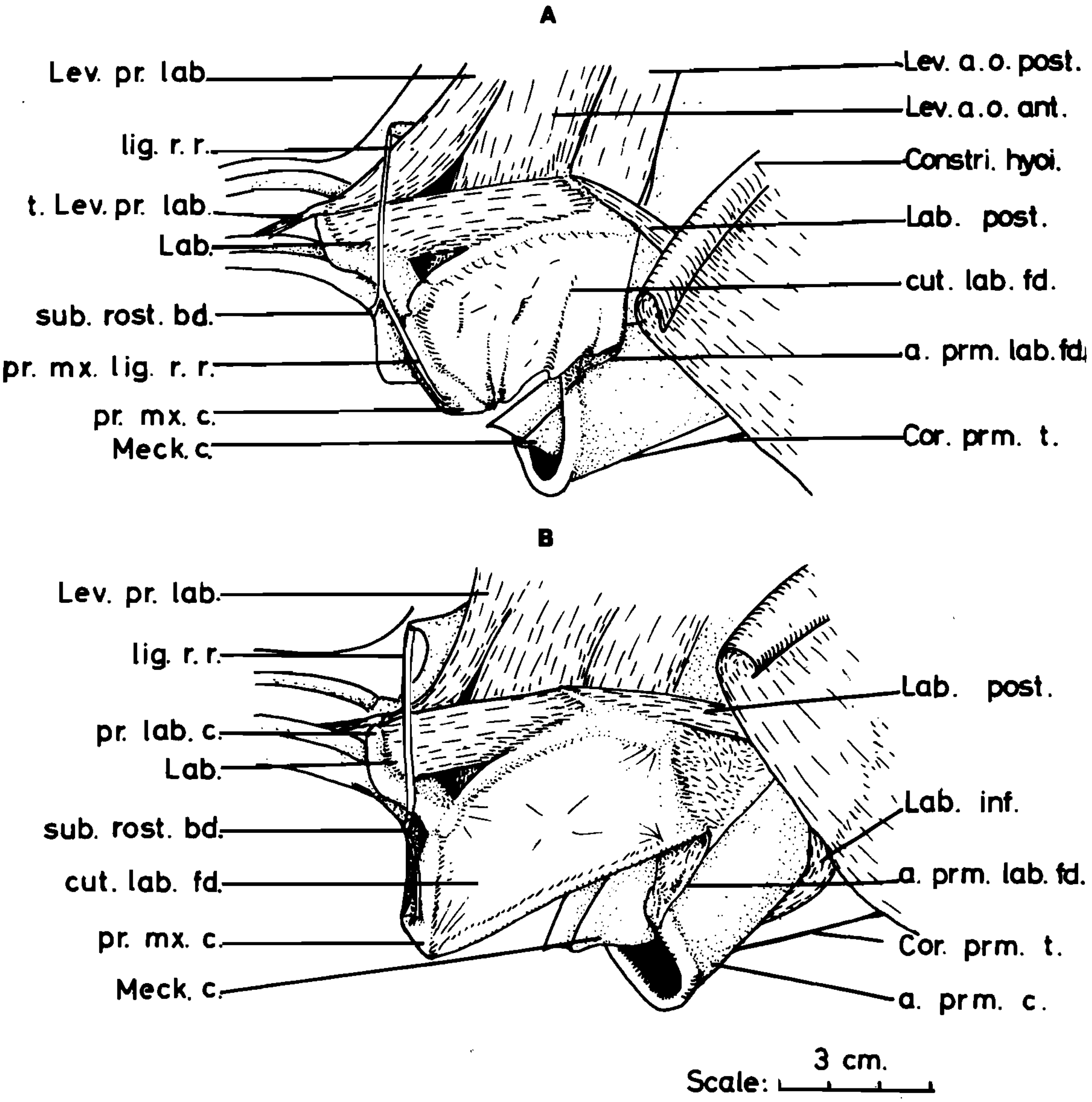

FIGURE 4

4A. The labial "skirt" in the closed position. 4B. The labial "skirt" in the open position. The relative positions of the labial muscles and the ligamentum radicis rostri are shown. For abbreviations see p. 69.

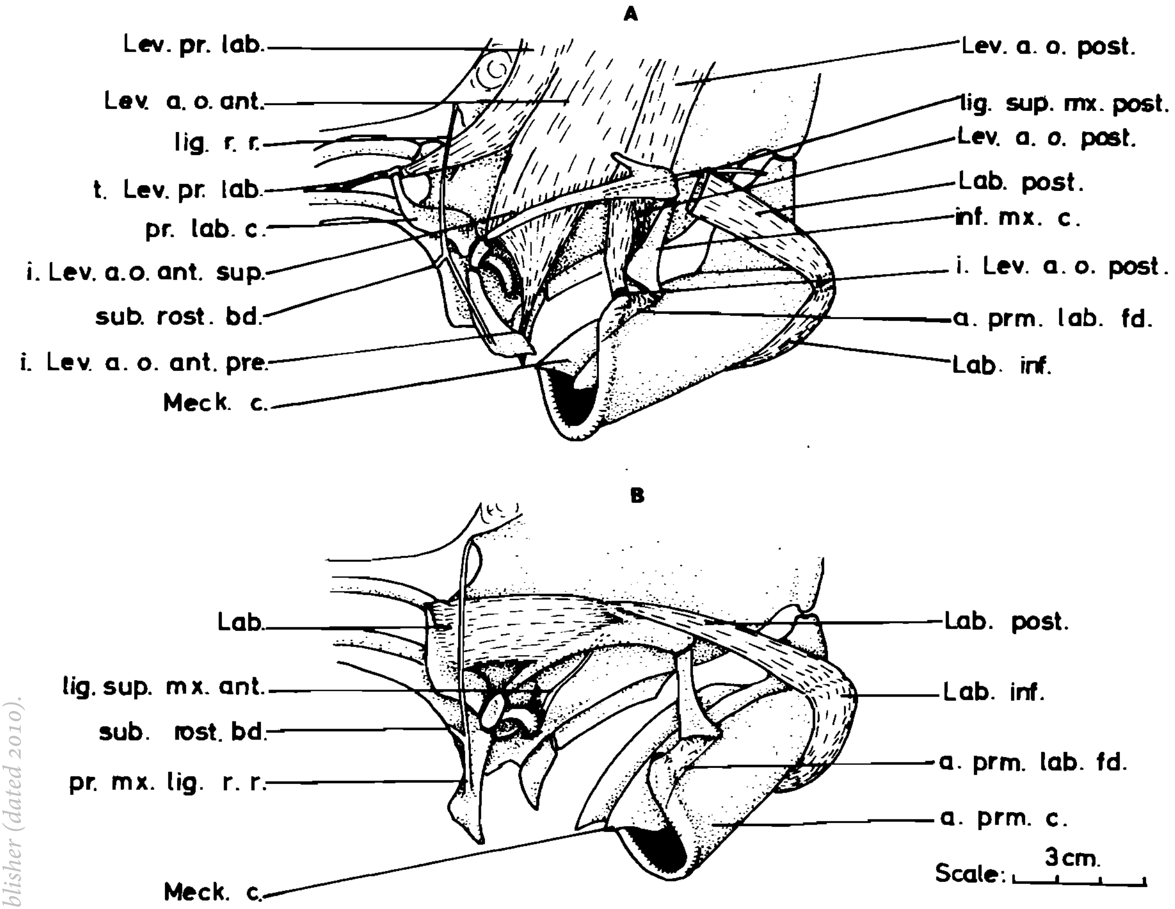

FIGURE 5

5A. The insertions of the vertically oriented labial muscles, and the position of the ligamentum superioris maxillaris posterior are illustrated in the closed position. 5B. The labialis muscles and ligamentum superioris maxillaris anterior are illustrated in the open position. For abbreviations see p. 69.

cartilage upon the pedicle and premaxillary cartilages, because the heel of the prelabial cartilage pushes the pedicle and premaxillary cartilages downwards.

The upper end of the inferior maxillary cartilage is pulled forwards and outwards by tension on the labial folds due to the movements of the premaxillary cartilage. Furthermore the ventrocaudal movement of the accessory premandibular cartilage (to be discussed below) further increases the tension on the labial "skirt" by pulling the lower end of the inferior maxillary cartilage backwards consequently increasing the diameter of the "skirt" (Figs. 5a, 5b and 7).

The overall effect of the contraction of the labialis anterior is to open the labial skirt by

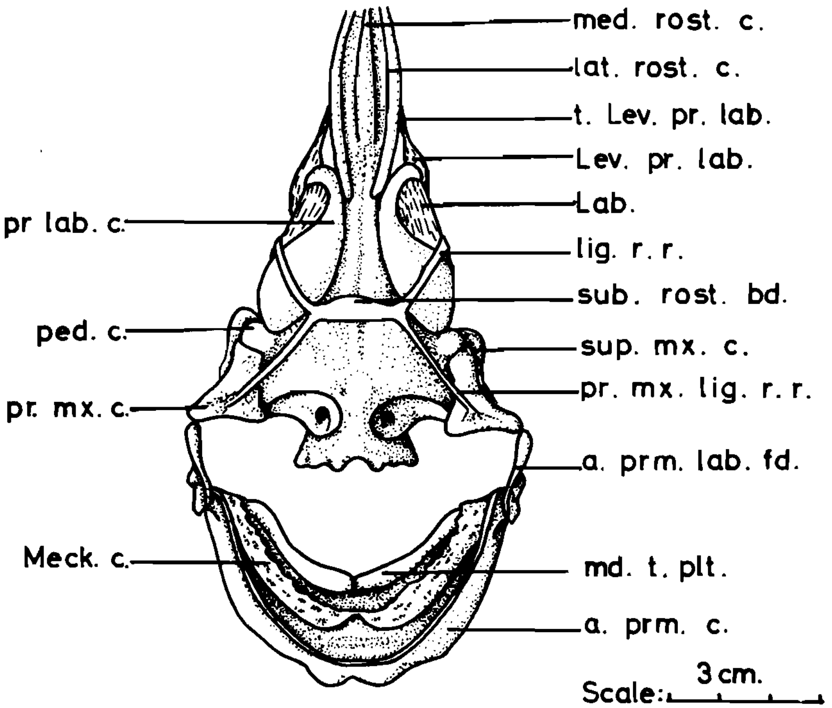

FIGURE 6
The sub-rostral band and the ligamentum radicis rostri are illustrated in antero-ventral aspect. The sub-rostral connective tissue has been removed. For abbreviations see p. 69.

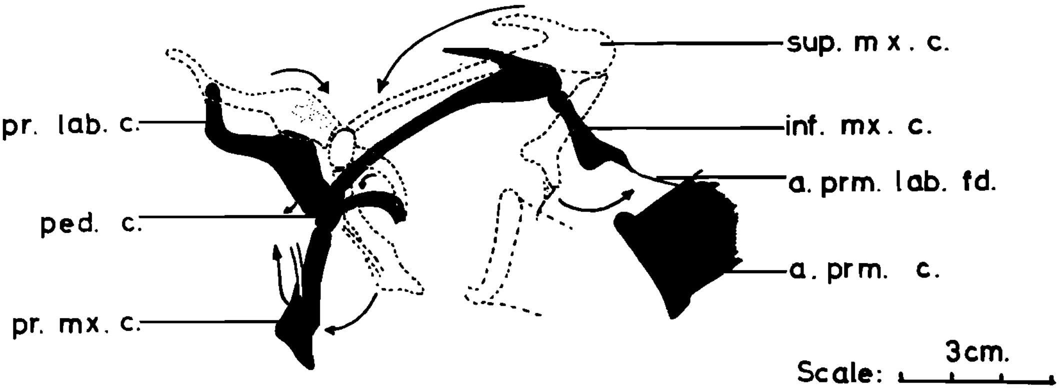

FIGURE 7
The relative positions of the labial cartilages in closed (dotted) and open (blackened) positions. The arrows indicate the movements of the cartilages from the closed to the open position. For abbreviations see p. 69.

moving those cartilages attached to the pedicle cartilage forwards. This movement is controlled and limited by the ligamenta superiores maxillares anterior and posterior; stretching forwards and backwards from the superior maxillary cartilage (Fig. 5a, b).

The labialis posterior pulls the posterior rim of the accessory premandibular cartilage forwards and upwards. Simultaneously the coraco-premandibularis (see hypobranchial muscles below) would pull the lower lip caudally (Figs. 4, 5 and 7). These two muscles rotate the accessory premandibular cartilage into the open position, whereas the labialis inferior pulls the accessory premandibular cartilage downwards so that the lower lip protrudes when in the open position. Furthermore the labialis inferior pulls the inferior edges of the caudal region of the accessory premandibular cartilages medially inwards in a similar manner to the intermandibularis (proper) of other fish (Fig. 8).

B. Closing

Closure of the labial complex involves movement in the reverse direction. The accessory premandibular cartilages are lifted into the closed position by the levator anguli oris posterior. They are guided by the overlying constrictor hyoideus and velum. (The velum is a muscular-cutaneous flap which lies external to the labial complex, see Figs. 9 and 10.) The slip of the levator anguli oris posterior retracts the inferior maxillary cartilage.

Contraction of the levator anguli oris anterior lifts the superior maxillary cartilage upwards and caudally, and swings the premaxillary cartilage into the closed position. The retro-movement of the superior maxillary cartilages rotates the pedicle cartilage inwards so that it comes to lie flush against the nasal capsule. Consequently the entire labial complex is brought in towards the cranium.

The levator cartilaginis prelabialis lifts the prelabial cartilage into its closed position and elevates the rostrum. Since the cutaneous rostral flap (Fig. 3) is sufficiently long to be caught in the mouth during food manipulation it is essential that the rostrum remains elevated throughout the duration of feeding. For this reason the muscles associated with both extension and retraction (labialis anterior and levator cartilaginous prelabialis respectively) have the additional function of holding the rostrum away from the mouth. The principal function of these muscles is nonetheless considered to be manipulation of the labial cartilages.

Although there is considerable independence of jaw and labial cartilages, the movement of Meckel's cartilage does depress or elevate the labial cartilages to a certain extent, because connective tissue links the upper and lower labial cartilages to the lower jaw. Furthermore the accessory premandibular cartilages are also joined to Meckel's cartilages by the labialis inferior muscle.

THE EPIBRANCHIAL AND HYPOBRANCHIAL MUSCULATURE

During embryological development several of the anterior myotomes grow forward into the head (Edgeworth 1935). These muscles are considered to be "intrusive elements into the head", thereby implying that there was a stage in vertebrate phylogeny when they were absent from the head. These muscles have retained their spinal innervation as they are innervated by the plexus cervicalis, which is formed from two or more spinal nerves.

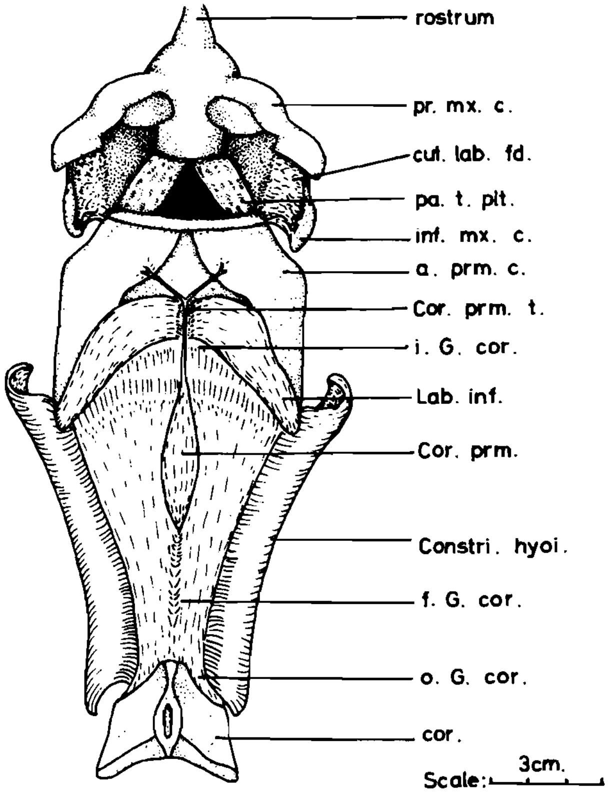

FIGURE 8
Ventral aspect of the origins and insertions of the genio-coracoidei and coraco-premandibularis.
For abbreviations see p. 69.

The Epibranchial Spinal Muscles

The subspinalis runs backwards and inwards from its origin on the ventral surface of the neurocranium to insert upon the first and second pharyngobranchial cartilages (Fig. 3). The interpharyngobranchial* muscles link the second and third pharyngobranchial elements. These myotomes give rise to the genio-coracoideus and the rectus cervicis found in the adult (Fig. 2).

The Hypobranchial Spinal Muscles

The genio-coracoideus is a large muscle system consisting of five portions, namely paired ventral sections, paired dorsal sections and an unpaired ventral section. The last is called the coraco-premandibular. It lies between the paired ventral sections, emerging in front (Fig. 2).

The paired ventral genio-coracoidei originate from the coracoid portion of the pectoral girdle (Figs. 2 and 8). They run forward as a fused muscle, but separate anteriorly to pass on either side of the coraco-premandibularis to insert broadly upon the caudal edges of Meckel's cartilages by means of a tendon.

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* Not illustrated.

The dorsal pair of genio-coracoidei (Figs. 2 and 8) arise from the scapular region of the pectoral girdle. They pass forwards and downwards to join with the ventral genio-coracoidei posterior to the emergence of the coraco-premandibularis. The junction between the dorsal and ventral portions is achieved by extensive mingling of muscle fibres, and is substantially strengthened by a strong aponeurotic sheath which envelops and binds both sets of muscles (Fig. 2).

The coraco-premandibularis, which arises from within the ventral genio-coracoidei, emerges in midline as a slender muscle (Figs. 2 and 8). It then runs forwards forming a thin tendon which passes mid-ventrally beneath Meckel's cartilages. The tendon bifurcates and inserts upon the fronto-lateral edges of each of the accessory pre-mandibular cartilages (Fig. 8).

The rectus cervicis (sternohyoid of many authors) is composed of two fused muscle bands. They originate together as a flat tendon from the aponeurotic tissue which binds the dorsal and ventral genio-coracoidei (Fig. 2), and insert upon the basihyal.

The hypobranchial spinal muscles open the mouth and increase the buccal cavity. The genio-coracoidei depress the mandible. The ventral pair of muscles supply the caudally directed vector, whereas the dorsal pair provide the component of lift.

The rectus cervicis pulls the basihyal and enflanking skin of the buccal floor downwards, thereby enlarging the buccal cavity. Since the rectus cervicis probably contracts in conjunction with the coraco-branchiales (to be discussed below) it would also participate in the enlargement of the branchial cavity.

The coraco-premandibularis pulls the accessory premandibular cartilages ventrally backwards, thereby moving the lower lip into the open position.

It is probable that the hypobranchial muscles would function in phase with one another, since they are all innervated by the N. hypobranchialis S. plexus cervicalis from which motor roots to the rectus cervicis and genio-coracoideus arise.

THE BRANCHIAL MUSCLES

The Coraco-branchialis

Kesteven (1933) found that the "coraco-branchialis" of *Callorhynchus antarcticus* "is composed of five slips, each of which is easily divisible throughout its length from the others". This was not found to hold true for *Callorhynchus capensis*, in which the coraco-branchiales arise as a strongly developed muscular sheet from the most lateral rim of the pectoral girdle. The muscular sheet then passes anteriorly upwards to insert separately upon the ventral ends of the branchial bars (Fig. 3).

Edgeworth (1935) found that the five coraco-branchiales of the Holocephali develop separately, but during the later stages of embryological development the five muscle bands grow together to form a sheet that remains separate only at their insertions. It appears as though the coraco-branchiales of *Callorhynchus capensis* conform with Edgeworth's embryological studies, whereas the same muscles in *Callorhynchus antarcticus* do not. It would be of interest to have Kesteven's (1933) findings confirmed.

Contraction of the coraco-branchiales causes the ventral part of the branchial skeleton to move downwards and backwards, thereby expanding the buccal and branchial cavities.

The N. hypobranchialis S. plexus cervicalis arches forwards under the most caudal coraco-branchialis as a single stem and gives off motor roots to the coraco-branchiales. The hypobranchial spinal muscles are innervated by more anterior roots of the N. hypobranchialis S. plexus cervicalis than the coraco-branchialis.

The Cucullaris

During the embryonic development of *Callorhynchus* the cucullaris separates into two muscles —the cucullaris profundus and the cucullaris superficialis (Edgeworth 1935).

The cucullaris* superficialis originates from the postorbital process as a broad muscle band which narrows as it passes backwards and downwards to insert upon the lower, outer edge of the scapula. A tendinous slip from the insertion of the muscle continues downwards to insert upon the coracoid.

Contraction of this muscle pulls the entire pectoral girdle upwards and forwards, closer to the opercular cavity. Vetter (1878) suggests that this movement would assist in the closure of the opercular cleft of *Chimaera*. The function of the cucullaris superficialis in *Callorhynchus capensis* may be the same as in *Chimaera.*

The cucullaris* profundus originates ventro-medially from the subotic process and inserts upon the postero-dorsal edge of the third pharyngo-branchial cartilage. It lifts the third pharyngo-branchial cartilage upwards and forwards, thereby co-operating with the subspinalis (which lifts the first and second pharyngo-branchial cartilages) to lift and expand the branchial arches.

The cucullaris profundus is innervated by the X3 branch of the vagus which also innervates the 4th branchial arch. The cucullaris superficialis is innervated by the most caudal root of the vagus (X4).

THE HYOID MUSCULATURE

The constrictor hyoideus is an extensive but thin muscular sheet, which lies immediately beneath the skin of the opercular and rostral regions. Ventrally it is divided into a deep and a superficial layer.

The embryonic hyoid muscle plate gives rise to the constrictor hyoideus which spreads over the operculum and downwards to meet the muscular sheet from the opposite side (Edgeworth 1935). The mid-ventral junction forms a raphé which becomes attached to the genio-coracoidei above it.

Only in the later stages of development does the constrictor hyoideus extend forwards onto the rostrum (Edgeworth 1935).

Although the constrictor hyoideus is essentially a single muscle it does have several parts which differ in function. These portions were allotted names, for convenience, by Kesteven (1933). These names will be used in this paper.

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* Edgeworth (1935) writes that both cucullaris muscles "in *Callorhynchus* arise from the lateral edge of the palato-quadrate." This statement appears to be erroneous, being inconsistent with his diagrams which appear to be correct.

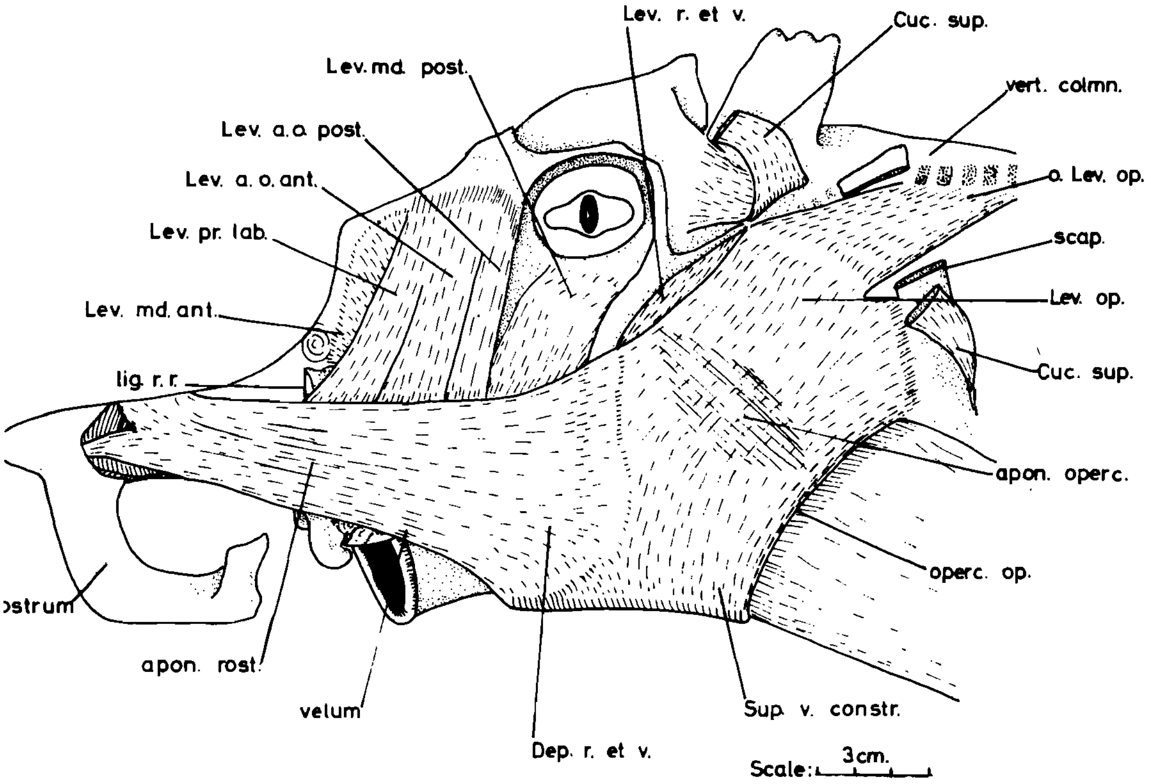

FIGURE 9
The components of the constrictor hyoideus. The cucullaris superficialis is reflected in order to show the insertion of the levator operculi upon the vertebral column. For abbreviations see p. 69.

Levator operculi (Kesteven)
The levator operculi originates as a tendinous sheet from the vertebral column medial to the pectoral girdle, and also from the scapula (Fig. 9). The muscle then appears on the surface from between the two sections of the cucullaris muscle and runs anteriorly downwards to insert widely upon the fascia of the operculum.

Kesteven suggested that the origin of this muscle in *Callorhynchus antarcticus* was the superficial fascia of the pectoral muscles.

Contraction of the levator operculi lifts the operculum posterodorsally upwards, as the name implies.

Superficial Ventral Constrictor (Kesteven)
This portion of the constrictor hyoideus originates from the mid-ventral raphé. It then passes round from the ventral surface to insert upon the ventero-lateral border of the aponeurotic tissue which covers the operculum. Muscle fibres from the superficial ventral constrictor cross the opercular aponeurosis to join fibres from the levator operculi. The muscular connections

linking these two portions are especially thick along the posterior rim of the operculum.

Contraction of the superficial ventral constrictor would pull the operculum downwards. Simultaneous contraction of this muscle and the levator operculi would result in a constriction of the opercular cavity, and probably an elevation of the floor of the branchial cavity.

Depressor Rostri et Veli (Kesteven)

This muscle originates from both the anterior part of the median raphé, where it is mingled with the origin of the superficial ventral constrictor, and from the fascia of the anterior border of the operculum. From its wide origin the muscle runs rostrally to roof over, and insert dorsolaterally upon, the rostrum (Fig. 9). As the muscle traverses the rostrum it develops a broad superficial aponeurotic band (Fig. 9 and 10).

The depressor rostri et veli can depress the rostrum and pull the velum downwards provided the muscles on both sides of the rostrum contract simultaneously. If they contracted independently of one another they would probably move the rostrum sideways. Luther (1938) expresses the opinion, "Der ,Depressor rostri' dürfte kaum die im Namen ausgedrückte Funktion haben, sondern wohl eher den Mundboden heben helfen". However it is unlikely that the depressor rostri elevates the floor of the mouth to any great extent, since it passes beneath the angle of the jaw which cannot be lifted. Its primary function therefore does appear to be one of constriction of the branchial cavity and depression of the rostrum.

Anterior deep constrictor (Kesteven)

This muscle originates from the median raphé where it is anterior to and continuous with the superficial ventral constrictor. The fibres separate from those of the superficial constrictor and travel with them for a short distance before inserting deeply upon the velum and operculum.

This muscle assists with the constriction of the branchial cavity and may also pull the velum, and hence the rostrum, downwards.

Posterior deep constrictor (Kesteven)

This portion of the constrictor hyoideus arises deeply from the median longitudinal raphé behind Meckel's cartilages. At its origin the posterior deep constrictor is fused with the superficial constrictor, however as it passes upwards it separates from the superficial constrictor to insert upon the deep fascia of the opercular cover. This muscle also constricts the branchial chamber.

The primary function of the superficial musculature is to constrict the opercular cavity. It appears as though this constriction might also depress the jaw and elevate the buccal floor since the constrictors would tend to lift the genio-coracoideus to which they are attached. This is to be discussed more fully below.

Levator rostri et veli (*Depressor mandibulae superior of Kesteven*)

Beneath the antero-dorsal part of the levator operculi is a thickened part of the hyoid musculature which appears to have been omitted from all but Kesteven's descriptions of the Holocephali. Kesteven (1933) called this muscle the "depressor mandibulae superior".

This muscle originates from the ventral surface of the sub-otic and sub-ocular process.

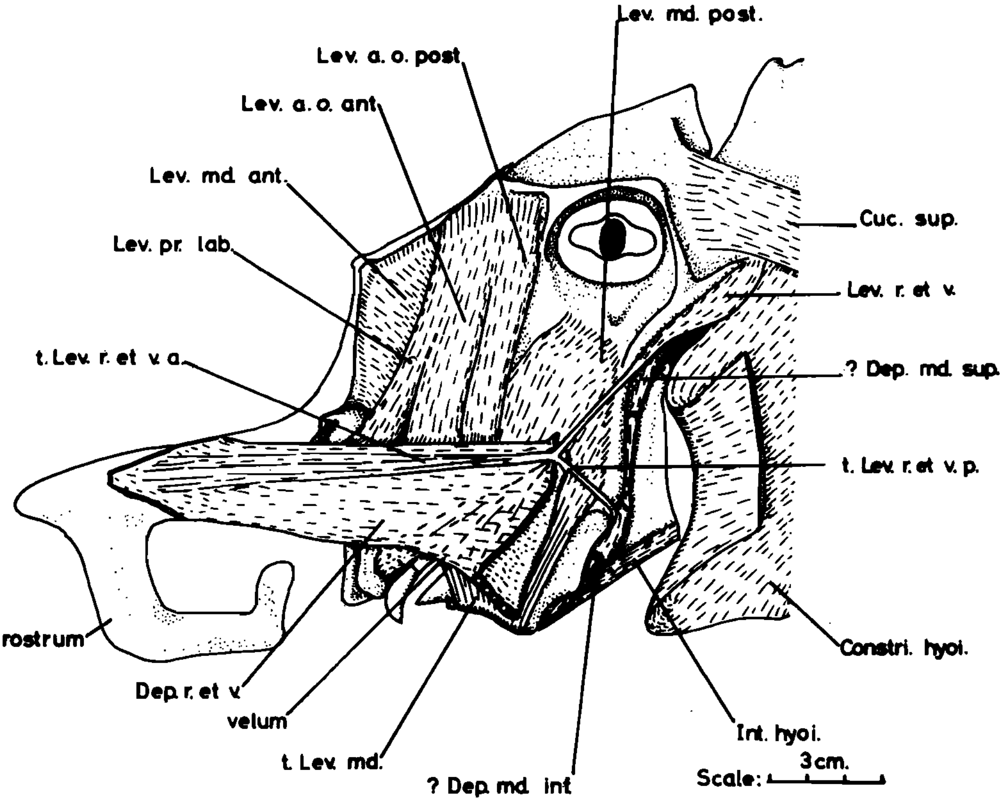

FIGURE 10
The posterior components of the constrictor hyoideus are reflected to illustrate the deeper components of Kesteven's ?depressor mandibulae, and also the t.Lev. r. et v.p. The superficial aponeurotic tissue of the Dep. r. et v. has been removed to illustrate the t. Lev. r. et v.a. The accessory premanidibular cartilages are not illustrated in order to show the ?Dep. md. inf. For abbreviations see p. 69.

It then runs forwards and downwards to dive under the superficial constrictor sheet. As the muscle passes over the suspensorial lamina it narrows into a tendon which continues for a short distance and then bifurcates to give rise to an anterior and posterior component. The posterior component passes obliquely backwards and downwards to attach to the postero-dorsal edge of Meckel's cartilage. The anterior component passes forwards onto the rostrum, where it widens to insert upon the superficial rostral aponeurotic tissue and the velum (Figs. 9 and 10).

This muscle could not possibly depress the mandible as Kesteven's nomenclature implies. The posterior tendon is attached to Meckel's cartilage in order to provide a ventro-caudal vector component for the muscle. A simultaneous contraction of the muscle on both sides of the head would elevate the rostrum and velum. The suggested name for this muscle is the levator rostri et veli.

Kesteven found a second part to his "depressor mandibulae superior" which lies ventro-

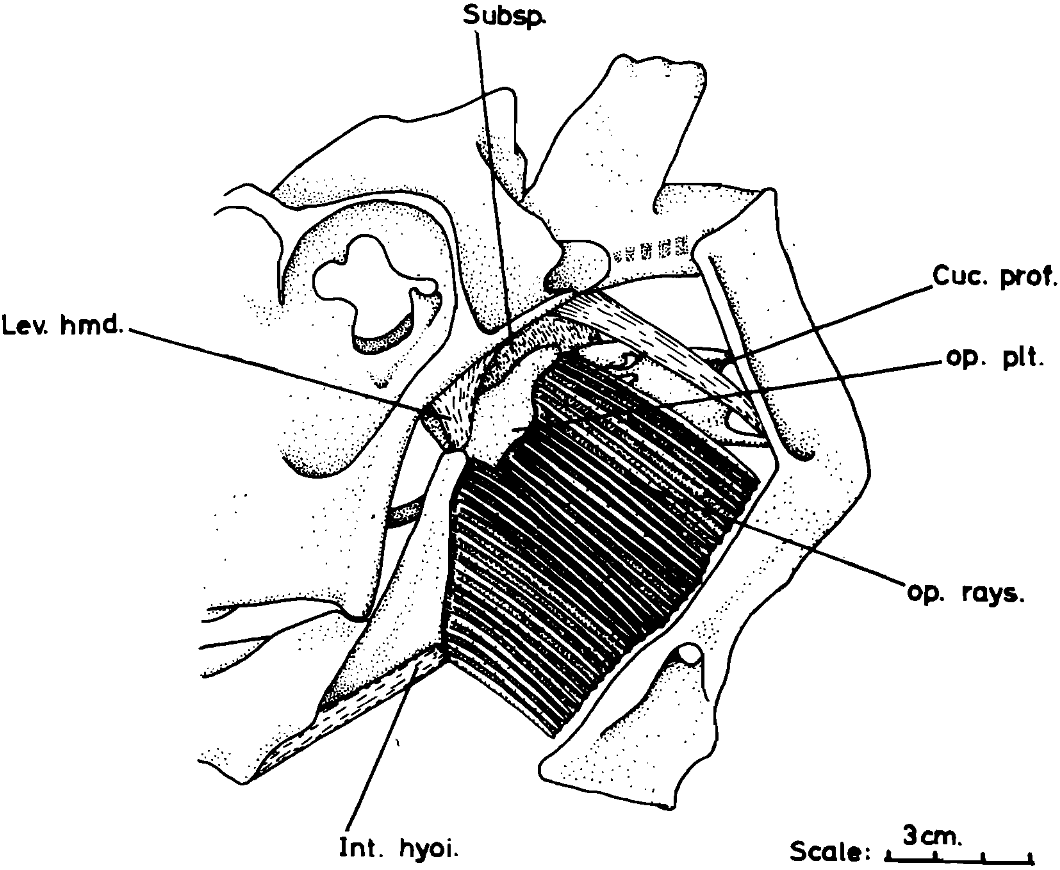

FIGURE 11
An illustration of the levator hyomandibular, interhyoideus, subspinalis and opercular rays. For abbreviations see p. 69.

medial to the portion already described. This second part passes downwards behind the suspensorial lamina and in front of the hyoid arch, becoming fibrous and narrower as it proceeds. Prior to reaching Meckel's cartilage the muscle widens again to form a third belly (inferior part of the superior mandibular depressor—Kesteven) which inserts by means of a tendon to the median inferior edge of Meckel's cartilage. Kesteven was of the opinion that this muscle would assist the genio-coracoidei to depress the mandible. It is extremely difficult to ascertain whether this muscle is a separate entity from the constrictor hyoideus. There is no definite demarcation between the two and at least some of the fibres are continuous. It is concluded that the so-called deep section of the depressor mandibulae superior and its inferior part are not separate entities in *Callorhynchus capensis*, but represent anterior thickenings of the levator operculi and the anterior deep constrictor respectively. In this case the anterior deep constrictor might have the additional function of partially depressing the mandible. This, however, seems unlikely since the mouth would probably be closed during the exhalation (Hughes and Ballintijn 1965). Meckel's cartilages could serve as an additional origin for the constrictor sheet.

The Levator Hyomandibulae and the Interhyoideus

These two muscles separate from the hyoid sheet fairly early during development. "The levator hyomandibulae separates from the upper part of its anterior edge and the interhyoideus from its lower part" (Edgeworth 1935).

The levator hyomandibulae in the adult *Callorhynchus capensis* originates from the ventral edge of the sub-ocular shelf and runs downwards and outwards to insert upon the hyomandibular cartilage (Fig. 11). Vetter (1878) found that the insertion of this muscle in *Chimaera* extended onto the pharyngobranchial cartilage. This is not so in *Callorhynchus capensis*.

The function of this muscle acting alone is to pull the hyoid arch and attached gill rays upwards and inwards thereby constricting the opercular chamber.

The interhyoideus stretches from the outer ventral edge of the hyoideum to the inferior caudal symphysis of Meckel's cartilages and to the median raphé just behind the lower jaw (Figs. 10 and 11). The closed jaw during exhalation would act as the origin for the muscle which, acting alone, pulls the hyoideum medially inwards and downwards.

It appears as though the levator hyomandibulae and interhyoideus acting together can pull the hyoid arch medially inwards. Observations of live animals showed a respiratory pulsation in the hyoid region. It is possible that the muscles of the hyoid arch initiate the exhalent respiratory rhythm.

The constrictor hyoideus is innervated principally by the VIIth (hyomandibular) nerve; however, Kesteven (1933) also found twigs from the trigeminal.

DISCUSSION OF MODES AND MECHANISMS OF FEEDING

Graham (1939) found that the diet of *Callorhynchus milii* Bory was composed of pelecypod and prosobranch molluscs, Crustacea and fish. The gut contents of *Callorhynchus capensis* were found to be similar to its New Zealand counterpart. Table 1 lists the food organisms found in a total of 134 fish.

Gorman (1963) is of the opinion that the Callorhynchidae are benthonic feeders. This opinion is supported by the fact that the mouths of the Callorhynchidae are ventrally orientated, which is considered by Alexander (1967) to be an adaptation to bottom feeding. Further substantiation is provided by Table 1, which shows that the prey species are benthonic sand- or mud-dwellers; also quantities of sand are frequently found in the gut.

The fish probably swim close to the floor of the sea having chosen a sandy substrate in which to forage. As the eyes are postero-dorsally situated they would not be of much use in prey detection; it is therefore suggested that the rostral flap would be drawn over the sand to locate the prey, since it is well innervated, and probably highly sensory. Lateral movement could be effected by unilateral contraction of the rostral muscles. It is probable that the velum would be lifted and held out of the way of the mouth by the levator rostri et veli throughout the duration of feeding.

On location of a large, buried prey species, the labial cartilages would be moved into the

TABLE 1

GUT CONTENTS AND THE HABITAT OF PREY SPECIES

Identified and Partially Identified Prey Species	*Depth at Which Caught (metres)*	*Habitat of Prey Species*
CRUSTACEA		
Brachyura		
× *Ovalipes punctatus*	0–15	Sandy (beach) substrate
× *Hymenosoma orbiculare*	0–15	Sandy (beach) substrate
× *Goniplax rhomboides*	80–100	Green mud
Anomura		
× *Diogenes extricatus*	0–15	Sandy (beach) substrate
(Molluscan shells in which *Diogenes* were found are not included as a possible dietary supplement.)		
Isopoda		
Exosphaeroma truncatitelson	0–15	Sandy (beach) substrate
Exosphaeroma spp.	0–15	Sandy (beach) substrate
?Zuzaria furcifer	0–15	Sandy (beach) substrate
× *Paridotea spp.*	0–15	Sandy (beach) substrate
Amphipoda		
Perioculoides ?longimanus	0–15	Sandy (beach) substrate
Mysidacea		
Gastrosaccus psammodytes	0–15	Sandy (beach) substrate
Cumacea		
Bodotria ?lata	0–15	Sandy (beach) substrate
Iphinoe spp.	0–15	Sandy (beach) substrate
MOLLUSCA		
Pelecypoda		
× *Pitaria hebraea*	0–15	Sandy (beach) substrate
× *Donax serra*	0–15	Sandy (beach) substrate
× *Schizodesma spengleri*	0–15	Sandy (beach) substrate
Choromytilus meridionalis	0–15	Sandy (beach) substrate
Gastropoda		
× *Bullia laevissima*	0–15	Sandy (beach) substrate
× *Bullia digitalis*	0–15	
× *Nassa analogica*	80–100	Green mud
ANNELIDA		
Polychaeta		
?Sabella penicillus	80–100	Green mud

KEY × Found only in gut of specimens exceeding 35 cm in length.

NOTE: The majority of the crabs, bivalves and prosobranchs bury themselves in the sand-surface, whereas the smaller Crustacea live between or on top of the sand-grains. The information regarding the habitat of the prey species was obtained from the University of Cape Town Ecological Records; and from Day (1969) and Jones (1959).

open position. The most important of these are the accessory premandibular cartilages, which combine to form a shovel-like lower lip that could be driven into the sand in order to dislodge the prey. The propulsive force of the swimming fish would dig the lower lip into the sand, and minor manipulations could be made. Once the prey is dislodged it may then be scooped up with small quantities of sand by the lower lip, and manipulated back into the mouth by the entire labial complex. The shell of the prey species would be crushed between the tooth-plates by contraction of the levator mandibulae, and the fragments plus quantities of sand then swallowed. Large unburied prey species would merely be scooped off the bottom and then crushed.

It is of interest to note that, in common with several other bottom-feeding fish, *Callorhynchus* may obtain additional movement of the jaw, and an increased gape by moving the head vertically backwards on the vertebral column.

Although both the intermandibularis muscles (labialis posterior and inferior) and the labialis anterior are concerned with opening the mouth it is nonetheless suggested that the intermandibularis appeared earlier in the evolutionary history of the Callorhynchidae than the labialis anterior. This is supported by the sequence of embryological development (see page 52. In addition the intermandibularis muscles appear to be more basically concerned with food manipulation and prey capture than does the labialis anterior which merely manipulates food fragments. It thus seems possible that the evolution of the upper labial complex followed a step behind the development of the lower labial system, and merely added refinements to the basic mechanisms of prey capture and feeding implemented by the lower labial system.

It appears as though *Callorhynchus* may employ a different mode of feeding for the small Crustacea which live on the sand surface, since these species are found to be uncrushed and unaccompanied by sand in the gut. This indicates that the small prey species are not scooped out from within the sand.

Since the small Crustacea are often the same size and colour as the surrounding sand-grains (Jones 1959), it is unlikely that they would be detected when stationary. Probably the rostral flap disturbs the prey which would swim upwards. It would come into the visual fields of the fish and consequently be taken into the mouth by one or all the methods outlined by Alexander (1967) for teleosts, namely

(*a*) by swimming up to and engulfing the prey;
(*b*) by sucking the prey into the mouth and
(*c*) by a combination of engulfing and sucking.

The parallel between the teleosts and Holocephali is probably acceptable since both groups possess an operculum. For the capture of small prey species the labial "skirt" would be opened, and the bucco-branchial cavities rapidly expanded to create a negative pressure. This would involve a sudden contraction of the rectus cervicis (which depresses the basihyal and enflanking buccal floor) and the coraco-branchiales. The genio-coracoideus would then open the mouth to allow water to rush through to equalise pressures.

It is probable that the hypaxial muscles would sharply retract the pectoral girdle thereby reinforcing the action of the coraco-branchiales and genio-coracoideus.

As the hypo- and epibranchial muscles are all innervated by the N. hypobranchialis S.

plexus cervicalis, it is probable that these muscles act either simultaneously or in a rhythm which begins anteriorly and passes backwards. Hughes and Ballintijn (1965) found this sort of rhythm in the branchial muscles of the dogfish. In *Callorhynchus* one might suggest that the rectus cervicis would contract first followed by the branchial muscles and the genio-coracoidei.

It is likely that the cucullaris superficialis and the cucullaris profundus would contract in phase. From the position and insertion of the superficialis it could pull the dorsal end of the pectoral girdle upwards and forwards while the hypaxial muscles pull the ventral end backwards, thus co-operating with the cucullaris profundus to expand the branchial chamber. This is a slightly different interpretation from that of Vetter (1878) for *Chimaera*. The negative pressure within the branchial cavity would draw the soft opercular flap inwards, thus sealing the opercular cleft to prevent water from entering posteriorly.

During normal respiration a sudden violent expansion of the orobranchial cavities would be unnecessary. Hughes and Ballintijn (1965) found very little electrical activity in the hypobranchial muscles of the dogfish during normal respiration. However they could evoke electrical activity in these muscles if they forcefully moved the jaw or induced hyperventilation. They therefore suggested that the elasticity of the branchial skeleton was sufficient to expand the branchial cavity for normal respiratory movements. These findings might be applicable to *Callorhynchus*.

Matthes (1963) described the forceful expulsion of a jet of water through the mouths of certain teleosts as "blowing" or "spitting". Possibly *Callorhynchus* could exhibit "blowing" and this process could be utilised in feeding as follows. Once the branchial cavity is filled with water the hypaxial muscles would relax and the cucullaris superficialis, genio-coracoidei and possibly the coraco-branchiales would draw the whole of the pectoral girdle forwards decreasing the opercular aperture. The small mouth would remain open to permit the powerful contraction of the constrictor sheet to force a jet of water outwards through it. This jet could be utilised for either disturbing small prey species or to "blow" sand away from buried prey species, such as *Ovalipas* or *Donax*, to expose them.

During normal expiration one anticipates that the mouth would be closed and that the contraction of the constrictor hyoideus would force exhalent water out via the opercular cleft.

Patterson (1965) considers that the Holocephali became dorso-ventrally deepened and laterally compressed in order to become mid-water feeders, thus avoiding the increasing competition from the emerging durophagous, benthonic skates and rays. Patterson's view may hold for other families of Chimaeroidei, but the Callorhynchidae are undoubtedly benthonic feeders. Furthermore the Callorhynchidae appear to be the only chimaeroid family which possess enlarged accessory premandibular cartilages (premandibular cartilages of Holmgren, 1942) and separate pedicle cartilages. It is therefore possible that the Callorhynchidae returned to a shallow-water benthonic existence as active predators capable of digging their prey from the substrate, thus managing to compete successfully with the skates and rays which are unable to dig out their prey. Presumably the other Chimaeroidei have remained mid-water feeders and differ also in their mode of feeding.

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SUMMARY

The muscles concerned with manipulating the jaw and labial complex are described and their probable functions discussed. The accessory premandibular cartilage is considered to be utilised for digging the large prey species from the substrate, whereas the upper labial complex manipulates the food back into the small mouth. The labial "skirt" as a whole enlarges the buccal opening.

The muscles responsible for closing the labial skirt, and the problem of the elevation of the rostrum during feeding, are discussed.

Contraction of the levator mandibulae crushes the large prey species between the tooth plates.

Small prey species are considered to be sucked into the mouth and swallowed whole. The sucking mechanism, which would involve a rapid contraction of the hypo- and epibranchial muscles, the hypaxial muscles and probably both cucullaris components, is discussed.

It is possible that prey location may be dependent upon the innervated rostral flap assisted by a "blowing" mechanism. It is not known whether the large eyes are used for prey location.

It is suggested that the velum is held away from the mouth by the levator rostri et veli during feeding.

EXPLANATION OF ABBREVIATIONS

a. prm. c.	accessory premandibular cartilage
a. prm. lab. fd.	cutaneous labial fold linking the Accessory premandibular cartilage to the inferior maxillary cartilage.
apon. fusion	aponeurotic fusion of Rectus cervicis and the dorsal and ventral Genio-coracoidei
apon. operc.	aponeurotic tissue overlying the operculum
apon. ros.	aponeurotic tissue of the Musculus depressor rostri et veli
ceratobr.	ceratobranchial elements
cor.	coracoid

Cor. br.	Musculus Coraco-branchiales
Cor. prm.	Musculus Coraco-premandibularis
Constri. hyoi.	The Constrictor hyoideus muscle sheet
comm. orig.	The common tendinous origin of the Labial muscles
Cor. prm. t.	Tendon of the Coraco-premandibular
Cuc. prof.	Cucullaris profundus
Cuc. sup.	Cucullaris superficialis
cut. lab. fd.	cutaneous labial folds
? Dep. md. inf.	inferior belly of Kesteven's Depressor mandibulae
? Dep. md. sup.	superior belly of Kesteven's Depressor mandibulae
Dep. r. et v.	Depressor rostri et veli
epibr.	epibranchial elements
f. G. cor.	fusion of ventral Genio-coracoidei
G. cor. dors.	dorsal pair of Genio-coracoidei
G. cor. vent.	ventral pair of Genio-coracoidei
hyomand	hyomandibular
inf. mx. c.	inferior maxillary cartilage
Int. hyoi.	Musculus Interhyoideus
i. G. cor.	insertion of Genio-coracoidei
i. Lev. a.o. ant. pre.	insertion of Levator anguli oris anterior on pre-maxillary cartilage
i. Lev. a.o. ant. sup.	insertion of Levator anguli oris anterior on superior maxillary cartilage
i. Lev. a.o. post.	insertion of Levator anguli oris posterior on lower lip
i. Lev. a.o. post. inf.	insertion of Levator anguli oris posterior on inferior maxillary cartilage
i. Lev. op. p.	insertion of Levator operculi on pectoral girdle
Lab.	Labialis anterior
Lab. inf.	Musculus labialis inferior
Lab. post.	Musculus labialis posterior
lat. rost. c.	lateral rostral cartilage
l.o.n.	lamina orbito-nasalis
Lev. a.o. ant.	Levator anguli oris anterior
Lev. a.o. post.	Levator anguli oris posterior
Lev. a.o. post. slp.	slip of Levator anguli oris posterior
Lev. hmd.	Levator hyomandibular
Lev. md. ant.	Anterior head of Levator mandibulae
Lev. md. post.	Posterior head of Levator mandibulae
Lev. op.	Levator operculi
Lev. pr. lab.	Levator cartilaginis prelabialis
Lev. r. et v.	Levator rostri et veli
lig. r. r.	ligamentum radicis rostri

lig. sup. mx. ant.	ligamentum superioris maxillaris anterior
lig. sup. mx. post.	ligamentum superioris maxillaris posterior
md. t. plt.	mandibular toothplate
Meck. c.	Meckel's cartilages
med. rost. c.	median rostral cartilage
nas. cap.	nasal capsule
nas. c.	nasal cartilage
nas. proc.	nasal process
operc. op.	opercular opening
op. plt.	opercular plate
op. rays.	opercular rays
orb.	orbit
o. Lev. op.	origin of Levator operculi upon the vertebral column
o. G. cor.	origin of ventral Genio-coracoidei
pa. t. plt.	palatine tooth plate
p.q.	palato-quadrate
p.q.-Meck. a.	palato-quadrate Meckelian articulation and mandibular suspension
ped. c.	pedicle cartilage
ph. br. c.	pharyngo-branchial cartilages
p.o.p.	post-orbital process
pr. lab. c.	prelabial cartilage
pr. mx. c.	premaxillary cartilage
pr. mx. lig. r.r.	premaxillary component of the ligamentum radicis rostri
pr. o. cr.	pre-orbital crest
pr. o.p.	pre-orbital process
Rect. cer.	Rectus cervicis
sag. cr.	sagittal crest
scap.	scapular
s.o.s.	sub-ocular shelf
s.ot.pr.	sub-otic process
sub. rost. bd.	sub-rostral band of Ligamentum radicis rostri
Subsp.	Subspinalis
sup. mx. c.	superior maxillary cartilage
Sup. v. constr.	Superficial ventral constrictor
susp. lam.	suspensorial lamina
t. Lev. md.	tendinous insertion of sling of Levatores mandibulae
t. Lev. pr. lab.	tendon of levator prelabialis
t. Lev. r. et v. a.	anterior tendon of Levator rostri et veli
t. Lev. r. et v. p.	posterior tendon of Levator rostri et veli
vert. colmn.	vertebral column
vom. t. plt.	vomerine tooth-plate

APPENDIX: LIST OF SYNONYMS

Nomenclature used herein	*Used by Edgeworth* (1935)	*Used by Kesteven* (1933)	*Used by Vetter* (1878)	*Used by Luther* (1938)
MASTICATORY MUSCLES				
Levator mandibulae anterior	Levator mandibulae anterior	Adductor mandibulae anterior	Adductor mandibulae or levator labii superior	Praeorbitalis
Levator mandibulae posterior	Levator mandibulae posterior	Adductor mandibulae posterior	Adductor mandibulae posterior	Adductor mandibulae
Levator cartilaginis prelabialis	Levator cartiliganis prelabialis	Levator rostri		Levator cartilaginis praelabialis
Levator anguli oris anterior	Levator anguli oris anterior	Levator labii superioris	Levator anguli oris (1)	Levator anguli oris anterior
Levator anguli oris posterior	Levator anguli oris posterior	Levator labii inferioris	Levator anguli oris (ii)	Levator anguli oris posterior
Labialis anterior	Labialis	Protractor labii superior	Labialis anterior	Labialis anterior
Labialis posterior	Labialis posterior	Protractor superior labii inferioris	Labialis posterior	Labialis posterior
Labialis inferior	Labialis inferior	Protractor inferior labii inferioris	Labialis inferior	Labialis inferior
EPIBRANCHIAL SPINAL MUSCLES				
Subspinalis	Subspinalis		Protractor arcus branchialis	
Interpharyingobranchiales	Interpharyngobranchiales	?Dorsal oblique interacual		
HYPOBRANCHIAL SPINAL MUSCLES				
Genio-coracoideus	Genio-coracoideus	Coraco-mandibularis	Coraco-mandibularis	Coraco-mandibularis
Coraco-premandibularis	Genio-coracoideus	Coraco-premandibularis	Coraco-mandibularis	
Rectus cervicis	Rectus cervicis	Coraco-hyoideus	Coraco-hyoideus	
Coraco-branchiales	Coraco-branchiales	Coraco-branchialis (x5)	Coraco-branchiales	
CUCULLARIS MUSCLES				
Cucullaris superficialis	Cucullaris superficialis	Cucullaris	Trapezius superficialis	Transversus superficialis
Cucullaris profundus	Cucullaris profundus		Trapezius profundus	Transversus profundus
HYOID MUSCLES (Superficial musculature)				
Levator hyomandibular	Levator hyomandibular		Hyoideus superior	Hyoideus superior
Interhyoideus	Interhyoideus	Genio-hyoideus	Hyoideus inferior	Hyoideus inferior
Constrictor hyoideus:			The different portions of the Constrictor Hyoideus were designated different lettering and numerals by both Vetter and Luther (1938)	
Part 1. Levator operculi	Constrictor hyoideus	Levator operculi		
Part 2. Superficial ventral constrictor	Constrictor hyoideus	Superficial ventral constrictor		
Part 3. Depressor rostri et veli	Constrictor hyoideus	Depressor rostri et veli		
Part 4. Anterior deep constrictor	Constrictor hyoideus	Anterior deep constrictor		
Part 5. Posterior deep constrictor	Constrictor hyoideus	Posterior deep constrictor		
Part 6. Levator rostri et veli	Constrictor hyoideus	?Depressor mandibulae superioris ?Depressor mandibulae inferior which has a dorsal and ventral body		

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