The Role of the Hyoid Apparatus in the Feeding Mechanism of the Coelacanth *Latimeria chalumnae*

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Previous investigators have suggested that depression of the lower jaw and the concomitant extension of the intracranial joint in the living coelacanth *Latimeria chalumnae* occurs by contraction of the coracomandibularis muscle. An alternative hypothesis is proposed in which posterodorsal hyoid movement accompanied by extension of the otico-occipital portion of the cranium on the vertebral column mediates mandibular depression. Movement of the hyoid apparatus, initiated by contraction of the sternohyoideus muscle, is transmitted to the lower jaw by the symplectic bone and by a strong ligament between the symplectic and the mandible. This hypothesis is corroborated both by a force analysis of the effect of coracomandibularis contraction which suggests that it functions to adduct the lower jaw, and by an electromyographic analysis of the homologous muscle in the primitive actinopterygians *Amia* and *Polypterus*.

THE feeding mechanism of the living coelacanth *Latimeria chalumnae* has been the subject of a rather extensive analysis in the last twenty years (Adamicka, 1976; Alexander, 1973; Millot and Anthony, 1958; Thomson, 1966, 1967, 1970). These investigators have analyzed the jaw in terms of a four-bar linkage model and have derived certain proposals concerning movement of the bones (especially the intracranial joint) during respiration and feeding. Thomson (1973) has described actual movements of the jaw during respiration based on movies taken of a live specimen.

The mechanics of the intracranial joint have been of the greatest interest, especially in light of possible parallels with the kinetic cranium of rhipidistian fishes. It now seems, however, that the coelacanth feeding mechanism is quite distinct from that of rhipidistians (Thomson, 1967). Bjerring (1973) suggested that the entire intracranial joint was non-homologous in the two groups and more recently Wiley (in press) has proposed that the dorsal portion of the intracranial joints in these two groups may not be homologous while the ventral part is a primitive feature of osteichthyians (Gardiner and Bartram, 1977).

In spite of these differences the jaw of *Latimeria* still occupies a position of considerable importance in any consideration of the evolution of vertebrate feeding mechanisms. A functional analysis of the coelacanth musculoskeletal system can, in addition to providing potentially testable biomechanical hypotheses, contribute greatly to our understanding of osteichthyian evolution.

A new hypothesis of the coelacanth feeding mechanism is proposed here which suggests that the hyoid apparatus is of fundamental importance in mediating both mandibular depression and extension of the intracranial joint. A similar mechanism is responsible for mandibular depression in primitive actinopterygian fishes as demonstrated by an electromyographic and cinematographic analysis of feeding in *Amia* and *Polypterus*.

LATIMERIA Feeding Mechanism

Previous hypotheses.—Millot and Anthony (1958) were the first to propose an hypothesis of jaw movements in *Latimeria*. They suggested that the only muscles acting to depress the lower jaw were the paired coracomandibularis muscles originating on the clavicle and extracleithrum and inserting on either side of the mandibular symphysis (Fig. 2A). Thomson (1967, 1970) and Trewavas (1959) have concurred with this
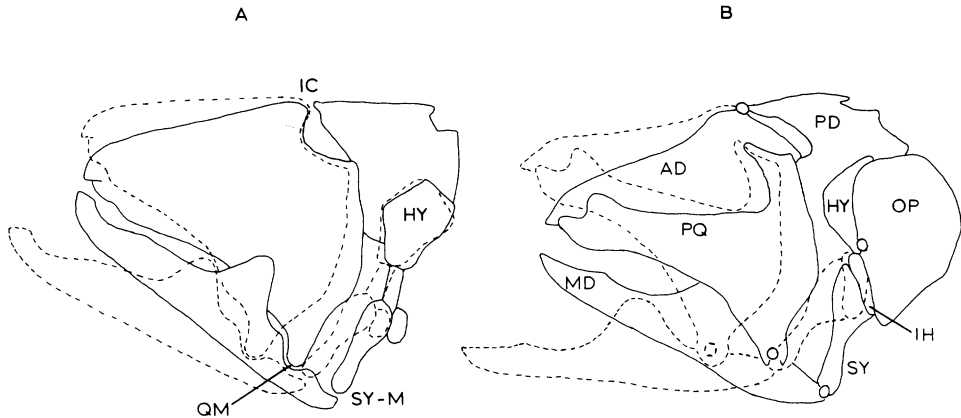
Fig. 1. A) Thomson's (1967) proposal of jaw movements in *Latimeria*. Note the anterior swing of the hyomandibular, protraction of the symplectic and interhyal, and extension of the intracranial joint. B) Alexander's (1973) proposal of *Latimeria* jaw mechanics. The hyomandibular is stationary during mouth opening and the fourth axis of the four-bar linkage mechanism is the diarthrosis between the hyomandibular and the interhyal. Solid lines indicate the position at the initial rest position. Dashed lines indicate the position at the point of maximum gape. Abbreviations: AD = anterior division of the cranium; HY = hyomandibula; IC = intracranial joint; IH = interhyal; MD = mandible; OP = operculum; PD = posterior division of the cranium; PQ = palatoquadrate; QM = quadratomandibular articulation; SY = symplectic; SY-M = symplectic-mandibular articulation.

hypothesis and further suggested that the coracomandibularis muscle is in fact the antagonist of the subcephalic muscles. Since the epaxial muscles insert only on the posterior (otico-occipital) portion of the cranium (Fig. 2A), no direct muscular mechanism acts to elevate the anterior cranial division. Thomson (1970:2) has noted that "by virtue of the mechanical arrangement of the various skull parts, the action of this muscle (the coracomandibularis [=geniocoracoideus of Thomson {1970}]) in retracting the mandibles and rotating them ventrally around the quadrate joint includes translation of the ventrally and posteriorly directed forces into a force pushing the palate and anterior portion of the braincase forward and upward."

Fig. 1 summarizes the proposals of Thomson (1967) and Alexander (1973). Thomson (1967) proposed that the jaw of *Latimeria* could be modelled essentially as a four-bar linkage system (Fig. 1A). The four key joints are 1) the intracranial joint, 2) the dorsalmost articulation of the hyomandibular with the neurocranium, 3) the articulation between the symplectic and the mandible and 4) the quadratomandibular articulation. By manipulating specimens which had not been preserved, Thomson (1966, 1970) discovered that manually depressing the lower jaw does result in elevation of the anterior cranial unit. A key feature of his proposal is the

mechanical link between lower jaw depression and intracranial joint extension. This occurs as a consequence of the four-bar linkage system. The elements of the hyoid arch are also protracted during mouth opening (Fig. 1A). As the intracranial joint is extended, it lifts the palatoquadrate anterodorsally carrying with it the quadratomandibular joint. This movement in turn carries the symplectic anterodorsally and since the ceratohyal articulates at the interhyal—symplectic junction, it too will move anteriorly.

Two additional points should be noted. Thomson (1970), based on movies of manipulations of a thawed (unpreserved) specimen, revealed a paradox regarding the length of the coracomandibularis muscle. He found that as the mouth was opened, the distance between the origin and the insertion of the coracomandibularis lengthened. He suggested that the pectoral girdle moves anteriorly as the lower jaw is depressed in order to allow the coracomandibularis to contract isometrically and open the mouth. A further feature of interest was observed by Thomson (1973). Not only was a clear correlation observed between mandibular depression and intracranial extension in movies of a respiring coelacanth, but the posterior cranial division was also found capable of moving through a 16° arc, pivoting dorsally on the ver-

tebral column. Both the length relationships of the coracomandibularis muscle and the significance of otico-occipital extension will be considered in detail below.

Alexander (1973) has elaborated on the work of Thomson and has suggested two additional features of the feeding mechanism (Fig. 1B). Alexander has redefined one of the joints in the four-bar linkage. Based on the manipulation of an unpreserved specimen the hyomandibular was found to have very limited anteroposterior mobility while the interhyal–hyomandibular articulation possessed a well developed diarthrosis (see Adamicka, 1976) allowing the interhyal–symplectic complex to pivot about a transverse axis. The four-bar linkage model remains intact with only a shift in one of the points of rotation.

Alexander (1973) further suggested that the orobranchial chamber may be expanded without opening the mouth. Since a hinge exists between the symplectic and the interhyal with an oblique axis lying roughly in the parasagittal plane (Fig. 1B) as the palatoquadrate is abducted, the mouth need not open due to adduction of the symplectic. This mechanism results in a potential decoupling of orobranchial expansion and mouth opening.

Robineau and Anthony (1973) have proposed yet another mechanism of intracranial joint extension in *Latimeria*. They suggest that the hypobranchial muscles (sternohyoideus and coracomandibularis) raise the posterior portion of the mandible and cause a "compression" of the hyoid arch elements. The force produced by hypobranchial muscle contraction is resisted by the hyoid arch and results in an anterior force transmitted to the anterior cranial division by the inferior quadratohyoid ligament connecting the quadrate to the symplectic. Depression of the mandible thus causes automatic intracranial joint extension. This proposal is similar to that of Cracraft (1968).

The role of the hyoid apparatus.—All of the above considerations of the coelacanth feeding mechanism suggest that mandibular depression occurs mainly by contraction of the coracomandibularis muscle and that the symplectic and interhyal move anterodorsally as the mouth opens. An analysis of the line of action of the coracomandibularis, however, reveals that this muscle actually should adduct the lower jaw (Fig. 2A).

Two relevant features of the coracomandib-

ularis pertain to its effect on the jaw elements. The line of action in the resting position of the jaw passes above the articulations of both the quadrate and the symplectic with the mandible (Fig. 2A). The line of action was determined both from radiographs of the head and pectoral girdle of *Latimera* and by dissection and measurement of a partially cleared and stained specimen (American Museum of Natural History, Department of Ichthyology 32949). Thus, contraction of this muscle will adduct the mandible and flex the intracranial joint. In fact, even though the line of action of the coracomandibularis passes ventral to both articulations of the mandible in the later stages of the feeding sequence (Fig. 2B, C) mandibular abduction still does not occur because of the moment arm of the coracomandibularis muscle around the intracranial and hyomandibular–interhyal joints. Contraction of the coracomandibularis at the position shown in Fig. 2C will still result in flexion of the intracranial joint and mandibular adduction. These two considerations strongly suggest that mechanically the coracomandibularis muscle cannot contribute to either mandibular depression or intracranial extension. There is, in addition, the question of how a posteroventral force applied at the mandibular symphysis could possibly be converted into an anterodorsal force at the quadratomandibular joint. These aspects of coracomandibularis action have been verified in a mechanical model of the coelacanth jaw.

Cracraft (1968) and Robineau and Anthony (1973) have suggested that a posterodorsal force applied at the symplectic (as a result of coracomandibularis contraction) will cause intracranial extension as a consequence of the resistance of hyoid elements to this force. This cannot occur both because the resisting force will be directed anteroventrally (Fig. 2A) and because the hyoid apparatus does not constitute a rigid bar (Alexander, 1973). There are two highly mobile articulations which attenuate any resisting force. Robineau and Anthony's (1973) mechanism also depends on the inferior quadratohyoid ligament (Fig. 2A) acting as a compression member and transmitting force to the anterior cranial unit against resistance.

What mechanism, then, can produce both mandibular depression and intracranial extension? I propose that an initial lateral and posterodorsal movement of symplectic mediated by contraction of the sternohyoideus exerts a posterodorsal force on the posterior aspect of
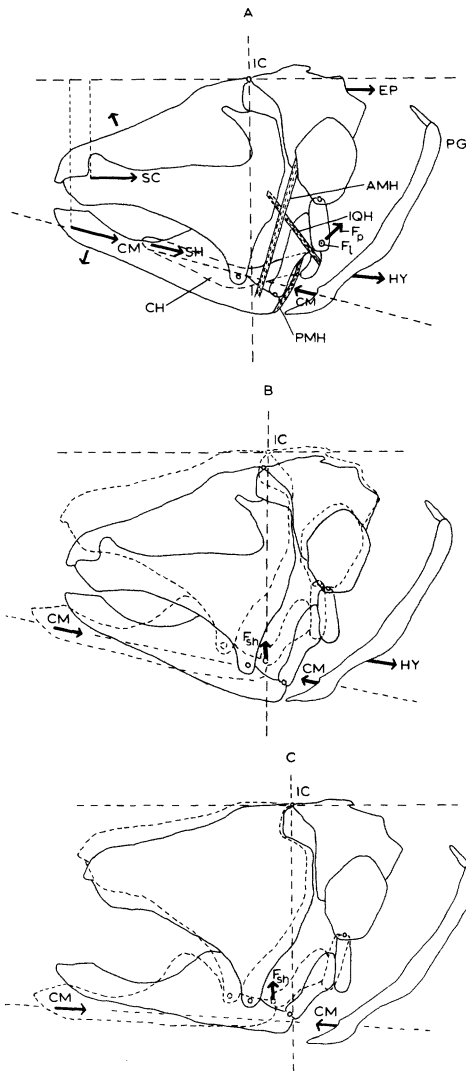
Fig. 2.   Hypothesis of *Latimeria* feeding mechanics presented here. This figure is derived from a mechanical model of the coelacanth jaw. The reader may wish to construct a model to aid in understanding the proposed movements by tracing part A onto a stiff surface and including the appropriate joints and articulations. Mobility of the symplectic–interhyal articulation should be maintained. Heavy arrows show the forces exerted by the principal muscles governing jaw movements. A) The position of the jaw elements in the initial rest state. Note that the line of action of the coracomandibularis muscle (CM) passes dorsal to both the quadratomandibular articulation and the symplectic–mandibular articulation. The sternohyoideus (SH) exerts both an anterior pull on the pectoral girdle during contraction and a posterodorsal force on the symplectic and interhyal by posterior movement of the ceratohyal. B) Initial position of the jaw

the mandible causing initial mandibular depression (Fig. 2B). Accompanying this movement is extension of the otico-occipital portion of the cranium on the vertebral column.

Specifically, this mechanism involves the following series of events (best understood with reference to Fig. 2 which has been reconstructed from a mechanical model of the coelacanth jaw) which may be divided into two phases.

In the initial rest position (Fig. 2A) the intracranial joint is flexed, the mandible adducted, and the line of action of the coracomandibularis passes dorsal to both articulations of the mandible. The first phase, represented by the transition between the solid and dashed outlines in Fig. 2B, consists of two components: mandibular depression and cranial extension. Cranial extension occurs through the action of the epaxial muscles (Fig. 2A:EP) which elevate the entire cranium. No extension of the intracranial joint occurs in this phase, elasticity of the notochord (Robineau and Anthony, 1973) resisting flexion of the intracranial joint. Extension of the entire cranium on the vertebral column in phase one also passively results in anterodorsal movements of the palatoquadrate and hyoid arch (Fig. 2B).

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elements (solid line) and their position following elevation of the posterior division of the cranium [by the epaxial muscles (EP)], retraction of the symplectic and interhyal (relative to the palatoquadrate), and lateral expansion of the symplectic and interhyal (dashed lines). At this point the symplectic–mandibular articulation is vertically aligned with the axis of the intracranial joint. C) The final stage of mouth opening. The solid lines correspond to the dashed line of B. The dashed lines represent the final position of the jaw at maximum gape. The vertical component of the force applied to the symplectic–interhyal articulation which acts at the symplectic–mandibular articulation now has passed anterior to the intracranial joint and causes extension of the joint and mandibular depression. Other abbreviations: AMH = anterior mandibulohyoid ligament; CH = ceratohyal; F_l = lateral force on the interhyal–symplectic articulation as a result of sternohyoideus contraction; F_p = posterodorsal force on the interhyal and symplectic as a result of sternohyoideus activity and rotation of the interhyal around the interhyal–hyomandibular articulation; F_{sh} = vertical component of F_p acting at the symplectic–mandibular articulation; HY = hypaxial muscles; IC = intracranial joint; IQH = inferior quadratohyoid ligament; PG = pectoral girdle; PMH = posterior mandibulohyoid ligament; SC = subcephalic muscles.

Mandibular depression, the second component of this first phase, is achieved by posterodorsal movements of the ceratohyal activated by contraction of the sternohyoideus muscle. The sternohyoideus (Fig. 2A:SH) exerts both a lateral force oriented perpendicular to the parasagittal plane on the interhyal–symplectic articulation (Alexander, 1973; Liem and Osse, 1975; Fig. 2:F_l) and a posterodorsal force on the interhyal and thus on the articulation between the symplectic and mandible (Fig. 2:F_p). This posterodorsal force results from the pivoting of the ceratohyal and interhyal around the hyomandibular–interhyal articulation in an exactly analogous way to the generation of a posterodorsal force on the retroarticular process of the lower jaw in teleosts (Fig. 3:SH, F_p). In *Latimeria*, this force is transmitted to the lower jaw by the symplectic and posterior mandibulohoid ligament and results in mandibular depression. The symplectic and interhyal are thus moved laterally and posteriorly relative to the palatoquadrate, although relative to a fixed point the whole jaw apparatus has moved anteriorly due to cranial extension by the epaxial muscles.

During this phase of jaw opening, the pectoral girdle remains stationary or may be slightly protracted due to antagonistic activity in the sternohyoideus and hypaxial muscles. Although at the end of phase one (Fig. 2B: dashed outline) the line of action of the coracomandibularis has shifted below both mandibular articulations, contraction of this muscle, as noted previously, would still result in flexion of the intracranial joint and mandibular adduction.

The second phase of mouth opening, the transition between the solid and dashed outlines in Fig. 2C, involves extension of the intracranial joint and mandibular depression. At the start of this phase, the dorsal component (F_{sh}) of the posterodorsal force (F_p) which acts at the symplectic–mandibular articulation aligns vertically with the intracranial joint (Fig. 2B). Due to extension of the entire cranium by the epaxial muscles in the first phase of jaw movement, this dorsal component comes to lie in line with the intracranial joint and as it passes anterior to it (Fig. 2C) causes intracranial extension and mandibular depression. During this phase the jaw apparatus moves further anterodorsally as the gape is widened and the interhyal–symplectic articulation continues to move posterior relative to the palatoquadrate. The further in
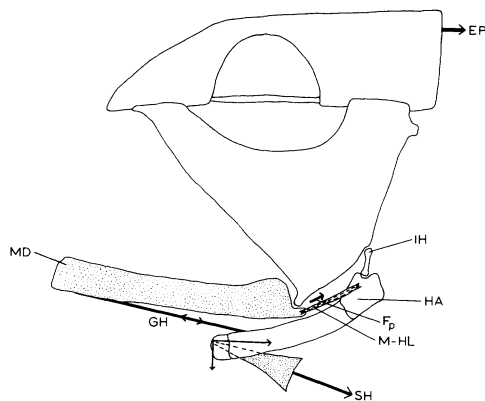

Fig. 3. Model of hyoid movement in primitive actinopterygians. From data on *Salvelinus fontinalis* (Lauder and Liem, in press). Posterior movement of the hyoid arch, initiated by contraction of the sternohyoideus muscle, causes a rotation around the interhyal–suspensorial articulation. This exerts a strong posterodorsal force on the mandibulohoid ligament causing mandibular depression. This mechanism is the only method of mandibular depression in *Lepisosteus* and *Polypterus*. Abbreviations: EP = epaxial muscles; F_p = posterodorsal force on the retroarticular process of the lower jaw resulting from contraction of the sternohyoideus muscle and posterodorsal rotation of the hyoid apparatus; GH = geniohyoideus; HA = hyoid arch; IH = interhyal; MD = mandible; M-HL = mandibulohoid ligament; SH = sternohyoideus.

crease in gape in phase two is due to a compression of the four-bar linkage system dorsally.

The sternohyoideus muscle, then, is both the antagonist of the subcephalic muscles and the prime mediator of mandibular depression. This mechanism produces a direct force acting dorsally to elevate the anterior cranial unit. Previous mechanisms generate a ventrally directed force actually resulting in intracranial flexion.

In addition to resolving the question of how the mouth is opened when the coracomandibularis muscle possesses an entirely unfavorable line of action, this hypothesis solves several other perplexing problems regarding the coelacanth feeding mechanism.

An extensive ligamentous network interconnects the hyomandibular, palatoquadrate, and mandible in *Latimeria* (Millot and Anthony, 1958). Thomson (1967) proposed that these ligaments, especially those from the hyomandibular and symplectic to the mandible (respectively the anterior and posterior mandibulohoid ligaments of Millot and An

thony, 1958; Fig. 2) function during mouth closing and act to restore the rest position of the intracranial joint and hyomandibular. I propose that the posterior mandibulohyoid ligament is an integral component of the mouth opening system. Posterodorsal and lateral movement of the ceratohyal and symplectic will exert a force on this ligament acting to depress the mandible. This force, since it is applied at a point close to the quadratomandibular articulation, will produce a large amount of mandibular depression for a relatively small displacement. The ratio of the distance from the symplectic–mandibular articulation to the quadratomandibular articulation and the distance from this articulation to the tip of the mandible is about 1:3.7. Thus the tip of the mandible will be depressed an amount 3.7 times greater than the initial posterodorsal movement of the posterior aspect of the mandible. This mechanism produces a relatively high velocity of mandibular depression relative to a system with an applied force far from the quadratomandibular joint (such as the coracomandibularis muscle). Mouth opening during feeding in *Latimeria* is probably a very rapid movement mediated by a velocity-efficient system while mouth closing is the result of a force-efficient system. Both the coracomandibularis and the subcephalic muscles have their insertion far from the axis of rotation (Fig. 2) and this suggests that adduction of the mandible and flexion of the intracranial joint produce powerful crushing forces.

The demonstration that the coracomandibularis muscle possesses a line of action acting to adduct the lower jaw suggests that manipulations of fresh or thawed specimens have provided misleading data on the jaw mechanics of *Latimeria*. The direct coupling observed between depression of the lower jaw and intracranial extension is an artifact of the direction in which force was applied to the lower jaw to cause mandibular depression. This can be simulated in a mechanical model. If an anteroventral force is applied to the mandibular symphysis, intracranial extension does indeed accompany mandibular depression. However, the line of action of the coracomandibularis muscle is posteroventral and passes above the jaw joint. The action of this muscle therefore, cannot be simulated accurately by manually depressing the lower jaw.

Based on the model of the coelacanth feeding mechanism involving the hyoid apparatus as the prime mediator of mandibular depression and intracranial extension, the following (potentially testable) sequence of events is proposed. Contraction of the sternohyoideus, epaxial muscles, and hypaxial muscles results in mandibular depression and lifting of both the anterior and posterior division of the braincase. The hypaxial muscles stabilize the pectoral girdle to allow sternohyoideus contraction to affect primarily the hyoid apparatus. The mechanical interrelationships of the hyoid arch, palatoquadrate, and mandible suggest that the first 5°–7° of mandibular depression will not result in significant direct intracranial extension. Robineau and Anthony (1973) have noted, however, that notochordal elasticity can act to raise the anterior division of the neurocranium by 5° following relaxation of the subcephalic muscles. Thus the direct correlation observed by Thomson (1973) between mandibular depression and intracranial extension during small respiratory movements need not be due to the mechanical interrelationships of the jaw elements. Mouth closing is effected by the adductor mandibulae complex and the subcephalic muscles while the coracomandibularis acts to compress the buccal cavity.

Evidence from primitive actinopterygians.—Although primitive actinopterygian fishes such as *Polypterus* and *Amia* are only very distantly related to *Latimeria*, analysis of the biomechanics of feeding in these fishes, and in the generalized primitive teleost *Salvelinus fontinalis*, provides powerful insights into primitive actinopterygian feeding mechanisms. In addition, the actinopterygian homologue of the coracomandibularis muscle in *Latimeria* is the so-called branchiomandibularis (Allis, 1897, 1922) found in *Amia* and *Polypterus* (Wiley, in press). An analysis of the activity of this muscle during feeding may furnish a test of the above hypothesis of coracomandibularis activity in *Latimeria*. In addition, an examination of feeding in primitive living fishes allows conclusions to be drawn concerning the role of muscles attaching to the pectoral girdle, hyoid, and mandible in the feeding mechanism.

Based on high-speed cinematography and electromyography of feeding in *Amia*, *Polypterus*, *Lepisosteus* and *Salvelinus*, Lauder (1978) proposed that control of mandibular depression by posterior movements of the hyoid apparatus is a primitive feature of actinopterygian fishes. This mechanism was conclusively dem-
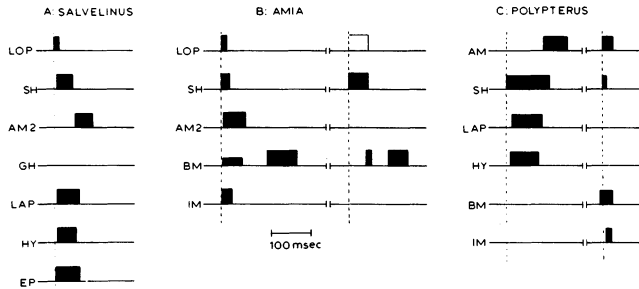
Fig. 4. Block diagram of electrical activity in cranial muscles during feeding in three actinopterygian fishes. Experimental methods were those of Lauder and Liem (in press). The black bar indicates the duration of electrical activity and the dashed lines indicate the onset of activity in the levator operculi (*Salvelinus, Amia*) and the sternohyoideus (*Polypterus*). Two sequences are shown for *Polypterus* and *Amia*: activity during the initial strike at the prey (first dashed line) and a sequence of buccal compression during chewing and swallowing (second dashed line). Open bars indicate variations observed in activity periods. In *Amia* during rapid strikes at the prey, all compressive and expansive muscles are active nearly synchronously. Abbreviations: AM = adductor mandibulae; AM2 = part two of the adductor mandibulae complex; BM = branchiomandibularis; EP = epaxial muscles; GH = geniohyoideus; HY = hypaxial; IM = intermandibularis posterior; LOP = levator operculi; LAP = levator arcus palatini; SH = sternohyoideus.

onstrated in *Salvelinus* (where it forms only one of two jaw opening couplings) by high-speed (200 frames per second) X-ray cinematography (Lauder and Liem, in press). They demonstrated (Fig. 3) that contraction of the sternohyoideus results in a posterodorsal movement of the ceratohyal and epihyal which pivot around the interhyal bone. This small styliform bone allows posterior movement of the hyoid to exert a force on the retroarticular process of the lower jaw via the mandibulohyoid ligament and cause mandibular depression. This mechanism operates in addition to the levator operculi muscle which initiates mandibular depression (Fig. 4A). Lauder and Liem (in press) also found that the geniohyoideus muscle, in spite of its biomechanically advantageous position to activate mandibular abduction (Fig. 3:GH) is never active during the mouth opening phase of the initial strike at the prey (Fig. 4:GH). The geniohyoideus is mostly active as a compressive muscle of the buccal cavity.

Amia calva and *Polypterus senegalus* both possess a pair of branchiomandibularis muscles originating lateral to the mandibular symphysis and inserting on the third hypobranchials. This muscle has been proposed to be the homologue of the coracomandibularis of *Latimeria* (Wiley, in press). Electromyograms of the branchiomandibularis during feeding in *Amia* and *Polypterus* (Fig. 4:B, C) reveal that this muscle also is active during compression of the buccal chamber. *Amia, Polypterus* (Allis, 1897, 1922),

and *Lepisosteus* (Wiley, 1976) all possess a strong ligament extending from the posterodorsal aspect of the hyoid to the retroarticular process of the mandible. Contraction of the sternohyoideus muscle in these fishes exerts a force on this ligament resulting in mandibular depression. In *Polypterus* and *Lepisosteus* this mechanism is the only mechanism causing mandibular depression and the sternohyoideus shows the first activity of all cranial opening muscles. Strong activity in the sternohyoideus is also accompanied by synchronous activity in the hypaxial muscles to stabilize the pectoral girdle (Fig. 4:A, C).

The pattern which emerges from a functional analysis of feeding in primitive actinopterygians is that the sternohyoideus (and hypaxial) muscles are the agents responsible for mandibular depression. The occurrence of strong ligamentous connections between the hyoid and mandible in all generalized primitive living actinopterygians, dipnoans, and *Latimeria* strongly argues for a key role of the sternohyoideus muscle and hyoid apparatus in the osteichthyian feeding mechanism. Furthermore, it is a general conclusion for all primitive fishes so far examined that the ventral head muscles inserting on the mandible from the hyoid and pectoral girdle, in spite of a potentially significant mechanical advantage, are rarely active during mouth opening. It thus seems highly likely, given that the coracomandibularis of *Latimeria* lacks any mechanical advantage, that it is active

only in compressive movements of the buccal cavity, not in mouth opening.

These results resolve the problem of the increase in distance between the origin and insertion of the coracomandibularis muscle in *Latimeria* noted by Thomson (1970). Any muscle between either the hyoid or pectoral girdle and the mandible will lengthen as the mandible is protruded and the hyoid moves posteriorly. This clearly occurs for the geniohyoideus muscle of teleosts. If these muscles are not active during the lengthening process, this problem is not encountered. Lengthening contractions, however, are quite common in vertebrate musculoskeletal systems (Alexander and Goldspink, 1977) and no physiological constraints would prevent the coracomandibularis muscle from contracting as the lower jaw was protracted.

Based on data from primitive living actinopterygians, it also is highly likely that, following prey capture, manipulatory movements of the prey could be performed prior to deglutition with the lower jaw adducted and with alternate compressive (by coracomandibularis contraction) and expansive (by sternohyoideus contraction) movements of the hyoid apparatus.

DISCUSSION

The model of the coelacanth feeding mechanism proposed here is fundamentally different from those proposed previously. The main features of this model are the central role of the hyoid apparatus in controlling both mandibular depression and extension of the intracranial joint, and the suggested compressive function of the coracomandibularis muscle in regulating the volume of the buccal cavity. The functional analysis of primitive actinopterygian fishes has revealed that a mechanism involving the sternohyoideus, hyoid apparatus, and ligamentous connections to the mandible is probably a primitive feature of the actinopterygian feeding mechanism. The occurrence of similar ligaments joining the hyoid to the mandible in Dipnoi (Edgeworth, 1935; Huxley, 1876; pers. obs.) and in *Latimeria* (Millot and Anthony, 1958) suggests that the hyoid apparatus has played a fundamental role in the evolution of the osteichthyian feeding mechanism.

Viewed in this light, the feeding mechanism of *Latimeria* is not merely a unique system far removed from the morphology of the rhipidistian jaw and rather disappointing in what it reveals about the evolution of vertebrate feeding mechanisms. The jaw of *Latimeria*, in spite of several specialized features including the unique articulation of the mandible with both the quadrate and the symplectic, has retained a fundamental feature of the osteichthyian feeding mechanism: mandibular depression mediated by the sternohyoideus muscle and ligamentous interconnections between the hyoid arch and the mandible. The feeding mechanism of *Latimeria* thus has much greater generality than previously suggested and sheds considerable light on the extent to which modifications can occur in the musculoskeletal couplings of the osteichthyian jaw without disrupting a key primitive functional component of the feeding mechanism.

Several aspects of this specific hypothesis of hyoid movement in *Latimeria* are relatively easily tested and the more general hypothesis of the role of the hyoid apparatus in osteichthyian fishes is now being tested by a functional analysis of the hyoid in living Dipnoi.

Two specific predictions may be made. 1) The sternohyoideus and epaxial muscles will be the first muscles active during mouth opening while activity in the coracomandibularis will occur only as the jaws close or perhaps only during chewing and swallowing of the prey. 2) Extension of the entire cranium on the vertebral column will occur prior to actual extension of the intracranial joint. The effect of notochordal elasticity on movements of the anterior cranial division may partially mask the later occurrence of intracranial extension. Depression of the mandible will have to be accurately measured independently of cranial elevation and movements of the anterior cranial division must be separated from movement of the otico-occipital division in testing these predictions.

During respiration and perhaps also during the initial stages of mouth opening in feeding the opercular bone may rotate posteriorly due to contraction of the so-called levator operculi muscle (Millot and Anthony, 1958) and (more probably) from compression of the hyoid arch resulting from sternohyoideus contraction. This movement could be directly translated to the posteroventral margin of the lower jaw by the anterior mandibulohyoid ligament and cause mandibular depression.

Given the present lack of available living specimens on which to test the hypotheses presented here, only correlations between structures in *Latimeria* and similar structures and

functions in other living fishes can be used to test hypotheses directly. This procedure has been followed for the coracomandibularis muscle of *Latimeria* but it is hoped that these hypotheses will be further tested in the near future on a living specimen.

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