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Evolution of jaw depression mechanics in aquatic vertebrates: insights from Chondrichthyes

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The widely accepted phylogenetic position of Chondrichthyes as the sister group to all other living gnathostomes makes biomechanical analyses of this group of special significance for estimates of skull function in early jawed vertebrates. We review key findings of recent experimental research on the feeding mechanisms of living elasmobranchs with respect to our understanding of jaw depression mechanisms in gnathostome vertebrates. We introduce the possibility that the ancestral jaw depression mechanism in gnathostomes was mediated by the coracomandibularis muscle and that for hyoid depression by the coracohyoideus muscle, as in modern Chondrichthyes and possibly placoderms. This mechanism of jaw depression appears to have been replaced by the sternohyoideus (homologous to the coracohyoideus) coupling in Osteichthyes following the split of this lineage from Chondrichthyes. Concurrent with the replacement of the branchiomandibularis (homologous to the coracomandibularis) coupling by the sternohyoideus coupling as the dominant mechanism of jaw depression in Osteichthyes was the fusion and shift in attachment of the interhyoideus and intermandibularis muscles (producing the protractor hyoideus muscle, mistakenly refereed to as the geniohyoideus), which resulted in a more diversified role of the sternohyoideus coupling in Osteichthyes. The coracohyoideus coupling appears to have been already present in vertebrates where it functioned in hyoid depression, as in modern Chondrichthyes, before it acquired the additional role of jaw depression in Osteichthyes.

ADDITIONAL KEY WORDS:—Chondrichthyes – Osteichthyes – jaw mechanics – evolutionary morphology – gnathostomes.

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INTRODUCTION

The vertebrate jaw has proven to be a model subject of research on the evolution of functional systems. This complex system of muscles and skeletal elements that serves as a crucial interface between vertebrates and their environment has provided the material for several major concepts and repeating themes in the evolution of organismal design (Gans, 1961; Shaeffer & Rosen, 1961; Osse, 1969; Crompton & Parker, 1978; Barel, 1983; Lauder & Liem, 1983, 1989; Bramble & Wake, 1985; Frazzetta, 1986; Aerts *et al.*, 1987; Lauder *et al.*, 1989; Aerts, 1991). However, our understanding of the evolution of vertebrate jaws has been limited because functional morphological research on the sister group to all other living gnathostomes, the Chondrichthyes, has lagged behind work on other major clades. Because of the phylogenetic position of Chondrichthyes, establishing details of jaw mechanics in this group is vital to our understanding of the feeding mechanism in the earliest jawed chordates. In this paper we discuss some implications of recent research on the functional morphology of feeding in elasmobranchs (Haller, 1926; Moss, 1972; Motta, Hueter & Tricas, 1991; Frazzetta, 1994; Motta & Wilga, 1995; Motta *et al.*, 1997; Wilga, 1997; Wilga & Motta, 1998a,b, 2000) for our understanding of gnathostome jaw evolution.

We focus on the history of mouth opening mechanisms and particularly the systems of muscles and skeletal elements that are involved in depression of the lower jaw. One of the general conclusions from comparative studies of aquatic feeding mechanisms in bony fishes and salamanders is that the major biomechanical couplings involved in mouth opening have been largely retained throughout the radiation of these vertebrate groups (Reilly & Lauder, 1990; Lauder & Shaffer, 1993). The primary mechanism mediating lower jaw depression in all groups of living fishes and salamanders that have been studied to date, with the exception of Chondrichthyes, is a linkage involving a ligamentous connection between the hyoid bar and mandible that transmits posterior rotation to the mandible (Lauder, 1980a; Lauder & Shaffer, 1985; Bemis & Lauder, 1986; Bemis, 1987). Recent research on chondrichthyans has revealed that this linkage is not a viable mechanism of jaw depression in this group (Ribbink, 1971; Moss, 1972; Motta *et al.*, 1991, 1997; Motta & Wilga, 1995; Wilga, 1997; Wilga & Motta, 1998a,b, 2000). Our primary purpose in this paper is to review this observation and discuss its implications for our understanding of early vertebrate feeding systems in the light of current estimates of vertebrate interrelationships. We introduce and explore the possibility that the ancestral jaw

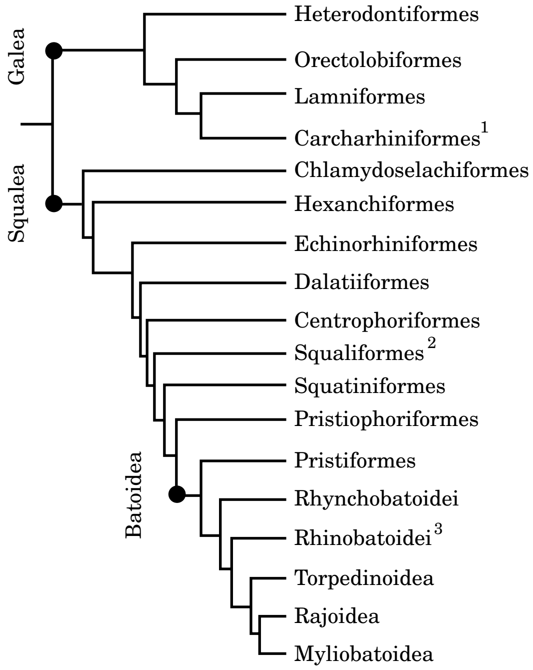


Figure 1. Elasmobranch phylogeny (after Shirai, 1996) showing taxa investigated functionally. 1, *Negaprion brevirostris*, *Sphyrna tiburo*; 2, *Squalus acanthias*; 3, *Rhinobatos lentiginosus*.

depression mechanism in gnathostomes was mediated by the coracomandibularis muscle and that of hyoid depression by the coracohyoideus as seen in modern Chondrichthyes.

METHODS

The morphology and function of the muscles involved in the coracomandibularis and coracohyoideus couplings in lower vertebrates was compiled from the literature. Muscle synonymies are from Edgeworth (1935), Winterbottom (1974), and Miyake, McEachran & Hall (1992). We reserve the chondrichthyan terms 'coracomandibularis' and 'coracohyoideus' couplings as general term for those couplings commonly referred to as the 'geniohyoideus' and 'rectus cervicis'. In this paper, we use the term 'hyoid' to refer to the ventral elements of the hyoid arch, which usually consist of the ceratohyal and the basihyal in most groups, but includes the hyomandibula in chondrichthyans. Schematic diagrams of musculoskeletal couplings in elasmobranchs were produced from anatomical dissections of at least five fresh-frozen specimens each of four species of elasmobranchs: the lemon shark *Negaprion brevirostris* (63–229 cm TL); the bonnethead shark *Sphyrna tiburo* (56–82 cm TL), the spiny dogfish *Squalus acanthias* (46–65 cm TL), and the Atlantic guitarfish *Rhinobatos lentiginosus* (52–63 cm TL) (Motta & Wilga, 1995; Motta *et al.*, 1997; Wilga, 1997; Wilga & Motta, 1998a,b, in review). These species represent each of the three major elasmobranch radiations (Fig. 1).

Computer axial tomography scans and photographs of intact heads approximating the location of the jaws in the resting position (jaws closed) and with the jaws and hyoid maximally depressed were used to measure the angle of the hyoid relative to the lower jaw (for more detail see Motta & Wilga, 1995). Hyoid rotation in degrees was calculated as the difference between the resting position and its position at peak lower jaw depression in one fresh-frozen specimen each of *N. brevirostris* (102 cm TL), *Squalus acanthias* (70 cm TL), and *Sphyrna tiburo* (84 cm TL). This angle was measured at the intersection of lines drawn along the dorsal edge of the teeth on the lower jaw and the dorsal edge of the ceratohyal.

Motor activity and kinematics of head movements during feeding in *N. brevirostris* (5 individuals, 36 capture trials), *Sphyrna tiburo* (3 individuals, 12 capture trials), *Squalus acanthias* (8 individuals, 44 capture trials), and *R. lentiginosus* (5 individuals, 42 capture trials) were studied using simultaneous electromyography and high-speed video (for more detail see: Motta *et al.*, 1997; Wilga, 1997; Wilga & Motta, 1998a, b, in review). Lateral and ventral video recordings were made during feeding experiments using a NAC 200 high-speed video camera at 200 fields per second. Bipolar electrodes were implanted in select cranial muscles using 26 gauge hypodermic needles. Fish were anaesthetized for surgery using 0.065 g/l of tricaine methanesulfonate (MS 222) and maintained on this solution during surgery. After surgery, fish were returned to the experimental tank to recover. Feeding trials were begun after normal swimming behavior was observed for at least one hour post-recovery and continued until the fish was satiated. Prey items found naturally in the diet were offered as follows: Atlantic thread herring (*Opisthonema oglinum*) and crevalle jack (*Caranx hippo*) for *N. brevirostris*; Pacific herring (*Clupea pallasii*) for *Squalus acanthias*; speckled crab (*Arenaeus cribrarius*), pink shrimp (*Penaeus duorarum*) and Atlantic thread herring (*Opisthonema oglium*) for *Sphyrna tiburo*; pink shrimp (*Panaeus duorarum*) for *R. lentiginosus*. Electrode wires were attached to differential amplifiers set at a gain of 1000, bandpass 100–3000 Hz with a 60 Hz notch filter. Signals were simultaneously monitored on a four-channel oscilloscope and an eight-channel thermal array recorder and recorded on a pulse code modulator that multiplexed the signals to a videocassette recorder. The EMG and video recordings were synchronized using a unit that directed a preprogrammed repeating pulse simultaneously to one channel of the tape recorder and to LED strobes that were recorded by the video camera. Chart recordings of electromyographic data from each muscle were analysed by measuring burst duration and burst onset relative to the start of lower jaw movement as determined by the pattern of synchronization pulses on the video images and EMG tracings. At the termination of each experiment, sharks were euthanized by MS-222 overdose according to Institutional Animal Care and Use Committee guidelines of the University of Washington, Friday Harbor Laboratories, the University of South Florida, and Mote Marine Laboratory. Positions of the electrodes were verified by dissection and body length measured. The following muscles were recorded from: epaxialis, coracomandibularis, coracohyoideus (not implanted in *Sphyrna tiburo*), coracoarcualis (*N. brevirostris* and *Squalus acanthias* only), quadratomandibularis, depressor mandibularis (*R. lentiginosus* only), coracohyomandibularis (*R. lentiginosus* only) and depressor hyomandibularis (*R. lentiginosus* only). The time of the following kinematic events was determined from the video recording: onset of lower jaw depression, onset of hyoid depression, peak hyoid depression, onset of lower jaw elevation, onset of upper jaw protrusion, onset of upper jaw retraction and complete jaw closure.

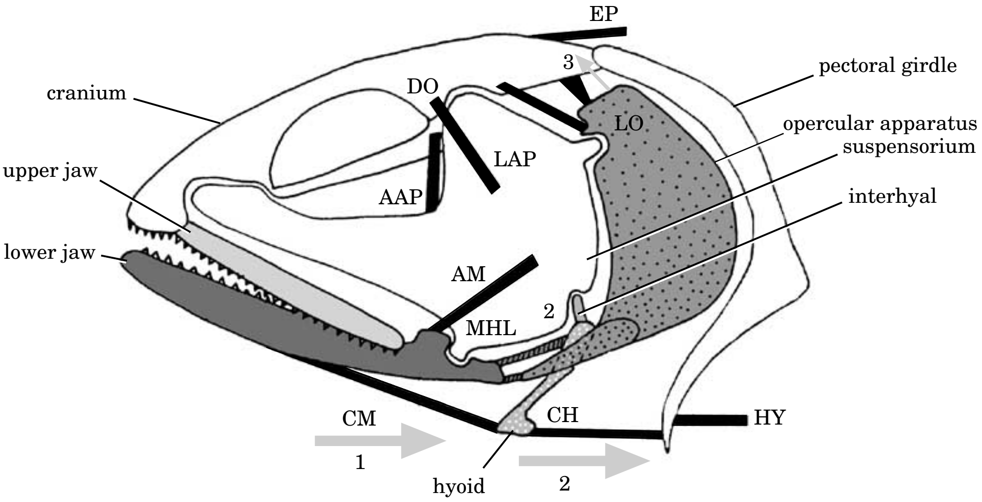


Figure 2. Jaw depression couplings in a teleost (after Lauder, 1985). 1, CM-coupling: hyoid–protractor hyoideus muscle–lower jaw; 2, CH-coupling: hypaxialis–pectoral girdle–sternohyoideus muscle–hyoid–MHL–lower jaw; 3, opercular coupling. Shading patterns indicate skeletal elements: light grey, upper jaw; dark grey, lower jaw; dark grey/black stipples, opercular apparatus; white, suspensorium (hyomandibula and other elements); light grey/white stipples, hyoid (ceratohyal); dark grey/barred, mandibulohyoid and interopercular-mandible ligaments. Muscle name abbreviations: AAP, adductor arcus palatini; AM, adductor mandibularis; DO, dilator operculi; EP, epaxialis; CM, coracomandibularis; HY, hypaxialis; LAP, levator arcus palatini; LO, levator operculi; MHL, mandibulohyoid ligament; CH, sternohyoideus.

Our comparisons of motor patterns among species are based on major qualitative differences concerning the synchrony of motor activity with specific kinematic events. In the jaw depression analysis, lower jaw depression and hyoid depression partially overlap in time, however the onset and completion of these kinematic events consistently occurred independently and allow differences in the motor pattern and the corresponding kinematic event to be detected. Muscle morphology, function and motor pattern were mapped by hand onto a cladogram of gnathostomes. The resulting phylogenetic distribution of these traits was used as a basis for inferring evolutionary sequences of change in these components of the feeding mechanism.

RESULTS

Schematic diagrams of a teleost and a dogfish shark illustrating the lower jaw depression couplings are shown in Figures 2 and 3 respectively. 'Coupling two' is the coracohyoideus coupling (hereafter referred to as the CH-coupling) and in teleosts is composed of the hypaxialis–pectoral girdle–sternohyoideus–hyoid–mandibulohyoid (MH) ligament–mandible linkage (see Fig. 2). In the teleost system, contraction of the sternohyoideus retracts the hyoid, which rotates the anterior-medial confluence of the left and right hyoid elements

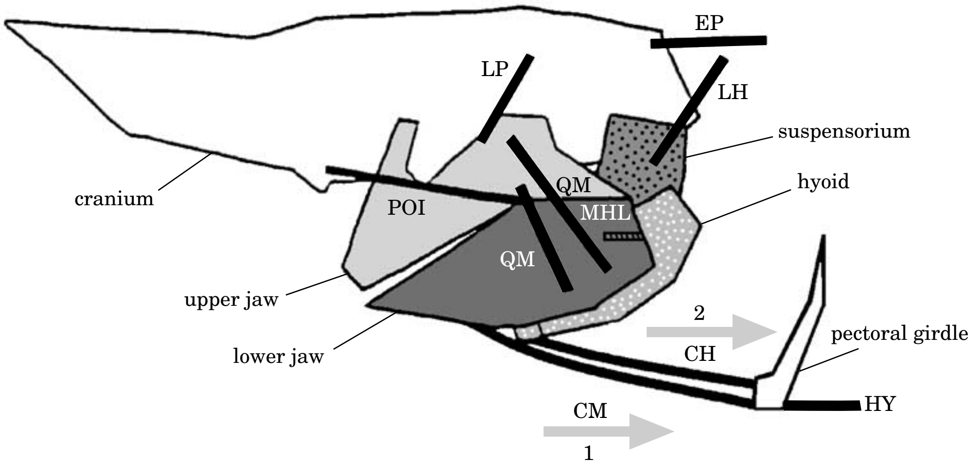


Figure 3. Jaw depression couplings in the dogfish (from Wilga & Motta, 1998a). 1, CM-coupling: pectoral girdle–coracomandibularis muscle–lower jaw; 2, CH-coupling: hypaxialis–pectoral girdle–coracohyoideus–coracoarcualis muscle–hyoid; light grey, upper jaw; dark grey, lower jaw; dark grey/black stipples, suspensorium (hyomandibula); light grey/white stipples, hyoid (ceratohyal-basihyal); dark grey/barred, mandibulohyoid ligament. Abbreviations: EP, epaxialis; CM, coracomandibularis; HY, hypaxialis; LH, levator hyomandibularis; LP, levator palatoquadrati; MHL, mandibulohyoid ligament; POI, preorbitalis I; QM, quadratomandibularis; CH, coracohyoideus-coracoarcualis complex.

posteroventrally. This causes posterodorsal rotation of the proximal end of the hyoid, which is transmitted to the posterior end of the mandible through the MH ligament. As a result, the anterior tip of the mandible rotates posteroventrally around the quadratomandibular joint to depress the lower jaw. Contraction of the hypaxialis muscles may fix or retract the pectoral girdle allowing the CH-coupling to work more effectively (Lauder, 1985).

The CH-coupling in sharks consists of the hypaxialis–pectoral girdle–coracoarcualis–coracohyoideus–hyoid linkage (see Fig. 3) (Motta *et al.*, 1997; Wilga, 1997; Wilga & Motta, 1998a, 2000). The origin of the coracohyoideus is from the coracoarcualis and the insertion is onto the hyoid, while the insertion of the coracoarcualis is onto the coracohyoideus and the origin from the pectoral girdle, thus they are linked functionally and morphologically as a coracohyoideus complex. Functional analyses have revealed that in sharks, contraction of the coracohyoideus complex pulls the anterior-medial end of the hyoid posteroventrally, as in teleosts. However, unlike the teleost hyoid, the proximal end of the shark hyoid does not move dorsally with contraction of the rectus cervicis, rather, it rotates anteriorly and ventrally (Fig. 4). This anteroventral rotation of the proximal hyoid is seen in the CAT scans, radiographs, and photographs of the head skeleton of sharks with the mouth closed and with the hyoid maximally depressed (see Fig. 4). Such images reveal that the distal hyoid is rotated posteroventrally around the mandibular-ceratohyal articulation through an angle of 55° in *N. brevirostris*, 60° in *Squalus acanthias*, and 70° in *Sphyrna tiburo* (Motta & Wilga, 1995; Wilga & Motta, 1998a, 2000). The hyoid appears to rotate around the articulation to the lower jaw as well

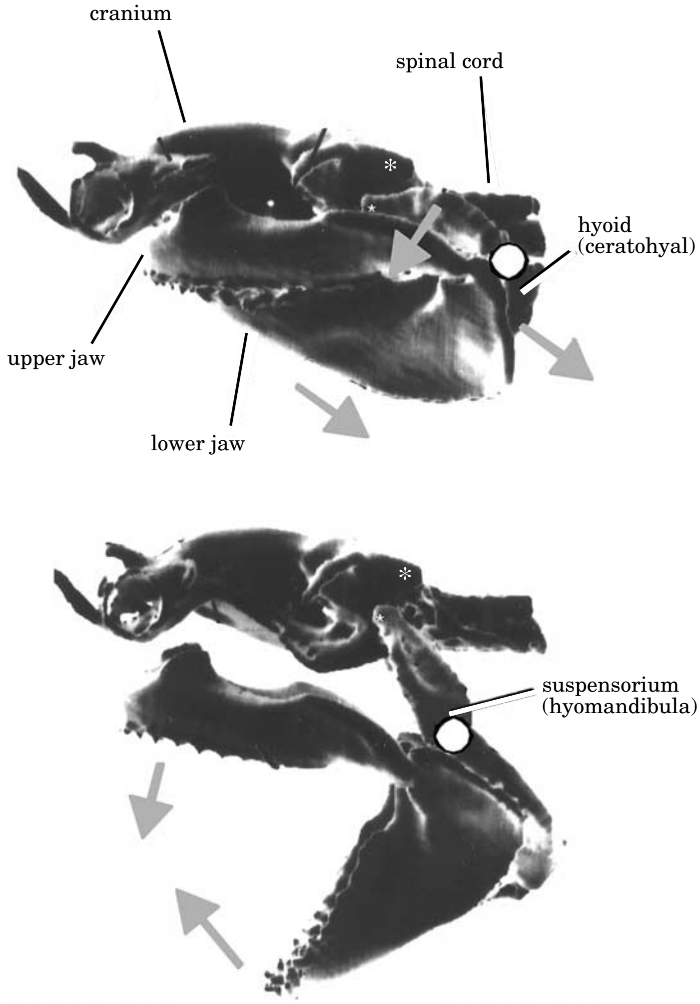


Figure 4. Lateral view of 3D-CAT scans of a *N. brevirostris* with the jaws closed (top) and open (bottom) (from Motta & Wilga, 1995). Grey arrows show direction of movement of skeletal elements to depress the lower jaw from the closed position and to adduct the jaws from the open position, white asterisks indicate fixed point on cranium, white dot indicates proximal end of the hyoid.

as, and independently of, the hyomandibular-ceratohyal articulation, thus the MH ligament does not appear to transmit rotation to the mandible.

The coracomandibularis coupling (CM-coupling) in teleosts, coupling 1 in Figure 2, consists of the hyoid–protractor hyoideus–mandible linkage. Contraction of the protractor hyoideus may either elevate or protract the hyoid compressing the buccal cavity or depress the lower jaw if the hyoid is fixed by coupling 2. The CM-coupling in elasmobranchs is composed of the hypaxialis–pectoral girdle–coracomandibularis–mandible linkage (coupling 1 in Fig. 3). As the pectoral girdle in sharks is fixed in position by the hypaxialis, contraction of the coracomandibularis pulls the anterior tip of the mandible posteroventrally. The coracomandibularis in

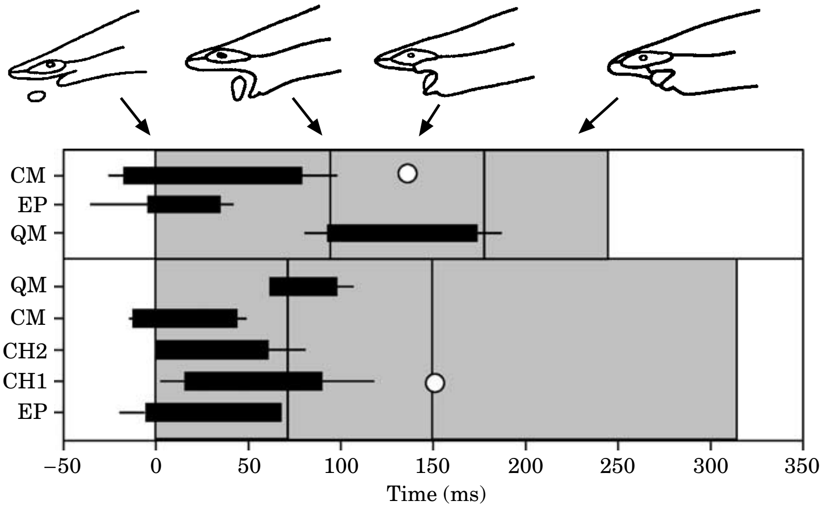


Figure 5. Bar diagrams of motor activity in two galean elasmobranchs, *Sphyrna tiburo* (top) and *N. brevirostris* (from Wilga and Motta, 2000; Motta *et al.*, 1997). Black boxes indicate the motor pattern with left and right error bars showing one standard error of the burst onset and duration times respectively. White circles indicate time of peak hyoid depression. The first grey region in each row indicates the expansive phase of mouth opening from the start to maximum lower jaw depression. The middle grey region indicates the compressive phase of mouth closing from maximum lower jaw depression and the start of upper jaw protrusion to complete jaw closure and maximum upper jaw protrusion. The last grey region indicates the recovery phase from jaw closure and maximum upper jaw protrusion to complete retraction of the upper jaw. Muscle name abbreviations: EP, epaxialis; CM, coracomandibularis; QM, quadratomandibularis; CH1, coracohyoideus; CH2, coracoarcualis.

elasmobranchs is not linked to the hyoid as it is in Osteichthyes and its line of action is always below the jaw joint and thus it always acts to depress the lower jaw.

The above interpretations of function in the CM-coupling and the CH-coupling in sharks are supported by electromyographic data from four species of elasmobranchs (see Figs 5 and 6). Motor activity in the coracomandibularis always precedes that of the coracohyoideus and coracoarcualis and always begins prior to the onset of lower jaw depression. Motor activity in the coracohyoideus and coracoarcualis may not begin until after the onset of lower jaw depression and may not continue throughout lower jaw depression. However, motor activity in these muscles begins just before the start of hyoid depression and ends prior to peak hyoid depression. In *N. brevirostris*, peak hyoid depression often occurs after activity in the coracohyoideus and coracoarcualis muscles have stopped. The extended duration of hyoid depression is probably due to water influx pushing against the hyoid when the mouth is opened and the shark is swimming. Note that peak hyoid depression occurs during elevation of the lower jaw.

DISCUSSION

The mechanisms of jaw action during feeding have now been studied in representatives of most of the major living non-amniotic, aquatic vertebrate lineages.

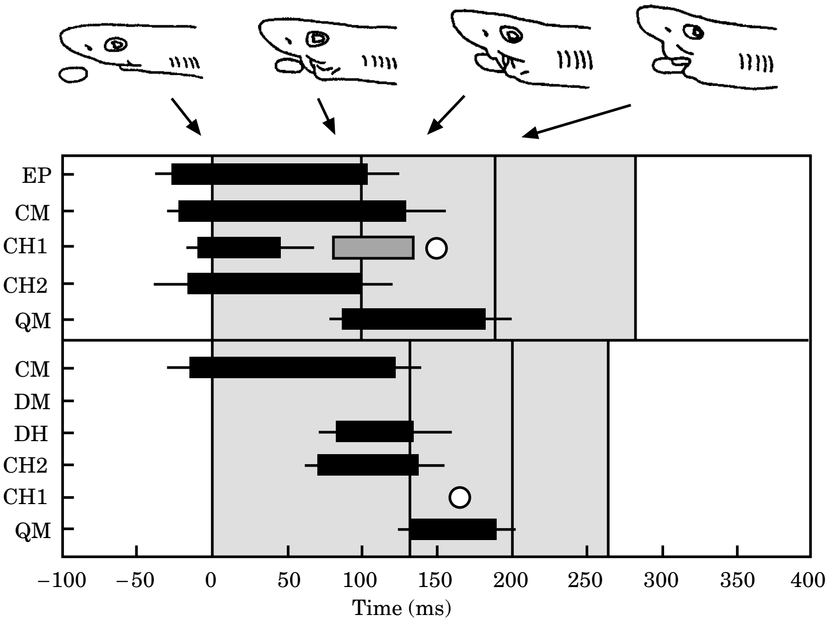
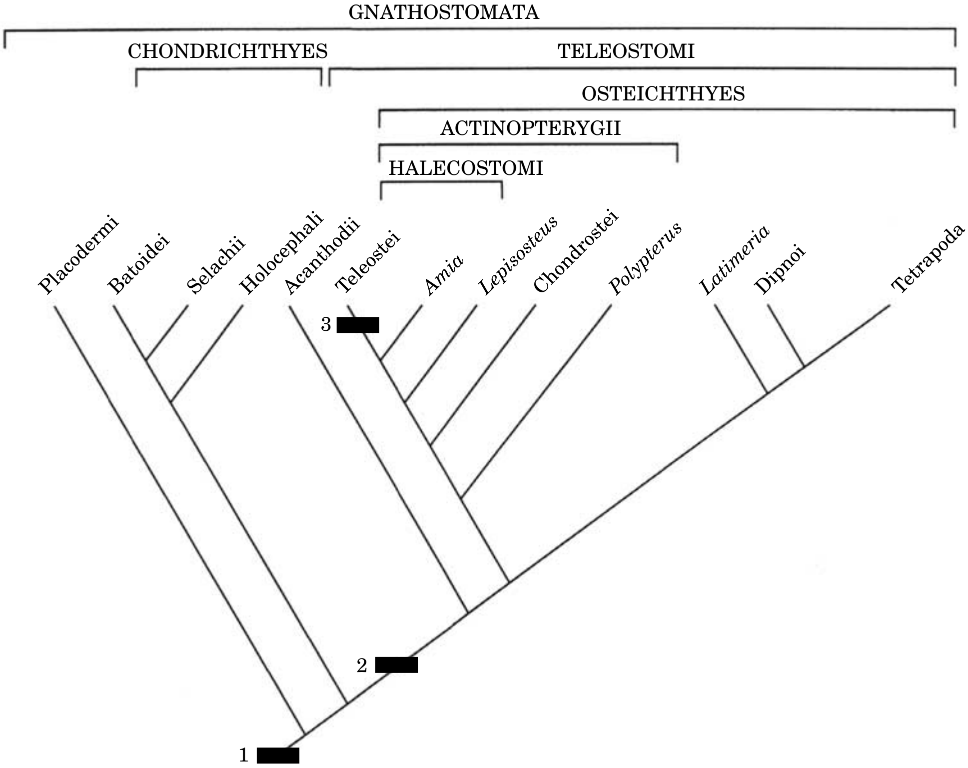


Figure 6. Bar diagrams of motor activity in a squalean and batoid elasmobranch, *Squalus acanthias* (top) and *R. lentiginosus* (bottom) (from Wilga & Motta, 1998a,b). Black boxes indicate the motor pattern with left and right error bars showing one standard error of the burst onset and duration times respectively. Dark grey box indicates a second burst of activity. White circles indicate time of peak hyoid depression. The first grey region indicates the expansive phase of mouth opening from the start to maximum lower jaw depression. The middle grey region indicates the compressive phase of mouth closing from maximum lower jaw depression and the start of upper jaw protrusion to complete jaw closure and maximum upper jaw protrusion. The last grey region indicates the recovery phase from jaw closure and maximum upper jaw protrusion to complete retraction of the upper jaw. Muscle name abbreviations: EP, epaxialis; DM, depressor mandibularis; DH, depressor hyomandibularis; CM, coracomandibularis; QM, quadratomandibularis; CH1, coracohyoideus; CH2, coracoarcualis; CH3, novel division coracohyomandibularis. Note the lack of activity in CH1 in *R. lentiginosus* even though the muscle was correctly implanted and was active during other behaviours.

This body of research includes experimental work with living specimens of salamanders (Lauder & Shaffer, 1985; Reilly & Lauder, 1990), lungfishes (Bemis & Lauder, 1986), actinopterygians (Lauder, 1979, 1980a), and now chondrichthyans (Motta, Hueter & Tricas, 1991; Frazzetta, 1994; Motta *et al.*, 1997; Wilga, 1997; Wilga & Motta, 1998a,b, 2000). Of the major living aquatic gnathostome lineages, only *Latimeria* lacks a thorough functional description based on work with living specimens (Lauder, 1980b). Work with extinct lineages is limited by our inability to observe jaw kinetics, but detailed morphological studies have been conducted with placoderms (Heintz, 1932; Edgeworth, 1935; Stensio, 1959; Miles & Westoll, 1968; Miles, 1969; Denison, 1978) and acanthodians (Miles, 1964; 1968), two basal gnathostome groups. Below we attempt to summarize observations made on the mechanisms of jaw depression in lower vertebrates and we attempt to recreate the evolutionary history of this (Fig. 7).



1. Coracomandibularis coupling (depressor gnathalis in Placodermi) attaches mandible to the pectoral girdle and functions to depress the mandible. Coracohyoideus coupling attaches pectoral girdle to hyoid and functions to depress hyoid. Mandibulohyoid ligament present but does not function in mandibular depression.
2. Coracomandibularis coupling (branchiomandibularis in Osteichthyes; geniothoracis in Dipnoi; geniohyoideus in Amphibia) attaches mandible to hyoid and other branchial arches and functions in buccal compression, hyoid protraction and limited depression of the mandible. Coracohyoideus coupling (sternohyoideus in Actinopterygii and Sarcopterygii; rectus cervicis in Dipnoi and Amphibia) depresses hyoid and mandible via the mandibulohyoid ligament.
3. True coracomandibularis coupling lost, analogous coupling (protractor hyoideus, formed from fusion of intermandibularis posterior and interhyoideus muscles) attaches mandible to hyoid and functions primarily to protract hyoid or compress buccal cavity, although it may contribute to mandible depression.

Figure 7. Lower jaw depression mechanisms mapped onto a gnathostome phylogeny (modified after Lauder & Liem, 1983; Lauder & Shaffer, 1993). Note that we differ from Lauder and Shaffer (1993) in the placement of character 2, but our interpretation is consistent with Lauder and Liem (1983).

Anatomical features of jaw depression couplings

The lower jaw depression couplings in aquatic gnathostomes involve the coracomandibularis and coracohyoideus muscles and their derivatives. The muscles that are believed to be homologous to the coracomandibularis and the coracohyoideus are known by a variety of names in the different vertebrate clades (Tables 1, 2). In keeping with our hypotheses that chondrichthyans possess the ancestral mechanisms and to simplify discussion throughout this paper, when we refer to couplings that involve these homologous muscles, we will refer to them using the terms

TABLE 1. A synonymy of the coracomandibularis muscle in lower vertebrates

Taxa	Coracomandibularis	Function	Literature
Placoderms			
*Dinichthyes**	depressor gnathalis	depresses lower jaw	Heintz (1932)
*Coccosteus**	depressor gnathalis	depresses lower jaw	Miles (1969), Miles & Westoll (1968)
Arctolepida*	depressor gnathalis	depresses lower jaw	Stensio (1959)
Brachythoraci*	depressor gnathalis	depresses lower jaw	Stensio (1959)
Chondrichthyans			
Holocephalans*	coracomandibularis	depresses lower jaw	Ribbink (1971), Didier (1995)
Sharks			
Negaprion	coracomandibularis	depresses lower jaw	Motta *et al.* (1991, 1997)
Squalus, *Sphyrna*	coracomandibularis	depresses lower jaw	Wilga & Motta (1998a, 2000), Wilga (1997)
Batoids			
Rhinobatos	coracomandibularis	depresses lower jaw	Wilga & Motta (1998b)
Acanthodians*	branchiomandibularis	depresses lower jaw and/ or compresses buccal cavity	Miles (1968)
Actinopterygians			
Cladistians			
Polypterus	branchiomandibularis	compresses buccal cavity	Lauder (1980a)
Chondrosteans			
*Acipenser**	branchiomandibularis	depresses lower jaw and compresses buccal cavity	Stengel (1962)
*Polyodon**	branchiomandibularis	depresses lower jaw and compresses buccal cavity	Danforth (1913)
Ginglymodians			
Lepisosteus	absent		Lauder (1980a)
Halecomorphs			
Amia	branchiomandibularis	depresses lower jaw and compresses buccal cavity	Lauder (1980a)
Teleostei	absent**, but uses the protractor hyoideus	protracts hyoid and compresses buccal cavity	Osse (1969), Lauder (1979), Liem (1980), Wainwright *et al.* (1989), Wainwright & Lauder (1986)
Sarcopterygians			
*Latimeria**	coracomandibularis	compresses buccal cavity	Lauder (1980b), Thomson (1967, 1970)
	coracomandibularis	depresses lower jaw	Millot & Anthony (1958)
Dipnoans			
Lepidosiren	geniothoracis	depresses lower jaw and compresses buccal cavity	Bemis & Lauder (1986)
Amphibians			
Ambystoma	geniohyoideus	depresses lower jaw and compresses buccal cavity	Lauder & Shaffer (1985), Shaffer & Lauder (1985)

Muscle synonymies from Edgeworth (1935), Winterbottom (1974), and Miyake *et al.* (1992). * Based on anatomical studies. ** Note that the muscle commonly called the geniohyoideus in teleosts is actually the protractor hyoideus, which arises from fusion of the intermandibularis posterior and the interhyoideus muscles and therefore is not homologous to the geniohyoideus of other lower vertebrate groups; however, we use it in this study because it is analogous to the geniohyoideus (Edgeworth, 1935; Winterbottom, 1974; Miyake *et al.*, 1992).

coracomandibularis or coracohyoideus coupling as the general term and follow with the specific muscle by group in parenthesis when it differs from chondrichthyans.

The coracomandibularis originates from the pectoral girdle in chondrichthyans and *Latimeria*, from the hyoid or branchial arches in bony fishes (branchiomandibularis) (except *Latimeria*, teleosts and gars), from the hypaxialis muscle in

Table 2. A synonymy of the coracohyoideus muscle in lower vertebrates

Taxa	Coracohyoideus	Function	Literature
Placoderms*	unknown	unknown	Denison (1978)
Chondrichthyans			
Holocephalans*	coracohyoideus	depresses hyoid	Ribbink (1971), Didier (1995)
Sharks			
Negaprion	coracohyoideus-coracoarcualis	depresses hyoid	Motta *et al.* (1991, 1997)
Squalus, *Sphyrna*	coracohyoideus-coracoarcualis	depresses hyoid	Wilga & Motta (1998a, 2000)
Batoids			
Rhinobatos	coracohyoideus-coracoarcualis	depresses hyoid	Wilga & Motta (1998b)
	and coracohyomandibularis	depresses hyoid and lower jaw	
Acanthodians*	sternohyoideus	depresses hyoid and lower jaw	Miles (1964, 1968)
Actinopterygians			
Cladistians			
Polypterus	sternohyoideus	depresses hyoid and lower jaw	Lauder (1980a)
Chondrosteans			
*Acipenser**	sternohyoideus	depresses hyoid and lower jaw	Stengel (1962)
*Polyodon**	sternohyoideus	depresses hyoid and lower jaw	Danforth (1913)
Ginglymodians			
Lepisosteus	sternohyoideus	depresses hyoid and lower jaw	Lauder (1980a)
Halecomorphs			
Amia	sternohyoideus	depresses hyoid and lower jaw	Lauder (1980a)
Teleostei	sternohyoideus	depresses hyoid and lower jaw	Osse (1969), Lauder (1979), Liem (1980), Wainwright & Lauder (1986), Wainwright *et al.* (1989)
Sarcopterygians			
*Latimeria**	sternohyoideus	depresses hyoid and lower jaw	Lauder (1980b)
	sternohyoideus	depresses hyoid	Millot & Anthony (1958), Thomson (1967, 1970)
Dipnoans			
Lepidosiren	rectus cervicis	depresses hyoid and lower jaw	Bemis & Lauder (1986)
Amphibians			
Ambystoma	rectus cervicis	depresses hyoid and lower jaw	Lauder & Shaffer (1985), Shaffer & Lauder (1985)

Muscle synonymies from Edgeworth (1935), Winterbottom (1974), and Miyake *et al.* (1992). * Based on anatomical studies.

lungfish (geniothoracis), and from the rectus cervicis muscle in salamanders (geniohyoideus) and inserts on both sides of the mandibular symphysis in all taxa (Marion, 1905; Danforth, 1913; Daniel, 1922; Edgeworth, 1935; Stengel, 1962; Lauder, 1980a; Lauder & Shaffer, 1985; Shaffer & Lauder, 1985a,b; Miyake *et al.*, 1992; Motta & Wilga, 1995, 1999; Didier, 1995; Wilga, 1997). The coracomandibularis coupling has been lost in teleosts and gars. It has been inferred, from attachment areas on the bones, that a depressor gnathalis muscle originated from the scapulocoracoid and inserted onto both sides of the mandibular symphysis in *Dinichthyes* and *Coccosteus* as well as other Arctolepida and Brachythoraci placoderms (Heintz, 1932; Stensio, 1959; Miles, 1969; Miles & Westoll, 1968). According to Edgeworth (1935), the depressor gnathalis resembles the primordium of the hypobranchial muscles, and bears a striking resemblance to the coracomandibularis muscle.

The protractor hyoideus muscle in teleosts is commonly, albeit mistakenly, referred to as the geniohyoideus muscle, which is involved in the coracomandibularis coupling. According to Edgeworth (1935) and Winterbottom (1974), the protractor hyoideus is composed of a fusion of the intermandibularis posterior and the interhyoideus muscles which resulted in the protractor hyoideus which spans the hyoid and mandible. The intermandibularis spans the mandible while the closely apposed interhyoideus spans the hyoid in other fishes. Furthermore, they concluded that any muscle that is homologous to the geniohyoideus (coracomandibularis coupling) in other lower vertebrates has been lost in teleosts, as well as gars. However, the protractor hyoideus muscle is functionally analogous to the coracomandibularis coupling of other vertebrates and so we use it in our discussion to show the phylogenetically broad roles of these couplings in jaw mechanics.

The coracohyoideus muscle originates from the pectoral girdle or hypaxialis muscle and inserts onto the hyoid arch in virtually all extant lower vertebrates: Chondrichthyes (coracohyoideus complex); Osteichthyes and amphibians (sternohyoideus); dipnoans and amphibians (rectus cervicis) (Marion, 1905; Danforth, 1913; Daniel, 1922; Edgeworth, 1935; Stengel, 1962; Lauder, 1980a; Miyake *et al.*, 1992). In fact, since osteichthyans lack a sternum, it is morphologically more accurate that the 'sternohyoideus' be called a 'coracohyoideus'. In the sister group to all other holocephalans, Callorhynchidae, the coracohyoideus originates from the aponeurosis overlying the coracomandibularis, while in the more derived groups, Rhinochimaeridae and Chimaeridae, it originates from the pectoral girdle; and it inserts onto the basihyal in all groups (Edgeworth, 1935; Ribbink, 1971; Didier, 1995).

Most gnathostomes have a mandibulohyoid ligament that extends between the proximal region of the hyoid and the proximal region of the mandible. Elasmobranchs have several ligaments interconnecting the two elements, while holocephalans have a single ligament (Gegenbaur, 1865; Gadow, 1888; Daniel, 1915; Allis, 1923; Nobiling, 1977; Motta & Wilga, 1995, 1999; Didier, pers. comm.). Coelacanths, lungfish, and most actinopterygians have a MHL (Lauder, 1980a,b; Bemis, 1986; Bemis & Lauder, 1986). While some salamanders lack a MHL, others have a single MHL or a multi-branched hyomandibular ligament (Lauder & Shaffer, 1985; Findeis & Bemis, 1990; Elwood & Cundall, 1994). Thus, the presence of a MHL has been hypothesized to be primitive for the Teleostomi (Lauder, 1980a,b).

Function of the coracohyoideus coupling

Anatomical and experimental evidence on Chondrichthyes supports the role of the CH-coupling in mediating hyoid depression in aquatic lower vertebrates. In Osteichthyes, the CH-coupling also functions to depress the lower jaw but this function has not been found in chondrichthyans (Fig. 7). The CH-coupling depresses the hyoid in both Chondrichthyes and Osteichthyes (sternohyoideus), which expands the buccal cavity and aids in suction feeding and directing food posteriorly. In sharks, as in other extant aquatic gnathostomes, the proximal end of the hyoid is connected to the proximal end of the lower jaw by several ligaments, but this linkage does not appear to effect jaw depression via hyoid retraction (Gadow, 1888; Daniel, 1915; Allis, 1923; Nobiling, 1977; Motta & Wilga, 1995, 1999). Manual manipulation of the hyoid does not depress the mandible beyond the effect of pushing on the ventral floor of the buccal cavity and the underlying coracomandibularis muscle. In video images of feeding sharks, a distinct ventral bulging of the hyoid is observed to travel posteroventrally from behind the mandibular symphysis shortly after the start of lower jaw depression (Wu, 1994; Motta *et al.*, 1997; Wilga, 1997; Ferry-Graham, 1998; Wilga & Motta, 1998a, 2000). As the hyoid is depressed, it rotates around the hyomandibular-ceratohyal and mandibular-hyomandibular articulations in *N. brevirostris*, *Squalus acanthias*, and *Sphyrna tiburo* through an angle between the mandible and the hyoid, from 0° to 55–70° at peak hyoid depression. Thus, the hyoid rotates independently of the lower jaw and the MHL ligaments do not appear to transmit hyoid rotation to the mandible.

When the mouth is opened in sharks, the proximal end of the hyoid does not move posterodorsally as in teleosts. Instead this element is rotated anteroventrally, displacing the entire jaw apparatus anteroventrally relative to the chondrocranium. Since posterodorsal elevation of the proximal end of the hyoid does not occur it cannot function to depress the lower jaw in a manner similar to that in bony fishes. Furthermore, peak hyoid depression occurs during elevation of the lower jaw in sharks, well after peak lower jaw depression has taken place.

Electromyographic data support this interpretation as activity in the coracohyoideus and coracoarcualis muscles do not begin until 25–43 ms after the onset of coracomandibularis activity and may not begin until well after the onset of lower jaw depression in *Squalus acanthias* and *N. brevirostris* (Wilga & Motta, 1998a; Motta *et al.*, 1997). Thus, the CH-coupling is unlikely to mediate lower jaw depression in elasmobranchs by transmitting movements of the hyoid to the mandible through the MH ligaments.

The CH-coupling does not mediate lower jaw depression in batoids and does not appear to do so in holocephalans, although experimental data on the latter group is lacking. These taxa present unique cases due to the distinctive morphology of their jaw suspension systems. The hyoid arch has separated in batoids with the ventral portion of the hyoid arch (ceratohyal) associated with the first branchial arch and the dorsal portion (hyomandibula) connected to and supporting the jaws (Gregory, 1904; Maisey, 1980). The coracohyoideus inserts onto the ventral portion of the hyoid arch, which is not connected to the jaws and therefore precludes it from mediating lower jaw depression (Wilga & Motta, 1998b). In support of this, the coracohyoideus (see CH1 in Fig. 6) is not active during lower jaw depression in *R. lentiginosus* (Wilga & Motta, 1998b). However, batoids have a novel division of the coracohyoideus muscle, the coracohyomandibularis that arises from the embryonic coracohyoideus along with the coracoarcualis and inserts onto the hyomandibula (Marion, 1905; Miyake *et al.*, 1992). The coracohyomandibularis depresses the hyomandibula and in doing so also depresses the jaw apparatus, but is not active until the latter half of lower jaw depression when the mouth has already been partially opened (Wilga & Motta, 1998b). Experimental evidence suggests that the role of the coracohyomandibularis muscle is to expand the orobranchial region for the production of suction (Wilga & Motta, 1998b).

Holocephalans are the only living gnathostomes to possess a morphologically complete hyoid arch that is not involved in suspending the jaws from the cranium and is free from the cranium (Gregory, 1904; Maisey, 1980; Didier, 1995). The coracohyoideus in holocephalans also appears to function in depressing the hyoid (Ribbink, 1971; Didier, pers. comm.). Although a MHL ligament is present that may assist lower jaw depression in holocephalans, this mechanism must work in conjunction with the coracomandibularis in those holocephalan groups in which the coracohyoideus originates from the coracomandibularis (Didier, 1995).

Although the visceral skeleton in placoderms is poorly known, the presence of hypobranchial muscles that depress the hyoid arch has been inferred in detailed morphological analyses of other researchers (Miles & Westoll, 1968; Denison, 1978). Thus, it appears that the CH-coupling in Chondrichthyes and possibly placoderms serves to expand the orobranchial cavity by depressing the hyoid. It is unclear whether the CH-coupling in placoderms included an MH ligament and if such a linkage was involved in jaw depression.

Experimental analyses of the coracohyoideus coupling in bony fishes (sternohyoideus) and aquatic salamanders (rectus cervicis) indicates that it functions to depress the hyoid (see Fig. 2) (Lauder, 1985; Lauder & Shaffer, 1993). During hyoid depression the proximal end of the hyoid is rotated posterodorsally, pulling the MH ligament which then pulls the proximal end of the lower jaw posterodorsally resulting in depression of the lower jaw (Liem, 1980; Lauder, 1979, 1980a, 1985; Shaffer & Lauder, 1985a; Bemis & Lauder, 1986). Although activity in all of the head muscles overlap broadly during feeding, activity in the sternohyoideus (coracohyoideus homologue) in bony fishes and rectus cervicis (coracohyoideus homologue) muscles in salamanders coincides with the mouth opening phase and thus the CH-coupling is the primary mechanism of lower jaw depression in bony fishes and salamanders (Osse, 1969; Liem, 1980; Lauder, 1979, 1980a; Barel, 1983; Shaffer & Lauder, 1985b; Lauder & Shaffer, 1985; Bemis & Lauder, 1986; Aerts *et al.*, 1987; Aerts, 1991). The hyoid arch is poorly known in acanthodians. However, a small accessory element between the hyomandibula and ceratohyal of *Acanthodes* is presumed to be an interhyal. The presence of this element indicates that the hyoid arch may have played a role in the jaw mechanism in *Acanthodes* similar to that in extant bony fishes (Miles, 1964, 1968), which suggests that it possessed a CH-coupling similar to that of extant bony fishes.

Secondary mechanisms for jaw depression that operate independently of the CH-coupling exist in various groups. Teleosts possess an opercular coupling (see Fig. 2) (Osse, 1969; Anker, 1974; Barel *et al.*, 1977), and batoids, lungfish and salamanders have independently evolved a depressor mandibularis coupling (Lauder & Shaffer, 1985; Shaffer & Lauder, 1985a,b; Bemis & Lauder, 1986).

Function of the coracomandibularis coupling

Functional analyses of feeding in *Squalus acanthias*, *N. brevirostris*, *Sphyrna tiburo* and *R. lentiginosus* indicate that the CM-coupling mediates depression of the lower jaw in this phylogenetically broad sample of elasmobranchs (Wilga & Motta, 1998a,b, in review; Motta *et al.*, 1997). Ribbink (1971) proposed that the coracomandibularis muscle is responsible for depressing the lower jaw in holocephalans. As illustrated by Didier (1995) and Ribbink (1971), the origin of the coracomandibularis muscle is ventral to the jaw joint in holocephalans, resulting in a line of action that would depress the lower jaw. Good evidence based on detailed morphological studies of placoderms show that a CM-coupling connected the pectoral girdle to the lower jaw, with a line of action ventral to the jaw joint (Heintz, 1932; Stensio, 1959; Miles, 1969; Miles & Westoll, 1968). As a result of these studies, the CM-coupling in placoderms has been hypothesized to depress the mandible (Heintz, 1932; Stensio, 1959; Miles, 1969; Miles & Westoll, 1968).

The role of the CM-coupling during feeding is variable in bony fishes and aquatic salamanders. The branchiomandibularis (coracomandibularis coupling) is active during lower jaw depression in *Amia* in capture events and during lower jaw elevation in manipulation events in *Polypterus* and *Amia* (Lauder, 1980a). Some insight into this apparent dual role is provided by Elshoud-Oldenhave and Osse (1976) and Lauder (1979, 1981), who noted that the function of the coracomandibularis coupling changes depending on its line of action. When the line of action is dorsal to the jaw joint it elevates the lower jaw and when it is ventral to the jaw joint it depresses the lower jaw. In an anatomical study of the head of *Acipenser*, Stengel (1962) proposed that the branchiomandibularis acts to depress the lower jaw. In teleosts, instead of a branchiomandibularis, the protractor hyoideus (analogous to the coracomandibularis coupling) protracts the hyoid and compresses the buccal cavity (Osse, 1969; Lauder, 1979; Liem, 1980; Wainwright & Lauder, 1986; Wainwright *et al.*, 1989). Perhaps, as the sternohyoideus (coracohyoideus coupling) took an increasing role in depressing the lower jaw, the branchiomandibularis (coracomandibularis coupling) atrophied until it was lost. Meanwhile, the protractor hyoideus evolved to function primarily in protracting the hyoid and compressing the buccal cavity.

In an anatomical study of *Latimeria*, Lauder (1980b) proposed that the coracomandibularis acts to elevate the lower jaw or compress the buccal cavity rather than to depress the lower jaw as reported by Millot and Anthony (1958), Thomson (1967, 1970), and Trewavas (1959). In *Ambystoma*, the geniohyoideus (coracomandibularis coupling) is active during lower jaw depression and buccal compression after the jaws have closed (Shaffer & Lauder, 1985a,b; Lauder & Shaffer, 1985). The geniothoracis (coracomandibularis coupling) is active throughout the feeding event from lower jaw depression through lower jaw elevation in *Lepidosiren* (Bemis & Lauder, 1986). Distinct muscle attachment sites have led researchers to the hypothesis that general ‘fish type’ mandibular and hyoid muscles can be restored in *Acanthodes* (Miles, 1968). If so, then this suggests that a protractor hyoideus (coracomandibularis coupling) that functioned similarly to that in Osteichthyes may have been present in *Acanthodes*. Thus, the role of the coracomandibularis coupling in basal bony fishes and acanthodians appears to be both jaw depression and buccal compression and that in teleosts is primarily in hyoid retraction and buccal compression.

Evolution of jaw depression couplings

We define the CH-coupling as a coracohyoideus muscle, or its derivative, originating on the pectoral girdle and attaching on the hyoid with a ligamentous connection between the hyoid and the mandible. This anatomical configuration exists in all living gnathostome groups, apparently existed in acanthodians (Denison, 1978), and may have existed in placoderms (Miles, 1968, 1969). We therefore hypothesize that the anatomical CH-coupling was present in the common ancestor of living gnathostomes (see Fig. 7, Bar #1). However, there is no clear indicaion of the functioning of the CH-coupling in lower jaw depression in placoderms. A CH-coupling that functions in jaw depression is not known from Chondrichthyes. However, the CH-coupling is the primary mechanism of jaw depression in actinopterygians, lungfishes, and aquatic salamanders. It has been inferred to function in *Latimeria* and acanthodians (Miles, 1964, 1968; Lauder, 1980a,b). Therefore, a CH-coupling that functions to depress the jaw appears to be primitive for the Teleostomi, as Lauder (1980a, b) suggested (see Fig. 7, Teleostomi = Acanthodii and Osteichthyes). This interpretation implies that the anatomical CH-coupling existed in gnathostomes before a role in jaw depression evolved.

To summarize our interpretation of the evolution of gnathostome jaw mechanics, we recognize two states of the CM-coupling in gnathostomes (see Fig. 7). A CM-coupling between the pectoral girdle and mandible that functions to depress the lower jaw is present in elasmobranchs plus holocephalans and is therefore inferred to be primitive for Chondrichthyes. Existing interpretations indicate that a coracomandibularis-like muscle in placoderms connected the pectoral girdle and mandible (Heintz, 1932) and we infer by similarity to living groups that this muscle may have been a jaw depressor in placoderms. If our functional interpretations of the fossil taxa are correct, and in light of the phylogenetic hypothesis presented in Figure 7 we note that this condition is estimated to have been present in the common ancestor of placoderms and living gnathostomes (Bar #1 Fig. 7). This conclusion must be tempered by the lack of unequivocal evidence for the mechanism of jaw depression in placoderms. In actinopterygians, coelacanths, lungfish, amphibians, and probably acanthodians the CM-coupling attaches onto the hyoid or branchial arch and is primarily involved with protraction of the hyoid and compression of the buccal cavity, but may also contribute to depression of the lower jaw in some groups. Determination of coracomandibularis muscle function in *Acipenser*, *Polyodon*, and *Latimeria* awaits experimental analyses. Thus, because this character state is shared by the major lineages of the Osteichthyes we hypothesize that it is primitive for the clade (see Bar #2, Fig. 7). These observations imply a transformation series of the jaw depression mechanism in gnathostomes that begins with jaw depression by the CM-coupling, as seen in living chondrichthyans. This mechanism was then replaced by the CH-coupling in Osteichthyes, in conjunction with a shift in attachment of the analogous CM-coupling which resulted in a more diverse role of the CH-coupling.

Future research should focus on two areas. First, a refined anatomical understanding of fossil lineages, such as placoderms, that pre-date the presumed split between Chondrichthyes and Osteichthyes is needed. Of particular interest will be estimates of the origin of the mandibulohyoid ligament, and attempts to test the hypotheses of coracomandibularis function in jaw depression. Because Chondrichthyes are the only living vertebrate lineages in which jaw depression is effected by the CM-coupling further functional analyses of holocephalans and basal elasmobranch taxa will be important to our interpretation of the fossil forms.

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