Evolutionary divergence in the feeding mechanism of fishes

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ABSTRACT:

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After the divergence of chondrichthyans and teleostomes, the structure of the feeding apparatus also diverged. Hyoid morphology varies considerably among fossil and extant elasmobranchs and has been hypothesized to be related to feeding style. How hyomandibular morphology affects function during feeding is of great interest since hyoid movement is a key component in the feeding mechanism. Cranial kinematics and buccal pressure during feeding was quantified in elasmobranchs and teleostomes. The feeding mechanism in elasmobranchs with anterior (AHY) or lateral (LHY) directed hyomandibulae differs from teleostomes primarily in hyoid movements due to morphological constraints. The hyoid expands ventrally during feeding in the species studied; however, the hyoid laterally compresses in AHY and LHY species but not in teleostomes or shark species with posterior directed hyomandibulae (PHY). Anterior and lateral hyomandibular orientation in elasmobranchs constrains them to adduct during feeding. This represents a fundamental difference in the feeding mechanism regardless of feeding style between elasmobranchs with AHY or LHY compared to sharks with PHY and teleostomes as a result of morphological divergence in hyoid morphology. It appears that posterior directed hyomandibulae may have evolved to increase the gape in specialized bite feeding sharks while lateral directed hyomandibulae evolved in specialized suction feeders.

Key words: Elasmobranchii, Teleostomi, Suction feeding, Jaw mechanism.

INTRODUCTION

After the divergence of chondrichthyan and teleostome fishes in the Ordovician period, the structure of the jaw apparatus and jaw suspension also diverged considerably between the two groups (WILGA 2002). Despite this, a general pattern of mouth opening, followed by expansion of the buccal cavity and then branchial expansion occurs during feeding in all fishes studied thus far (LAUDER & SHAEFFER 1993, WESTNEAT 2006, WILGA & *al.* 2007). Mouth shape also

varies widely and is typically associated with feeding style: biters tend to have relatively long jaws with large teeth while suction feeders tend to have relatively shorter jaws with smaller teeth. The hyoid arch is responsible for expanding the buccal cavity; however most studies of fish feeding only measure expansion in the vertical direction (LAUDER & SHAEFFER 1993, WESTNEAT 2006, WILGA & *al.* 2007), thereby hindering 3D analyses of hyoid function.

Jaw and hyoid morphology of chondrichthyans differs from that of teleostomes in several ways: num-
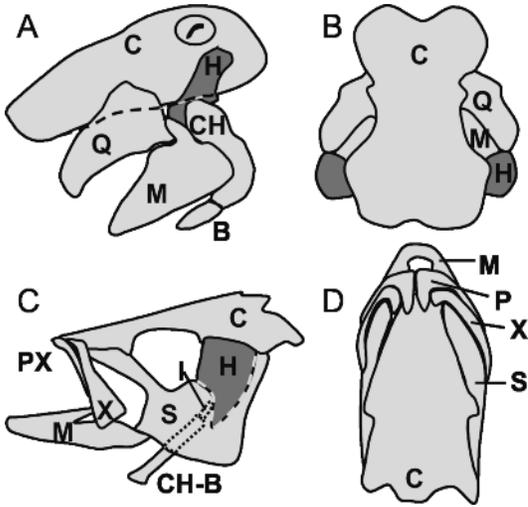
Fig. 1.Morphology of the cranium, jaws and hyoid arch in sharks and teleostomes. Lateral (A) and dorsal (B) views of a shark; lateral (C) and dorsal (D) views of a teleostome. B, basihyal; C, cranium; CH, ceratohyal; H, hyomandibula; I, interhyal; M, lower jaw; P, posteriorly directed hyomandibula; PX, premaxillary or upper jaw; Q, palatoquadrate or upper jaw; S, suspensorium; X, maxilla, part of upper jaw in some teleostomes. Note that H is part of the suspensorium (hyomandibula, pterygoids, symplectic) but has been delineated here for comparison

ber of elements, suspension, structural materials (GRE-GORY 1904, BOND 1996, WILGA 2002) (Text-fig. 1). Sharks have a chondrocranium from which the upper and lower jaws (palatoquadrate and Meckel's cartilages respectively) are suspended by the hyoid arch posteriorly and ligaments anteriorly. The hyoid arch is composed of hyomandibular cartilages that project laterally from the cranium and connect to underlying ceratohyal cartilages distally with a single interconnecting basihyal. Batoids are similar except they lack the anterior ligaments and the ceratohyal-basihyal cartilages are associated with the first branchial arch rather than the hyomandibular cartilage. In holocephalians, the hyoid does not suspend the jaws and is morphologically and functionally a branchial arch. Teleostomes have evolved many dermal bones overlying the now ossified cranium, the palatoquadrate has been subdivided and ossified with dermal bones now forming the upper jaw, Meckel's cartilage is reduced and overlaid by dermal bones now forming the lower jaw and the hyoid arch is ossified with an interhyal bone interconnecting the hyomandibula and ceratohyal. The hyoid arch projects ventrally from the cranium and is incorporated into the suspensorium and opercular series, which are composed of numerous dermal bones.
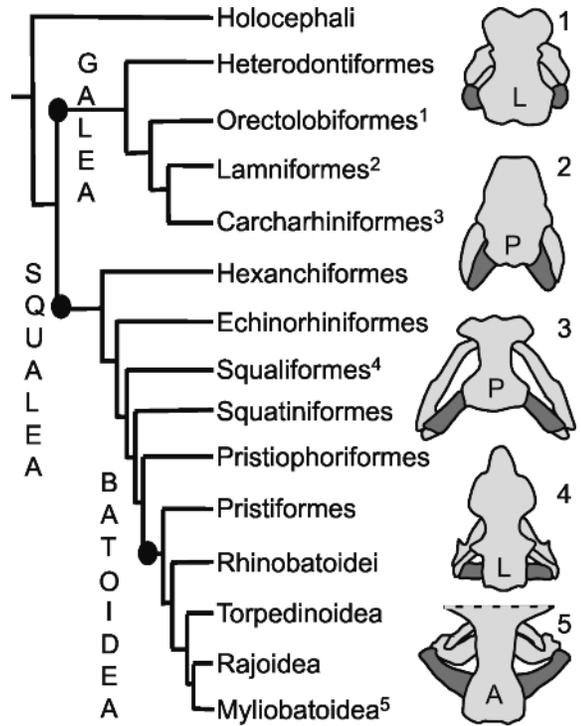

Fig. 2. Chondrichthyan phylogeny according to SHIRAI (1996) with hyomandibular cartilage orientation of major groups shown in dorsal view. Based on species from 52 genera, 29 families and all orders, except Centrophoriformes (DENISON 1937, MOSS 1977, GARMAN 1997, COMPAGNO 1973, 1988, SHIRAI 1992, WILGA 2002, 2005). A, anteriorly directed hyomandibula; C, cranium; H, hyomandibular cartilage; L, laterally directed hyomandibula; M, Meckel's cartilage; Q, palatoquadrate cartilage

A general pattern of jaw and hyoid movements occurs during feeding in all elasmobranchs studied thus far (WILGA & al. 2007). Just after the lower jaw is depressed, the basihyal is depressed posteroventrally causing the ceratohyal to pivot around the distal hyomandibula thus expanding the buccal cavity ventrally. As the basihyal clears the resting position between the lower jaws, the ceratohyal is also pulled posteroventrally, which in turn pulls the distal end of the hyomandibula ventrally as the proximal end of the hyomandibula moves like at hinge at the cranio-hyomandibular joint. A similar pattern occurs in teleostomes, except the vertically oriented hyomandibulae moves laterally outward with the suspensoria as the ceratohyal is depressed during feeding (LAUDER & SHAEFFER 1993, WESTNEAT 2006).

The orientation of the hyomandibulae differs greatly among elasmobranchs and has been hypothesized to be related to feeding style (MOSS 1977, WILGA & MOTTA 1998a, 1998b, 2000, DEAN &

MOTTA 2004, WILGA & SANFORD, in review) (Text-fig. 2). Heterodontiform and orectolobiform sharks have short laterally or slightly anteriorly directed hyomandibulae (L) that move ventrally and slightly anteriorly and when combined with very short jaws and labial folds facilitate suction feeding. Carcharhiniform and lamniform sharks have long jaws and long posterior directed hyomandibulae (P) that are thought to swing anterolaterally during feeding enabling a large bite. Squaliform sharks also have short jaws and labial folds with short laterally directed hyomandibulae (L) that are presumed to move only ventrally providing an effective cutting mechanism. Batoids have short jaws, which lack anterior ligaments to the cranium, and long anteriorly directed hyomandibulae (A) that presumably swing anteroventrally during feeding enabling extreme ventral jaw projection for feeding from the substrate. That hyoid vertical depth must increase is given since the basihyal must clear the opened jaws or deflect potential prey. What is not clear is the relationship of hyoid lateral width as the jaws open given the variation in hyomandibular orientation. The resting distance between the distal ends of the hyomandibulae determines hyoid lateral width and may increase, decrease or remain the same depending on the resting distance. If the distal tips of anteriorly directed hyomandibulae were to increase, then the two jaw joints would be placed in tension and would act to close the mouth. The distal tips of laterally directed hyomandibulae are already maximally distant; therefore the only option is to remain the same distance or decrease. However, the distal tips of posteriorly directed hyomandibulae may be pulled laterally if the jaw joints flare laterally when the lower jaw is depressed, if the jaws are pulled anteriorly or they may simply decrease.

How hyomandibular morphology affects function and thus influences feeding style in fishes is of great interest since hyoid arch movements have been shown to be a key component in the feeding mechanism of fishes, particularly in the generation of suction, which is the predominant mode of feeding in teleostomes (LAUDER & SHAEFFER 1993, WILGA 2002). In this study, hyoid mechanics in elasmobranchs are compared to that of teleostomes in an attempt to understand the functional and evolutionary changes that have taken place as the morphology of the jaw apparatus and suspension diverged between the two groups. More specifically, several hypotheses regarding orientation of the hyomandibula and function will be assessed. 1) Laterally directed hyomandibulae will move ventrally and medially resulting in lateral compression of the hyoid cavity. 2) Anteriorly directed hyomandibulae will move ventrally and medially resulting in lateral compression of the hyoid cavity or adduction of the distal hyomandibular tips. 3) Posteriorly directed hyomandibulae will move ventrally and laterally resulting in lateral expansion of the hyoid cavity or abduction of the distal ends of the hyomandibular tips. 4) Ventrally directed hyomandibulae will move laterally resulting in lateral expansion or abduction of the distal ends of the hyomandibular tips. 5) The relation of suction generation to hyomandibular orientation will be assessed.

METHODS

Internal jaw and hyoid kinematics and buccal pressure were quantified during feeding in three elasmobranch species (white-spotted bamboo shark, *Chiloscyllium plagiosum*, Orectolobiformes, Galea; spiny dogfish, *Squalus acanthias*, Squaliformes, Squalea; and Little skates, *Leucoraja erinacea* Rajiformes, Batoidea (WILGA & SANFORD, in review; WILGA & *al.* in preparation). The distance between moving skeletal elements in the elasmobranchs was recorded using sonomicrometry (see SANFORD & WAINWRIGHT 2002, WILGA & SANFORD, in revision). Crystals were placed to record changes in mouth opening distance, changes in hyoid area lateral width and vertical height, and distal hyomandibular tip movement relative to the anterior cranium. A pressure transducer was placed in the buccal cavity to record suction pressure generation simultaneously with kinematics (see SANFORD & WAINWRIGHT 2002, WILGA & SANFORD, in revision). At least five feeding sequences from at least four individuals were used.

To expand the data set, hyoid movements of two additional shark species was investigated using manual manipulation. The jaw and hyoid apparatus of a shortfin mako shark, *Isurus oxyrinchus,* and a sandbar shark, *Carcharhinus plumbeus,* were implanted with sonometric crystals as above. The specimens were manually manipulated under water to simulate at least four "bite capture" sequences, mimicking the positions of the jaw and hyoid apparatus during feeding in closely related species (TRICAS & MCCOSKER 1984, MOTTA & *al.* 1997).

The data collected on the elasmobranchs was compared to two published studies on teleostomes, *Micropterus salmoides* (SANFORD & WAINWRIGHT 2002) and *Amia calva* (LAUDER 1980). The kinematics of analogous internal skeletal movements and buccal pressure was reported for *M. salmoides* while only the
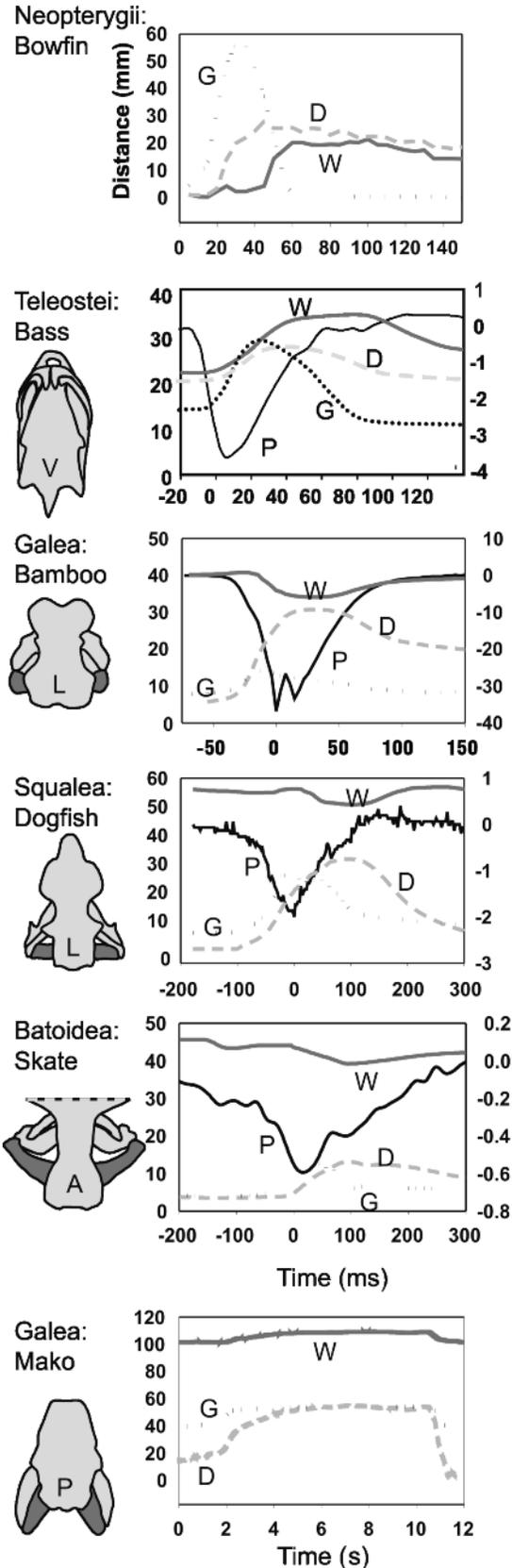
kinematics of external skeletal movements was reported for *A. calva.* Pressure in the anterior and posterior ends of the buccal cavity are similar in *C. plagiosum* (WILGA & SANFORD, in revision), thus the assumption is made for all species as well.

RESULTS

Hyoid arch movement during prey capture in *Amia calva* (vertical hyomandibula) is accomplished in two stages (LAUDER 1980). Mouth opening (gape) is followed by hyoid ventral depression and then when maximum hyoid depression is attained the hyoid begins to expand laterally (Text-fig. 3). The prey was observed to be drawn into the mouth of the fish, indicating that suction was used during capture. In contrast, during prey capture in *Micropterus salmoides* (vertical hyomandibula), mouth opening is rapidly followed by simultaneous ventral depression and lateral expansion of the hyoid (Text-fig. 3). Subambient buccal pressure rapidly declines and reaches a minimum (mean -5.2 kPa) prior to peak gape.

As the hyoid arch is ventrally depressed it is also medially compressed (adducted) during feeding in the three free feeding elasmobranch species: *Chiloscyllium plagiosum* (L)*, Squalus acanthias* (L) and *Leucoraja erinacea* (A) (Text-fig. 3). *Chiloscyllium plagiosum* generates greater subambient buccal pressure (mean -31 kPa) during prey capture than *S. acanthias* (mean -2 kPa) or *L. erinacea* (mean -0.45 kPa). During manual manipulation of *Isurus oxyrinchus* (P) and *Carcharhinus plumbeus* (P), the hyoid expanded both laterally and ventrally during mouth opening. The extent of expansion was typically greater in *I. oxyrinchus* than *C. plumbeus*. During hyoid expansion, the distance between the anterior cranium and distal hyomandibulae also increased indicating that the hyomandibulae swing outward, forward, and downward as the mouth opens. This will be verified in a future study on free feeding shark species with posteriorly directed hyomandibulae.

Fig. 3. Plots of jaw and hyoid kinematics and buccal pressure versus time during feeding in teleostome and elasmobranch fishes with hyomandibular orientation. Bowfin, *Amia calva*; Bass, *Micropterus salmoides*; Bamboo, *Chiloscyllium plagiosum*; Dogfish, *Squalus acanthias*; Skate, *Leucoraja erinacea*. Left Y axis is distance in mm and right Y axis is pressure when values are indicated. Thin black line, gape pressure; dotted line, gape opening distance; dashed gray line, hyoid ventral expansion distance; thick solid gray line, hyoid lateral width distance. B, gape distance; D, hyoid vertical distance; W, hyoid width distance; P, buccal pressure
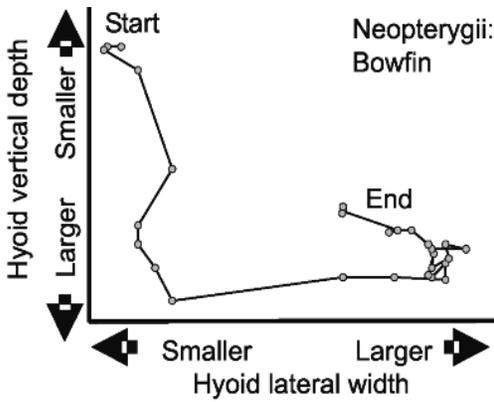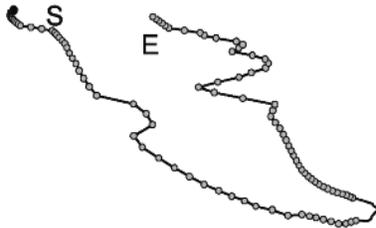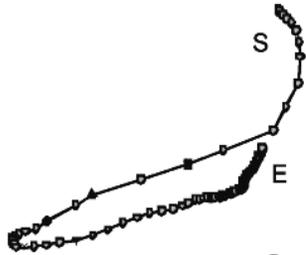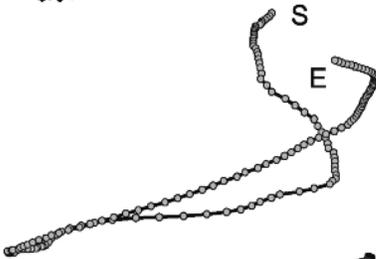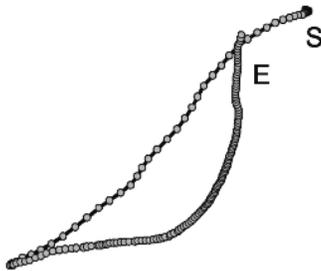
DISCUSSION

The prey capture mechanism in elasmobranchs differs from that of teleostomes primarily in hyoid arch movements based on resting orientation of the hyomandibulae. In all of the elasmobranch and teleostome species examined here, the hyoid is expanded ventrally during feeding as the basihyal is pulled posteroventrally. At the same time, the hyoid is also expanded laterally in the two teleostome species, *Amia calva* and *Micropterus salmoides*. In contrast, the hyoid is laterally compressed during feeding in the three elasmobranch species with lateral and anterior directed hyomandibulae, *Chiloscyllium plagiosum* (L), *Squalus acanthias* (L) and *Leucoraja erinacea* (L). Thus, those species with laterally or anteriorly directed hyomandibulae have a radically different pattern of hyoid lateral movement compared to the two teleostome species (Text-fig. 4). However, similar to the two teleostome species (ventral hyomandibulae) the hyoid is laterally expanded in the two species with posterior directed hyomandibulae during simulated feeding, *Isurus oxyrinchus* and *Carcharhinus plumbeus*.

This divergence in hyoid movements during prey capture in the elasmobranchs and teleostomes studied here appears to be due to morphological constraint. When the basihyal is depressed, the ceratohyal-hyomandibular joint is pulled ventrally, as in a 3D 6-bar linkage. The orientation of the hyomandibulae, when anterior or laterally directed constrains the distal tips of the hyomandibulae to adduct when the basihyal is depressed (Text-fig. 5). Laterally directed hyomandibulae are already or near maximally distant, therefore they can only move ventrally and this causes the inter-tip distance to decrease, more like a 2D 6-bar linkage. However, compression of the distal hyomandibulae laterally as the basihyal is depressed ventrally causes a temporal delay in the attainment of peak pressure during suction feeding (WILGA & SANFORD in revision). Compression of the lateral plane as the vertical plane expands acts to decrease or temporarily stall total volumetric expansion of the buccal cavity, compared to expansion of both planes. Indeed, a characteristic inflexion occurs in the pressure trace of the specialized suction feeder, *C. plagiosum*, as hyoid width begins to decrease and then again as it reaches a minimum. This is in direct contrast to teleostomes, in which lateral and ventral expansion of the hyoid arch functions simulta-

Fig. 4. Plots of hyoid vertical depth to hyoid lateral width in teleostome and elasmobranch fishes with hyomandibular orientation. Species as in Fig. 3. S, start of hyoid movement. E, end of hyoid movement

Elasmobranchs

Anterior and lateral directed hyomandibulae

Posterior directed hyomandibulae

Teleostomes

Vertical directed hyomandibulae
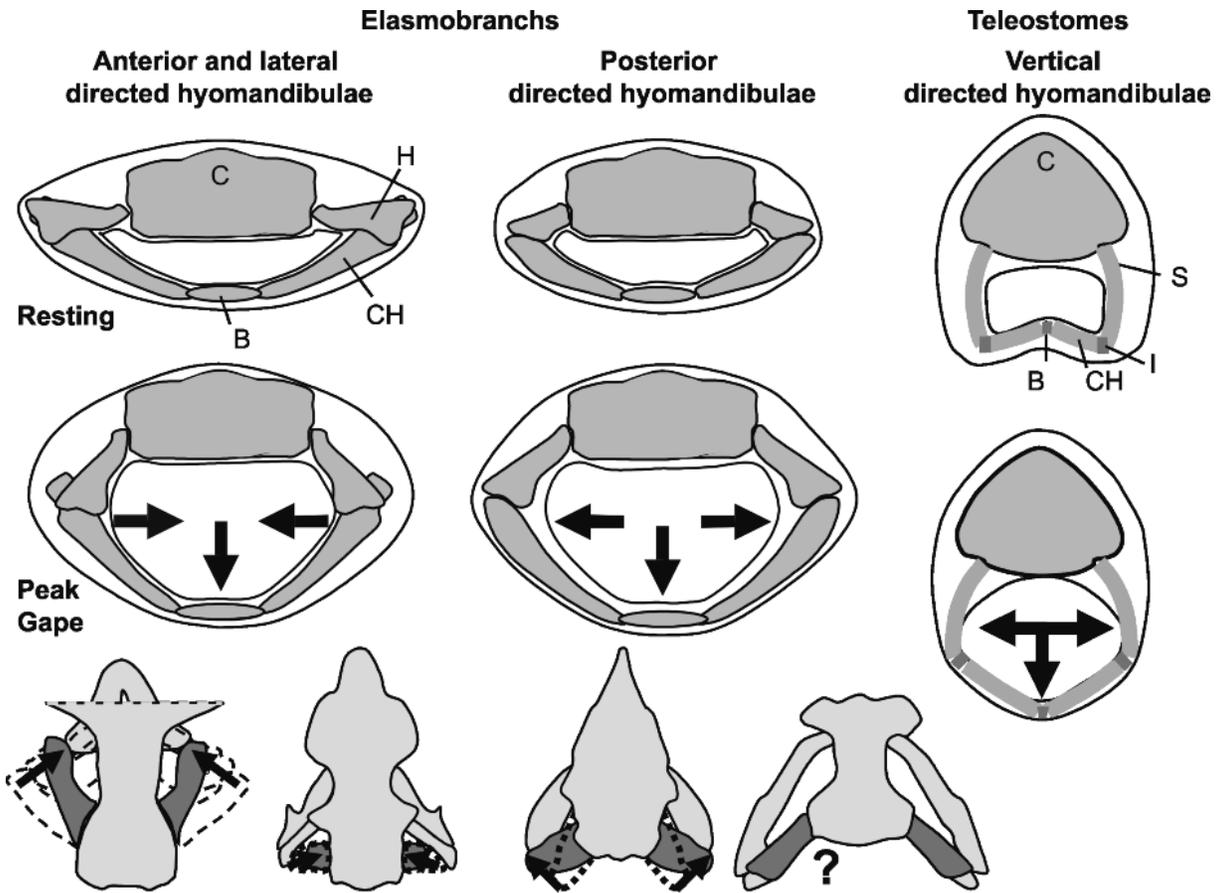
Fig. 5. Mechanics of hyoid expansion in elasmobranch and teleostome fishes. Top row show resting position, middle row peak gape position and bottom row shows hyomandibular orientation in resting (dotted) and peak gape position. Left column illustrates elasmobranchs with anteriorly and laterally directed hyomandibulae, middle column illustrates sharks with posteriorly directed hyomandibulae and right column illustrates teleostomes. B, basihyal; C, cranium; CH, ceratohyal; I, interhyal; S, suspensorium (hyomandibula, pterygoids, symplectic)

neously to expand the buccal cavity to generate suction (Text-figs 3, 4) (LAUDER 1980b, NORTON & BRAINERD 1993, NEMETH, 1997, SANFORD & WAINWRIGHT 2002, WILGA & *al.* 2007, WILGA & SANFORD, in revision; WILGA & *al.* in preparation). However, *C. plagiosum* (L) and *Narcine brasiliensis* (A) are able to generate considerable suction (both mean -21 kPa), as great or greater than that of teleostomes (mean -5 to -30 kPa), while paradoxically compressing the hyoid arch laterally (DEAN & MOTTA 2004, HIGHAM & *al.* 2006, WILGA & SANFORD in revision). This represents a fundamental difference in hyoid mechanics during feeding, particularly during suction, in elasmobranchs and teleostomes – compression vs expansion.

The morphological constraint does not appear to exist in the two species with posteriorly directed hyomandibulae, *Isurus oxyrinchus* and *Carcharhinus plumbeus*. Instead, the distal hyomandibulae abduct during simulated feeding as in teleostomes. Simulta-

neous lateral and ventral expansion of the hyoid arch in this case functions to produce a large mouth area. Depression of the basihyal and ceratohyal not only pulls the distal tips of the hyomandibulae ventrally, but they also appear to rotate anteriorly, much like unfolding a 3D 6-bar linkage. Anteroventral rotation of the hyomandibular tips increases the distance between the tips thereby increasing hyoid lateral width. It has long been suspected (MOSS 1977) and recently shown that shark species with long posteriorly directed hyomandibulae and long jaws have a larger mouth opening during feeding than those with lateral or anterior directed hyomandibulae (WILGA 2002). Lamniform and carcharhiniform sharks species have long posteriorly directed hyomandibulae and typically use grasping or biting to capture prey and do not rely as heavily on suction as orectolobiforms (L) and some batoids (A). However, the mechanism of hyoid movement must be tested experimentally during feeding in a car-
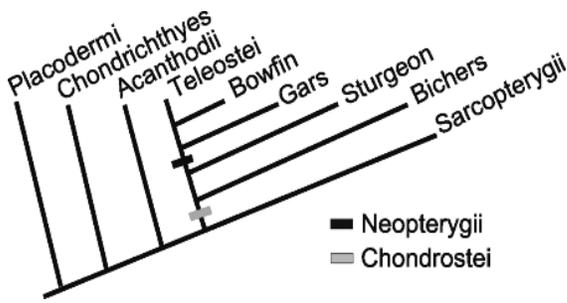
Fig. 6. Phylogeny of fishes (based on SHIRAI 1996 and BOND 2004)

charhiniform or lamniform species to verify that the simulations were accurate.

The question remains, what evolutionary mechanism has driven this divergence in hyomandibular orientation (horizontal vs vertical) between chondrichthyans and teleostomes? At what point did this mechanical and functional change occur? Lateral and ventral expansion of the hyoid arch occurs in *Amia calva* and *Micropterus salmoides*, therefore the trait is present in Neopterygii (LAUDER 1980, SANFORD & WAINWRIGHT 2002) (Text-fig. 6). Depression of the hyoid arch may be responsible for lateral orobranchial expansion in pallid sturgeon *Scaphirhynchus albus* (CARROLL & WAINWRIGHT 2003). If so, then the trait occurs in Chondrostei, even though they have retained the palatoquadrate and Meckel's cartilages as in chondrichthyans and have anteriorly directed hyomandibulae like batoids, but also have some of the dermal bones associated with the jaws as is typical of teleostomes. It appears that lateral and ventral expansion of the hyoid arch during suction feeding is an ancestral trait in Actinopterygii.

Similarly, what evolutionary mechanism has driven the alteration in hyomandibular cartilage orientation among elasmobranchs (Text-fig. 2)? Posterior or lateral oriented hyomandibulae is the basal state in various stem elasmobranchs. The orientation of the hyomandibulae in *Pleuracanthus* (Xenacanthida), *Palaeospinax* and *Chlamydoselachus* (Hexanchiformes) is posteriorly directed but that in *Hybodus* (Hyobodontida) appears to be more lateral directed than posterior (JOLLIE 1962, MILES 1968, MAISEY 1977, SCHAEFFER 1981, ZANGERL 1981). At some point a mechanical and functional change occurred from more posteriorly directed in stem selachians to the diversity of states in extant elasmobranchs. The trend is reversed in galean and squalean clades. Heterodontifomes and Orectolobiformes, which are both specialized suction feeders, are at the base of the galean clade and have laterally directed hyomandibulae. In contrast Carcharhiniformes, which are generalist feeders, and Lamniformes, which are specialized biters, are crown groups that have long posterior

oriented hyomandibulae. However, lamniform sharks have more acute posterior oriented hyomandibulae than carcharhiniform sharks. In contrast, hexanchiform sharks, which are at the base of the squalean clade, have long posterior directed hyomandibulae and are also biters, while the more derived Squaliformes, which are generalists have lateral directed hyomandibulae. The crown batoids are mostly generalists and have anterior directed hyomandibulae. Therefore posterior directed hyomandibulae may have evolved to increase the gape in specialized bite feeding sharks while lateral directed hyomandibulae evolved in specialized suction feeders with more generalized feeders having intermediate and anterior directed hyomandibulae. Future studies will include detailed morphological analyses of hyomandibular and joint structure in a broad range of elasmobranchs and more live feeding studies of carcharhininiform, lamniform and chondrosteans to better understand the evolution of morphology and function of the hyoid apparatus.

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