

# Functional Morphology of Prey Capture in the Sturgeon, *Scaphirhynchus albus*

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**ABSTRACT** Acipenseriformes (sturgeon and paddlefish) are basal actinopterygians with a highly derived cranial morphology that is characterized by an anatomical independence of the jaws from the neurocranium. We examined the morphological and kinematic basis of prey capture in the Acipenseriform fish *Scaphirhynchus albus*, the pallid sturgeon. Feeding pallid sturgeon were filmed in lateral and ventral views and movement of cranial elements was measured from video sequences. Sturgeon feed by creating an anterior to posterior wave of cranial expansion resulting in prey movement through the mouth. The kinematics of *S. albus* resemble those of other aquatic vertebrates: maximum hyoid depression follows maximum gape by an average of 15 ms and maximum opercular abduction follows maximum hyoid depression by an average of 57 ms. Neurocranial rotation was not a part of prey capture kinematics in *S. albus*, but was observed in another sturgeon species, *Acipenser medirostris*. Acipenseriformes have a novel jaw protrusion mechanism, which converts rostral rotation of the hyomandibula into ventral protrusion of the jaw joint. The relationship between jaw protrusion and jaw opening in sturgeon typically resembles that of elasmobranchs, with peak upper jaw protrusion occurring after peak gape. *J. Morphol.* 256:270–284, 2003. © 2003 Wiley-Liss, Inc.

**KEY WORDS:** Actinopterygians; Acipenseriformes; Acipenseridae; kinematics; feeding anatomy

The Acipenseriformes are basal ray-finned fishes (actinopterygians) often considered “living fossils” (Gardiner, 1984). However, they have a derived cranial morphology relative to other basal actinopterygians (Bemis et al., 1997). Despite their curious morphology and important phylogenetic position (Fig. 1), there have been no experimental studies of prey capture in sturgeon. Acipenseriformes are the only major lineage of actinopterygians and one of the few major lineages of vertebrates about which the functional morphology of feeding has not been studied in vivo. Functional interpretation of sturgeon anatomy can be found in Stengel (1962), Tessarsky (1992), Bemis et al. (1997), and Findeis (1993, 1997). Bemis et al. (1997) show frames from a feeding white sturgeon (*Acipenser transmontanus*) to illustrate jaw protrusion.

Sturgeon anatomy is distinctive among actinopterygians. The endochondral embryonic mandibular arch elements are retained as functional jaws,

the palatoquadrate does not fuse to the neurocranium, as in other actinopterygians, and the palatoquadrate and the lower jaw are suspended from a mobile hyoid arch (Edgeworth, 1935; Findeis, 1993; Bemis et al., 1997). The mobile hyoid arch and the independence of the jaws from the neurocranium allow the jaws to protrude a considerable distance away from the neurocranium. The complexity of sturgeon anatomy and the anatomical independence of its elements make it difficult to predict kinematics from anatomical investigation alone, as has been tried in the past (Stengel, 1962; Tessarsky, 1992).

The kinematics of aquatic prey capture have been studied in all members of the major vertebrate lineages except the Acipenseriformes. There have been several studies of chondrichthyes (Frazzetta and Prange, 1987; Motta et al., 1991, 1997; Ferry-Graham, 1997, 1998a,b; Wilga and Motta, 1998a,b 2000), dipnoans (Bemis and Lauder, 1986), tetrapods (Lauder and Reilly, 1988; Lauder and Shaffer, 1988), the basal actinopterygians *Polypterus*, *Amia*, and *Lepisosteus* (Lauder, 1979, 1980a), and several groups of basal teleosts (Lauder, 1979, 1980a; Van Leeuwen, 1984; Sibbing et al., 1986; Sanford and Lauder, 1989). The general feeding pattern for anamniotic vertebrates can be abstracted from these studies and has common and conserved features including: 1) the influx of water through the mouth resulting from dorsal, lateral, and ventral expansion of the orobranchial chamber; 2) gape opening by lower jaw depression and dorsal neurocranial rotation, with concurrent hyoid depression; and 3) a rostral to caudal wave of expansion, with maximum hyoid retraction following maximum gape and maximum opercular abduction following maximum hyoid retraction (Lauder, 1980a; Bemis and Lauder, 1986; Wilga and Motta, 1998a; Ferry-Graham and

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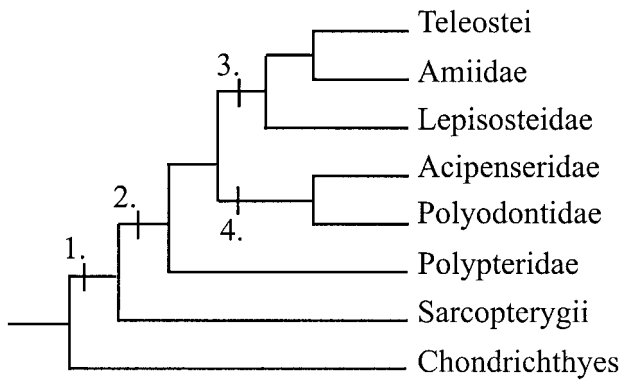


Fig. 1. Phylogenetic relationships of extant vertebrate lineages (Bemis et al., 1997). 1) Osteichthyes, 2) Actinopterygians, 3) Neopterygii, 4) Acipenseriformes. The two families of the Acipenseriform order are shown, the Polyodontidae (the paddlefish) and the Acipenseridae (the sturgeon). The kinematics of prey capture have been studied in each group except the Acipenseriformes.

Lauder, 2001). The influx of water created by these kinematic events draws prey through the mouth. This mechanism of prey capture, called suction feeding, has been hypothesized to be the primitive mechanism of prey capture in actinopterygians (Lauder, 1980a, 1982). It was not known, prior to this study, whether sturgeon use a kinematic pattern similar to that described in other vertebrates.

The use of upper jaw protrusion during suction feeding has been of historical and recent interest (Eaton, 1935; Alexander, 1966; Motta, 1984). Upper jaw protrusion evolved independently in several lineages of teleosts and in elasmobranchs, but its function seems to differ between these groups. In general, teleost upper jaw protrusion mechanisms are anatomically linked to mechanisms for jaw opening (Alexander, 1966; Motta, 1984; Westneat and Wainwright, 1989; Ferry-Graham et al., 2001). Peak upper jaw protrusion in teleosts is typically concurrent with peak gape and functions to move the mouth opening closer to prey before the prey is sucked in (Lauder, 1980b; Gillis and Lauder, 1995; Wainwright et al., 2001). In contrast, upper jaw protrusion in elasmobranchs involves a separate mechanism from jaw opening (Edgeworth, 1935; Motta et al., 1991; Motta and Wilga, 1999). In all elasmobranchs reported, jaw opening is complete before peak protrusion and upper jaw protrusion functions to help close the jaws (Ferry-Graham, 1997; Wilga and Motta, 2000). Sturgeon are actinopterygians but have a feeding apparatus resembling that found in elasmobranchs, including a mobile hyomandibula and protrusible jaws. Jaw protrusion in sturgeon evolved independently of both elasmobranchs and other actinopterygians with protrusible jaws. The relative timing of jaw opening and jaw protrusion in sturgeon is not described in the literature.

We conducted the first experimental investigation into the prey capture kinematics in an Acipenseriform

fish, the sturgeon *Scaphirhynchus albus*. Our most fundamental objective in this study was to use kinematic analysis to inform a functional interpretation of sturgeon anatomy and to postulate the anatomical mechanisms behind sturgeon prey capture kinematics. Additionally, we wanted to know whether Acipenseriformes shared the general pattern of aquatic feeding described in other vertebrates or whether the morphological divergence in the acipenseriform lineage had been paralleled by a divergence in prey-capture kinematics. Finally, we wanted to know whether the kinematics of jaw protrusion in sturgeon resembled those of teleosts, to which they are anatomically similar.

## MATERIALS AND METHODS

### Anatomy

Anatomical investigations were made on two species of sturgeon, the pallid sturgeon *Scaphirhynchus albus* (Forbes and Richardson) and the green sturgeon *Acipenser medirostris* (Ayres). *Scaphirhynchus albus* is native to the Mississippi and Missouri river drainages and *A. medirostris* to estuarine and river habitats in the Pacific Northwest (Findeis, 1993). Both feed primarily on benthic fish and invertebrates and grow in excess of 1 meter in length (Findeis, 1993). Specimens investigated were obtained from captive populations at the University of California at Davis and were hatched and reared in captivity. Specimens ranged in size from approximately 7 cm to 70 cm standard length (SL) for *A. medirostris* and between 10 cm and 40 cm SL in *S. albus*. Individuals were sacrificed by gradual overdose of tricaine methane sulfate (MS-222).

### Muscle Stimulation

Stimulation experiments were carried out on two sacrificed specimens of *Acipenser medirostris* (~50 cm SL). Individual muscles were artificially stimulated using a Grass S44 stimulator through wires embedded in the muscle. The sternohyoideus, the protractor hyomandibularis, the adductor mandibulae, the branchiomandibularis, and the epaxial musculature were stimulated at a frequency and voltage sufficient to produce repeated muscular contractions while the movement of anatomical elements was observed.

### Video

Kinematic data were collected from three *Scaphirhynchus albus* (SL 35 cm, 37 cm, 40 cm). Additionally, we collected video on a single 36 cm *Acipenser medirostris* for qualitative comparison. Fish were housed in a rectangular 200-L tank at 24°C and were cared for in accordance with U.C. Davis animal use and care protocols. The fish had been raised on

commercial particulate food and were introduced to more natural foods. A variety of dead shrimp (*Pandalus*), live earthworms (*Lumbricus*), and fish pieces (*Osmerus* and *Gambusia*) were offered. We found that *S. albus* fed most readily on small pieces of commercial smelt (*Osmerus*), so this prey was used during filming. Once a fish was readily feeding on natural prey the tank was readied for video recording. The tank was fitted with a false bottom of clear one-quarter inch thick Plexiglas that rested on weighted plastic columns. A 21 cm by 50 cm mirror was oriented at 45° to the false bottom. During video recording an NAC memrecam ci high-speed digital video camera was leveled and pointed directly at the false bottom so that it captured both the ventral and lateral images.

Fish were given at least a week to acclimate to the apparatus, during which time they were also introduced to the 600W lights necessary for video recording. During sequence collection prey items were placed over the feeding frame just before the sturgeon swam over it. Feeding events were considered to begin when the fish initiated mouth opening and to end when the jaws retracted. Feeding sequences usually lasted for about 100 frames (0.4 sec); 30–40 sequences were collected for each individual.

### Kinematic Analysis

Video sequences were converted into a series of image files with custom software and digitized using Scion image (Scioncorp, www.scion.com). Videos were made at 250 frames per second, but only every second frame was digitized, yielding a final sampling rate of one point every 8 ms. The locations of 12 points were recorded in each frame. These points were: (lateral image) the first scute, the lateral ethmoid process (LEP), the dorsal-caudal corner of the pectoral girdle, ventral tips of the upper jaw, lower jaw, and hyoid; (ventral image) the symphysis of the upper jaw and that of the lower jaw, the midpoint of the hyoid, the most anteromedial and posteromedial points on the opercular margin, the ventral corner of the pectoral girdle, and the prey (Fig. 2). We use the term *Hyoid* to refer the ventral components of the hyoid arch: the ceratohyals and hypohyals.

The following kinematic variables were calculated from the positions of the 12 digitized points: gape distance, opercular abduction, rostral-caudal and dorsal-ventral displacement of the hyoid, lower jaw and upper jaw displacement, and neurocranial rotation.

Gape distance was calculated from the two-dimensional (2D) distance between the upper to lower jaws in ventral view (points 7 and 8 in Fig. 2). This measurement is not a true measure of gape; rather, it is a projection of the true gape onto the ventral image. A 3D measure of gape was not used because the 3D position of the upper jaw could not be determined until it emerged from underneath the

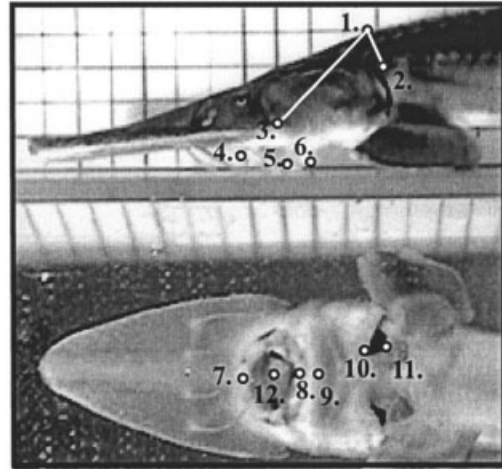


Fig. 2. Digitized points. These are: 1) the first scute; 2) the lateral ethmoid process (LEP); 3) the dorsal-caudal corner of the pectoral girdle; 4) ventral tip of the upper jaw; 5) lower jaw; 6) and hyoid; 7) the symphysis of the upper jaw; 8) symphysis of the lower jaw; 9) the midpoint of the hyoid; 10) the most anterior-medial point on the opercular margin; 11) the ventral corner of the pectoral girdle; and 12) the prey. Neurocranial angle was calculated as the angle between (3) and (1), and (1) and (2). Gape was calculated as the linear distance between points (7) and (8), not (4) and (5), for reasons explained in the text. Opercular abduction was defined as the distance between points (10) and (11). Notice that this will be less than the distance between the lateral edges of the operculum. The derivation of other measurements is given in the text.

neurocranium. Our reported measure of gape is an underestimate of true gape.

Opercular expansion was calculated as the distance from the pectoral girdle (point 10) to the opercular margin (point 12). Neurocranial elevation was calculated as the angle between the line from the LEP to the first scute and between the first scute and the corner of the pectoral girdle (points 1, 2, and 3). The minimum neurocranial angle for a sequence was defined as zero and subtracted from the other values to generate the final variable. Prey displacement was calculated as the prey's distance in the current frame from the last location at which it could be digitized.

Two X positional values were available for the hyoid, lower jaw and upper jaw. The ventral value was chosen because it was clearer than the lateral view and less sensitive to deviations from laterality. This X value was combined with the Y value from the lateral view. At each digitized frame the position of the lower jaw and the hyoid was subtracted from the position of the first scute (point 1) to remove translation of the fish. For the upper jaw a point combining the X value of the first scute and the Y value of the LEP (point 3) was used to remove both translation of the fish and neurocranial elevation. Each point was subsequently subtracted from its position in the first digitized frame. This centered the point's 2D path data at an origin defined by its value in the first frame.

Both total 2D displacement and displacement along the X or Y dimensions were calculated at each frame from the path data. Ventral displacement was defined as negative and caudal displacement was defined as positive, so that path traces were in the traditional anatomical position, with the anterior to the left.

Either five or six sequences were digitized for each fish. These data were combined to generate the final dataset. In order to reduce variation due to difference in timing, peak gape was defined as  $t = 0$  and the sequences were lined up accordingly. Peak gape was chosen as the first point within 2 mm of the maximum gape measured in each sequence. Average values at each point were calculated for each of the kinematic variables.

Maximum opercular expansion, maximum upper jaw protrusion, and maximum hyoid displacement were defined as the point at which those reached within 2 mm of the maximum in each sequence. Maximum neurocranial rotation was taken as the first point within 2° of the absolute maximum for that sequence.

## RESULTS

### Anatomy

Descriptions of sturgeon anatomy are available from the sources listed in the Introduction. We follow bone and ligament names from Findeis (1993) and Stengel (1962) except where otherwise noted. The names of muscles are from Edgeworth (1935) and Stengel (1962). Synonymies are given where appropriate. For interspecific and intergeneric anatomical differences among sturgeon, see Findeis (1993, 1997).

**Skeletal anatomy.** The cranial skeleton of *Scaphirhynchus albus*, like other Acipenseriformes, is largely cartilaginous, with some perichondral ossification. Additionally, numerous dermal bones and scales are associated with the head.

The neurocranium is characterized by a large triangular rostrum (Fig. 3A,B), the posterior corners of which are formed by the lateral ethmoid processes (LEP) (Findeis, 1993; = postorbital spur of Stengel, 1962). At the LEP the ventral surface of the neurocranium slopes sharply dorsally to about half the level of the fish's depth, forming a space for the orobranchial chamber (Fig. 3A). The orobranchial chamber is situated between the rostrum and the pectoral girdle (PG). At rest the jaws are retracted into the orobranchial chamber, just behind and below the orbits.

From proximal to distal, the elements of the hyoid arch are the hyomandibula (HY), the symplectic (Edgeworth, 1935; Stengel, 1962; = interhyal of Grande and Bemis, 1991; Findeis, 1993, 1997), the posterior ceratohyal (CH p) (= stylohyal of Stengel, 1962; and Sewertzoff, 1928; = interhyal of Edgeworth, 1935), the anterior ceratohyal (CH a) (= cera-

tohyal of Edgeworth, 1935; Stengel, 1962), and the hypohyals (HH) (Fig. 3). The hyomandibulae articulate with the neurocranium at a socket behind the spiracle.

The flat, wide, rectangular symplectic is the unifying element of the feeding apparatus, articulating with the jaws, the ventral hyoid, and hyomandibula (Fig. 3A). The symplectic articulates with the distal, anteromedial surface of the hyomandibula. The symplectic can rotate ventrally and medially about the hyomandibula.

The small, rectangular posterior ceratohyal articulates with the ventral-posterior corner of the symplectic. This bone projects medially, nearly orthogonal to the symplectic. Its anterior edge rests against the proximal end of the anterior ceratohyal (Fig. 3B). The posterior ceratohyal does not move relative to the symplectic and prevents the proximal anterior ceratohyals from sliding backward along the symplectic as they are retracted.

The anterior ceratohyals are the largest element of the ventral hyoid. In the unretracted position the anterior ceratohyals point rostrally, medially, and dorsally, forming the "chevron" shape found in most fishes (Fig. 3B). At their distal end they articulate with the small, flat, caudally pointed hypohyals. The hypohyals from both sides join each other at the dorsal edge of the midventral anterior basibranchial (basibranchial 1 of Findeis, 1993). The hypohyals and basibranchial are tightly connected to each other to form the ventral surface of the buccal cavity (see Findeis, 1993, for more detail). When the jaws are unprotruded, the hypohyals sit dorsal and caudal to the lower jaw in contact with the oral surface of the upper jaw.

There is no direct connection between the mandibular arch and the neurocranium. The jaws are suspended from the hyoid arch and only connected to the neurocranium through a loose invagination of skin between the upper jaw and ventral surface of the neurocranium.

Both jaws articulate with the symplectic on its distal margin. The upper jaw is composed of the joined contralateral palatoquadrate cartilages and several accessory dermal bones. The palatoquadrates extend transversely from their medial symphysis (Fig. 4B). The palatoquadrates are flat and wide at their medial symphysis but narrow laterally. Approximately two-thirds their length from the medial symphysis, the anteroventral surface tapers, takes a sharp posterior curve, before curving anteriorly again. At its distal edge the palatoquadrate deepens to form bulbous anteroventrally pointed process, the quadrate flange (Fig. 4B; Findeis, 1993). This curvature leaves a notch in the anterior surface of the palatoquadrate. A thin dermal bone (the dermopalatine) spans the notch as well as covering the distal edge of the palatoquadrates. The adductor mandibulae (AM) runs through this notch, from the aboral to oral side to insert on the lower jaw (Fig. 4).

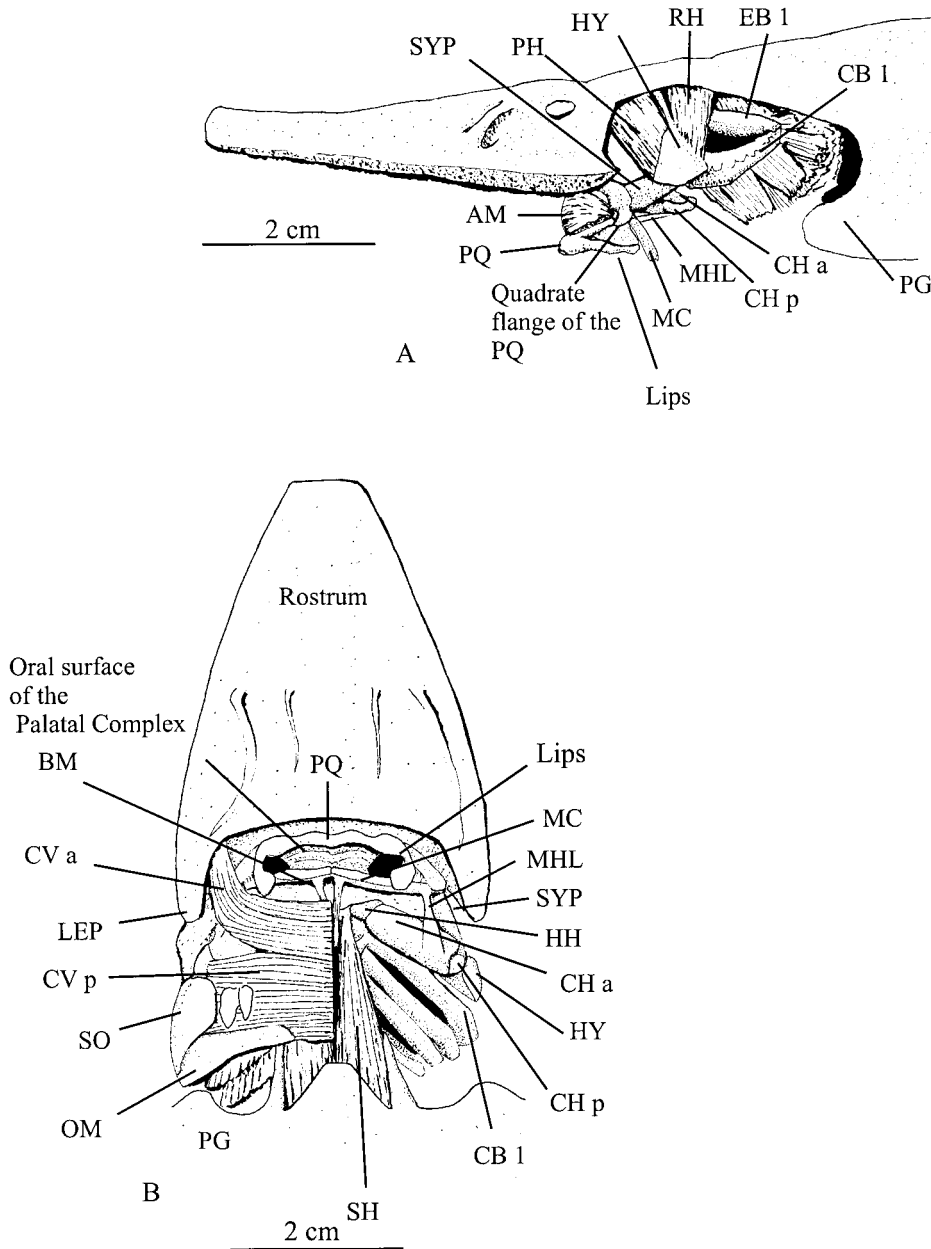


Fig. 3. Lateral and ventral skeletal and muscle anatomy of a 35-cm *Scaphirhynchus albus*. In the lateral view, the skin, much of the connective tissue, and the opercular series have been removed from the orobranchial chamber. The jaws are protruded to show the adductor mandibulae. The hyoid is not retracted and the sternohyoideus is not shown. In the ventral image the skin and much of the connective tissue have been removed from both sides; the superficial musculature and gills have been removed from the fish's left side. The jaws are partially protruded away from the hyoid. The fifth gill arch is not visible. AM, adductor mandibulae; BM, branchiomandibularis; CB 1, 1st ceratobranchial; CH a, ceratohyal anterior; CV a, anterior constrictor ventralis; CV p, posterior constrictor ventralis; EB 1, 1st epibranchial; HH, hypohyal; HY, hyomandibula; LEP, lateral ethmoid process; MC, Meckel's cartilage; MHL, mandibulohyoiod ligament; OM, opercular margin; PG, pectoral girdle; PH, protractor hyomandibularis; PQ, palatoquadrate; RH, retractor hyomandibularis; SH, sternohyoideus; SO, subopercle; SYP, symplectic.

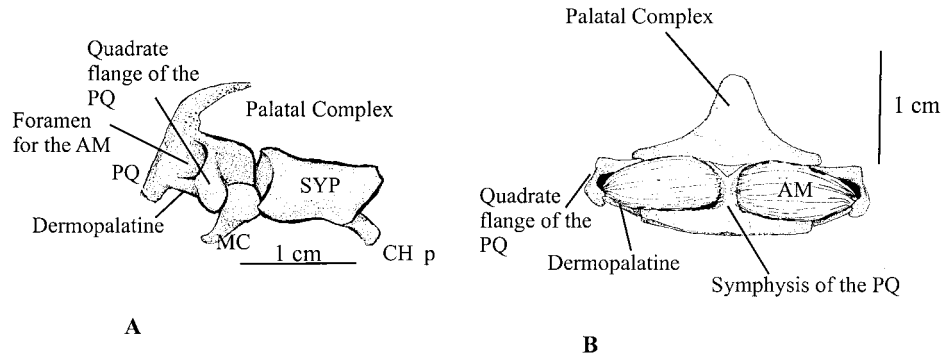
The ventral surface of the quadrate flange forms a partial ball-and-socket joint with the lower jaw (Fig. 4). The caudal surface of the palatoquadrate is extended by a triangularly shaped series of flat cartilages (Fig. 4B). This structure, called the palatal complex (= castilago impar of Edgeworth 1935; = median postpalatine cartilage of Weisel, 1979) develops independently from the palatoquadrate bar (Edgeworth, 1935; Findeis, 1993) and is a synapomorphy (among extant species) for the Acipenseridae (Findeis, 1993, 1997).

The straight, slender lower jaw is composed only of Meckel's cartilage (MC) and the small dentary bone on its oral side. Meckel's cartilage extends well past the margins of the mouth in the intact animal

to articulate with the upper jaw at the quadrate flange and with the distal edge of the symplectic (Fig. 4). Opening of the lower jaw requires rotation of the lateral head of Meckel's cartilage in its articulation with the quadrate flange. The distal ends of Meckel's cartilage articulate in a loose symphysis, so that the angle between contralateral cartilages is not fixed. The shape of the mouth in the intact animal is formed by large tuberous lips. These span the angle between the upper and lower jaws (Fig. 4).

The mandibulohyoiod ligament (MHL) runs from the lateral posterior corner of the anterior ceratohyal, across the flat ventral side of this bone, to insert onto Meckel's cartilage just distal to the insertion of the AM (Fig. 3B).

Fig. 4. Anatomy of the and jaw joint in lateral view (A), and upper jaw in aboral view (B) of a 35-cm *Scaphirhynchus albus*. The dermopalatine is not distinguished from the palatoquadrate where the two are contiguous. AM, adductor mandibulae CH p, ceratohyal posterior; MC, Meckel's cartilage; PQ, palatoquadrate; SYP, symplectic.



The branchial arches are similar to those of other actinopterygians, forming a caudally pointed cone with its base at the hyomandibula and the apex at the esophageal opening (Fig. 3B). The flat hypobranchials (not illustrated) are ligamentously bound to each other, to the hypohyals, and to the basibranchials (not illustrated) to form the floor of the buccal cavity. In cleared-and-stained or in unfixed specimens the branchial arches show three separate motions: flexion of the epibranchial-ceratobranchial joints, flexion of the ceratobranchial-hypobranchial joints, and rostrocaudal rotation of the entire arch at its dorsal connection to the neurocranium and ventral connection to the hypohyals. Flexion at the epibranchial-ceratobranchial and ceratobranchial-hypobranchial joints allows buccal floor retraction and depression.

The epibranchial of the first gill arch is tightly bound to the skin of the opercular margin dorsal to the subopercle. The branchial arches are bound to one another by strong ligamentous connections at their articulation with the neurocranium, through connections between the hypohyals, and through the basibranchials. In unfixed specimens movement of arches is uniform and is determined by the position of the hyoid arch; however, there are small muscles associated with individual branchial arches which may influence their movement in intact animals (see Stengel, 1962).

The opercular series is reduced to a flat, round subopercle (Findeis, 1993) embedded in the skin of the lateral-caudal cheek. Each hyomandibula is connected by wide ligament to the subopercle, such that when the hyomandibula rotates rostrally it pulls the subopercles along.

The pectoral girdle of *Scaphirhynchus albus* is composed of many dermal and endochondral bones, but these are not functionally distinct. The pectoral girdle is bound dorsally to the neurocranium. Ventral to the posterodorsal corner of the opercular chamber, the pectoral girdle can rotate caudally relative to the neurocranium.

**Ventral musculature.** The most superficial muscle of the ventral musculature is the constrictor ventralis (CV) (Stengel, 1962), which sits just beneath the skin between the lower jaw and posterior

margin of the opercular flap (Fig. 3B). This muscle originates at a midventral raphe superficial to the basibranchials. The anterior and posterior sections of this muscle (CV a and CV p) meet at the level of the proximal ends of the ceratohyals (Fig. 3B). The rostral-most fibers of the anterior CV continue around the margins of mouth to insert on the connective tissue of the neurocranium medial to the LEP. The fibers immediately caudal to these curve laterally and anteriorly around the corners of the mouth to insert on the strong connective tissue that is found lateral to the mouth between the LEP and the symplectic. The caudal-most fibers of the anterior CV insert onto the thin connective tissue that supports and encloses the cheek (Fig. 3B).

The posterior CV runs mediolaterally along the flat underside of the sturgeon's pharynx to connect to the aponerousis over the ceratohyals and hyomandibulae. Some fibers insert onto these bones. More caudal fibers run underneath the subopercles and branchiostegal bones, with some fibers inserting onto these bones.

The interhyoideus (not illustrated; = constrictor ventralis profundus of Stengel, 1962) lies directly between the proximal ends of the ceratohyal deep to the anterior fibers of the posterior CV. Its fibers originate from a median raphe and insert on the medial side of the proximal ends of the ceratohyals.

Two thin branchiomandibularis (BM) muscles run from the buccal floor at the level of the third gill arch, between the paired sternohyoideus muscles, through the thin skin behind the lower jaw to insert on the Meckel's cartilages near their symphysis (Fig. 3B). These are called the geniobranchialis by Sewertzoff (1928) and Edgeworth (1935) and are believed to be homologous to the coracomandibularis of sharks (Edgeworth, 1935).

The most prominent muscles of the ventral buccal chamber are the paired sternohyoideus (SH) muscles (= coracoarcualis of Stengel, 1962; = rectus cervicis of Edgeworth, 1935). These conical muscles originate from the dorsal surface of the midventral pectoral girdle and are continuous with posterior hypobranchial muscles. The primary insertion of the SH is through a large tendon onto the hypohyals (Fig. 3B).

**Lateral musculature.** The opercularis (not illustrated) (Edgeworth, 1935; Stengel, 1962) is a thin, sheet-like muscle that runs ventrally, laterally, and caudally from the neurocranium to the posterior half of the dorsal edge of the subopercle. The adductor mandibulae (AM) in sturgeon originates on the aboral surface of the palatoquadrate, where it is contained in a wide fossa. Its tendon runs through a notch in the palatoquadrate, described above, to insert on the lower jaw (Figs. 3, 4). The AM is not connected to either the neurocranium or the suspensorium.

The protractor hyomandibularis (PH) is a thick cylindrical muscle running caudally and ventrally from the neurocranium behind the orbit out to the rostral surface of the hyomandibula. The retractor hyomandibularis (RH) runs from the neurocranium rostrally and ventrally to insert on the caudal hyomandibula opposite the PH (Fig. 3A). The protractor hyomandibularis develops from the undifferentiated constrictor dorsalis and is homologous to its derivatives, the levator arcus palatini and dilatator operculi of the Neopterygii (Edgeworth, 1935). The retractor hyomandibularis develops from the constrictor hyoideus and is homologous to its derivative, the adductor arcus palatini.

### Muscle Stimulation

Artificial stimulation of the BM caused partial depression of the lower jaw. Stimulation of the SH depressed and retracted the hyoid, opened the branchial basket through connections described above, and apparently opened the jaws through the MHL. Stimulation of the PH protrudes both jaws on the stimulated side by causing rostromedial rotation of the hyomandibula, which is transferred to the jaws through the symplectic, although the actual movements of these cartilages could not be observed in intact fish. Stimulation of the AM pulled the jaws closed. Stimulation of the epaxials resulted in dorsal rotation of the neurocranium.

### Kinematics

All individuals swam continuously around the tank during the filming sessions. As the fish approached the prey it would often swing or roll its head toward it. The strike usually commenced when the prey contacted one of the sturgeon's barbels.

Before the onset of the strike the jaws were retracted into the neurocranium and angled rostrally (Fig. 5). A typical prey capture sequence began with rapid gape opening by lower jaw depression, with a partial protrusion of both jaws from within the orobranchial chamber (Fig. 5). The hyomandibula were seen to swing rostrally as the jaws were opened and protruded (Fig. 5). The lower jaw continued to depress until peak gape was achieved (Figs. 5, 6, 7, 8B). Ventral upper jaw protrusion during jaw open-

ing was not apparent in the kinematic data because dorsal-ventral movement of the upper jaw could not be analyzed until it descended from the neurocranium (Figs. 6, 8A). Anterior movement of the upper jaw was apparent (Fig. 6). At peak gape the mouth was usually angled rostrally and ventrally, with the upper jaw just below or flush with the underside of the neurocranium (Fig. 5). The fleshy lips surrounding the mouth spread between the jaws creating a round mouth aperture. The hyoid retracted ventrally and caudally as the lower jaw depressed (Figs. 5, 6, 7, 8C). Hyoid retraction was accompanied by lateral expansion of the anterior orobranchial chamber (Fig. 5).

After peak gape the lower jaw was held open (for ~50 ms) (Fig. 6, 8B). The hyoid continued retracting during this time, reaching its peak displacement 15 ms after peak gape (Table 1). Ventral upper jaw protrusion became visible at peak gape and continued as the lower jaw was held open (Fig. 8). Ventral jaw protrusion brought the jaws closer together, aiding in closing gape. Ventral jaw protrusion was accompanied by further rotation of the hyomandibulae, the impression of which, in the cheek of the fish, could be seen just caudal to the LEP (Fig. 5).

After the prey had been drawn into the mouth the lower jaw was rapidly swung rostrally to close the gape (Fig. 8B). The upper jaw continued to protrude ventrally as it rotated caudally (Fig. 8A) to meet the lower jaw. Peak ventral upper jaw protrusion was achieved during jaw closing and averaged 90 ms after peak gape (Table 1). The position of the ventral tip of the hyoid was maintained as the jaws were closed (Figs. 6–8), but the proximal ends of the hyoid were pulled forward (Fig. 5), apparently due to rostral rotation of the hyomandibulae. After jaw closing the hyoid slowly returned to its original position. Both jaws were slowly retracted to near their original positions. The jaws usually remained closed during this period (Figs. 5, 6).

Typically, the opercular margins were adducted but not completely closed at the onset of the strike. The opercular margins abducted throughout the strike reaching a maximum after peak gape (Figs. 5, 6). Full opercular abduction averaged 72 ms after the achievement of peak gape (Table 1). The opercular margins remained abducted after the jaws were closed and retracted.

Every sequence we observed involved prey movement towards the jaws, indicating that sturgeon generate a flow of water into their mouths during feeding. The prey generally began to move towards the mouth as the lower jaw descended and entered as the mouth was held open (Figs. 5, 6). Prey entry averaged 31 ms after peak gape (Table 1).

Neurocranial rotation was highly variable among strikes (Fig. 6). During some strikes it continued to rise throughout the strike, in others it decreased throughout the strike. Often, as in the strike shown in Figure 5, the head was angled dorsally to present

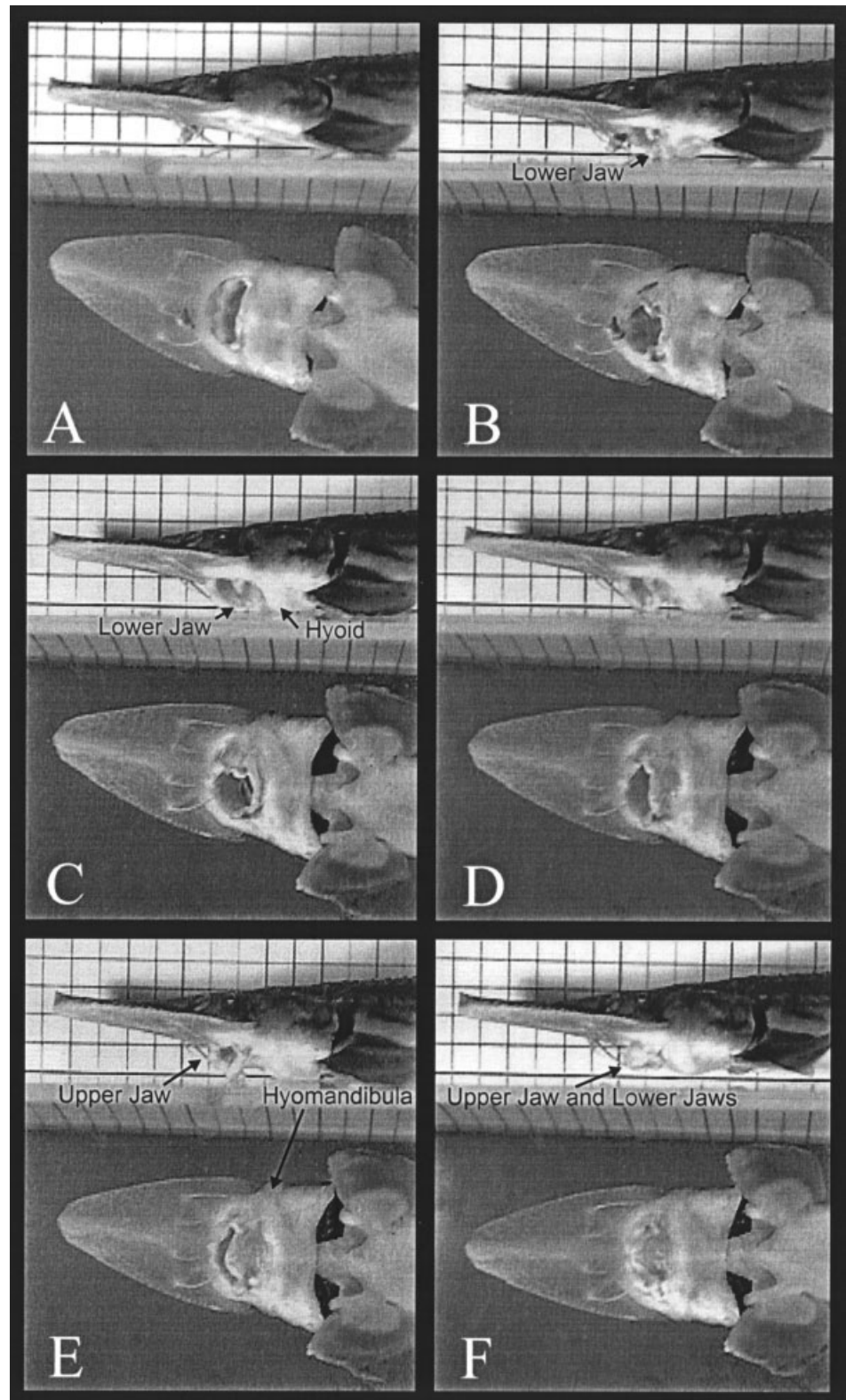


Fig. 5. Images from a typical feeding sequence in *Scaphirhynchus albus*. These images have been cropped to remove translational movement of the fish. During the feeding sequence the fish approaches the prey (A). The lower jaw is depressed, the hyoid is retracted, and the jaws are partially protruded (B). The mouth is held open while the prey enters. The upper jaw is protruded as the jaws are closed (C,D). The hyoid remains retracted as the jaws close, with the lower jaw swinging forward. Peak ventral upper jaw protrusion is achieved as the jaws are closed (E,F). The impression of the rostrally swinging hyomandibulae can be seen in the ventral image of frames C-F.

the mouth to the prey. Unanalyzed strikes from *Acipenser medirostris* show neurocranial rotation as a consistent component of the strike.

Although most strikes demonstrated the pattern described above, the relationship between jaw opening and upper jaw protrusion and the relationship



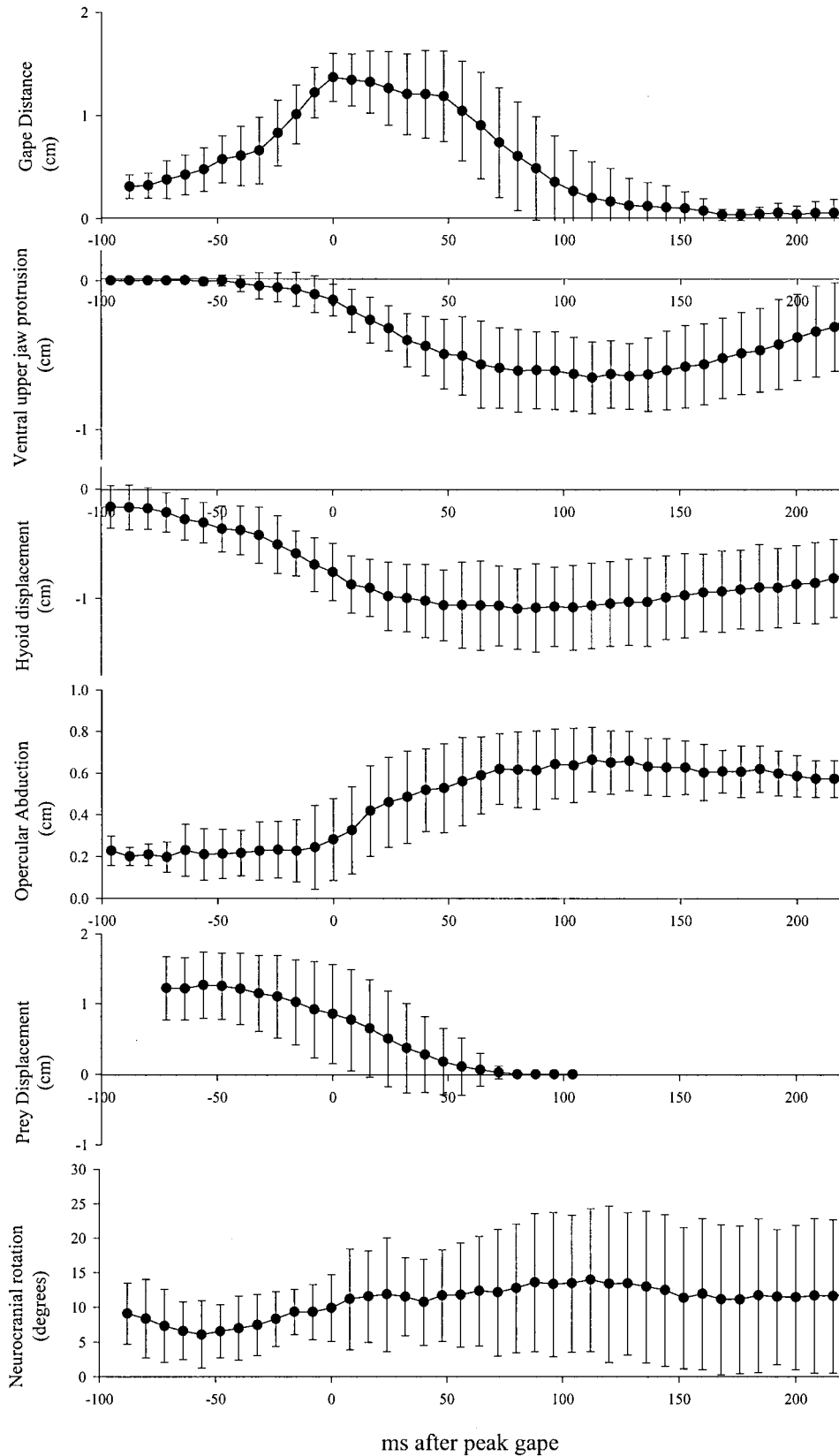


Fig. 6. Average kinematic variables at each frame. The time course of gape, hyoid displacement, ventral upper jaw protrusion, and opercular abduction. Points are the averages of at least 15 and no more than 16 sequences from three individuals. Sequences have been aligned at peak gape (time = 0 ms). The time between points is 8 ms. Prey moves from an average of 1.2 cm away to the last point it can be digitized (distance = 0). The calculation of other variables is described in the text. Hyoid displacement and jaw protrusion are graphed as a negative value in this figure. Gape is held open for about 50 ms between periods of rapid opening and closing. Peak hyoid displacement, peak upper jaw protrusion, and peak opercular abduction are all after peak gape. Neurocranial elevation is variable.

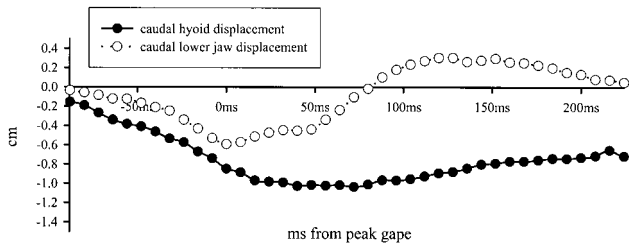


Fig. 7. Average hyoid rostrocaudal displacement and average lower jaw rostrocaudal displacement. These are the total horizontal displacements of points 8 and 9 in the ventral view. Caudal motion is considered negative for this figure. Motion of the lower jaw is coupled to the hyoid during jaw opening but uncoupled during jaw closing. The lower jaw retracts at the onset of the strike, reaching a maximum at time = 0 (peak gape). The hyoid also retracts but continues retraction after peak gape and does not return to its original position. The lower jaw begins to swing rostrally and does not stop until it passes its original lateral position to meet the upper jaw.

between upper jaw protrusion and jaw joint protrusion sometimes varied from the average pattern. Occasionally, prey were drawn in with little or no protrusion of the jaws. In other strikes upper jaw protrusion continued rapidly before peak gape was achieved. If peak ventral protrusion was reached before the onset of jaw closing, the upper jaw still contributed to jaw closing by rotating caudally toward the lower jaw.

## DISCUSSION

### Anatomy

The most important functional difference between sturgeon and other basal actinopterygians (as described in Edgeworth, 1935; Lauder, 1980a) involve the independence of the upper jaw from the neurocranium, the mobility of the hyomandibulae (HY), the presence of a mobile symplectic (SY), and the addition of the palatal complex to the dorsal edge of the upper jaw. Each of these differences is important

to the anatomical mechanisms underlying the kinematics of prey capture, as described below.

The sturgeon's musculature is reduced relative to other basal actinopterygians. Sturgeon have an undivided adductor mandibulae instead of the tripartite adductor muscle, hypothesized to be primitive to actinopterygians (Lauder, 1982). The muscular connections between the neurocranium and suspensorium are reduced to the protractor and retractor hyomandibularis, and the opercularis is the only muscle that connects directly between the neurocranium and opercular series. The reduction of musculature in Acipenseriform fish is consistent with the hypothesized importance of pedomorphosis in the evolution of this group (Bemis et al., 1997).

### Kinematics

Prey capture in *Scaphirhynchus albus* begins with simultaneous lower jaw depression, hyoid retraction, lateral expansion of the buccal cavity, and partial protrusion of both jaws from their resting position inside the orobranchial chamber. Lower jaw depression ends at peak gape, but the hyoid continues to retract before reaching its peak displacement. Opercular abduction starts after the jaws begin to open and reaches its peak after the jaws begin to close. Ventral protrusion of the upper jaw begins while the lower jaw is held open and reaches its peak as the jaws are closed. The prey item is sucked into the mouth before or just after the onset of jaw closing. The opercular margins are fully abducted after the onset of jaw closing. Neurocranial rotation in *S. albus* is variable both in duration and timing.

### Anatomical Mechanisms

We propose anatomical mechanisms behind retraction of the buccal floor, lateral and ventral expansion of the orobranchial chamber, gape opening and closing, jaw protrusion, opercular abduction,

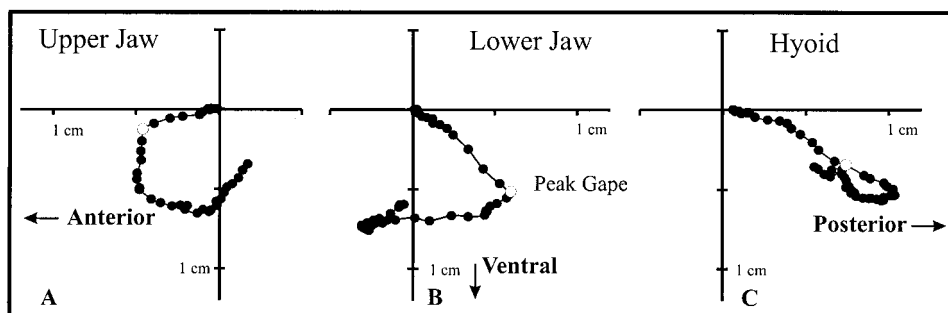


Fig. 8. Two-dimensional paths of the upper jaw (A), lower jaw (B), and hyoid (C). Each point is the position in each digitized frame of the anatomical element centered at the position of the element in the first digitized frame with the movement of the animal subtracted as described in the text. The white circle indicates peak gape. Because the ventral position of the upper jaw could not be digitized until it had descended below the level of the neurocranium, early ventral movement is not apparent in this figure. After peak gape the upper jaw descends further ventrally, although not as rapidly as before peak gape. Peak protrusion is reached and held as the jaws are brought together, the upper jaw rotates horizontally towards the lower jaw. The jaws are then partially retracted.

TABLE 1. Relative timings of kinematic events during prey capture by *Scaphirhynchus albus*: three individual averages (based on 5–6 sequences per individual) and averages of three individuals

Kinematic variables	1		2		3		Group	
	Avg.	SD	Avg.	SD	Avg.	SD	Avg.	SD
Timing (ms)								
Onset to peak gape	72	28	80	31	77	27	76	4
Onset to gape close	152	11	184	43	203	57	180	26
Prey entry*	38	41	19	32	37	30	31	11
Peak protrusion*	94	39	93	49	81	53	90	7
Peak hyoid displacement*	19	12	0	18	26	28	15	13
Peak opercular abduction*	62	17	72	45	83	43	72	10
Peak amplitudes (cm)								
Gape distance	1.6	0.1	1.3	0.3	1.5	0.3	1.5	0.1
Protrusion	-1.2	0.2	-1.0	0.2	-0.6	0.2	-0.9	0.3
Hyoid displacement	1.5	0.2	1.0	0.5	1.1	0.3	1.2	0.2
Opercular abduction	0.9	0.1	0.7	0.1	0.6	0.1	0.7	0.2

\*Expressed relative to peak gape (peak gape = 0 ms).

and neurocranial rotation. Our interpretations are based on the combined insights of manipulation of dissected and cleared-and-stained specimens, stimulation of muscles, and prey-capture kinematics.

**Hyoid-mediated anatomical mechanisms.** The retraction of the hyoid (= anterior and posterior ceratohyals and hypohyals) appears to be the result of contraction of the sternohyoideus. Retraction of the hyoid seems to be responsible for lateral orobranchial expansion, ventral orobranchial expansion, and lower jaw depression. Lateral expansion appears to be due to proximal ends of the hyoid pushing the hyomandibulae laterally as the hyoid is retracted (Fig. 9). Because the sturgeon's orobranchial chamber narrows anteriorly, anterior movement of the hyomandibulae in the sagittal plane also apparently results in lateral expansion (Figs. 5, 9).

Retraction of the hyoid results in ventral expansion of the orobranchial chamber by depression of

the buccal floor. The hypohyals (HH) are intimately connected to the buccal floor; ventral-caudal translation of the hyoid is transferred to these elements (Fig. 9). As the buccal floor ascends the distal ceratobranchials of branchial arches 1–4 follow by extension at ceratobranchial-epibranchial joint. Extension of these joints allows the branchial arches to bellow open, expanding the volume of the buccal cavity (also described by Stengel, 1962).

Retraction of the hyoid is kinematically associated with lower jaw retraction (Figs. 6–8), stimulation of the sternohyoideus causes both hyoid retraction and lower jaw depression and manual retraction of the hyoid in unfixed or cleared-and-stained specimens results in lower jaw depression. Therefore, we conclude that retraction of the hyoid is the primary lower jaw depression mechanism in the sturgeon, supporting both Stengel's (1962) anatomically based hypothesis and previous phylogenetic reconstructions that hyoid mediated jaw depression is primi-

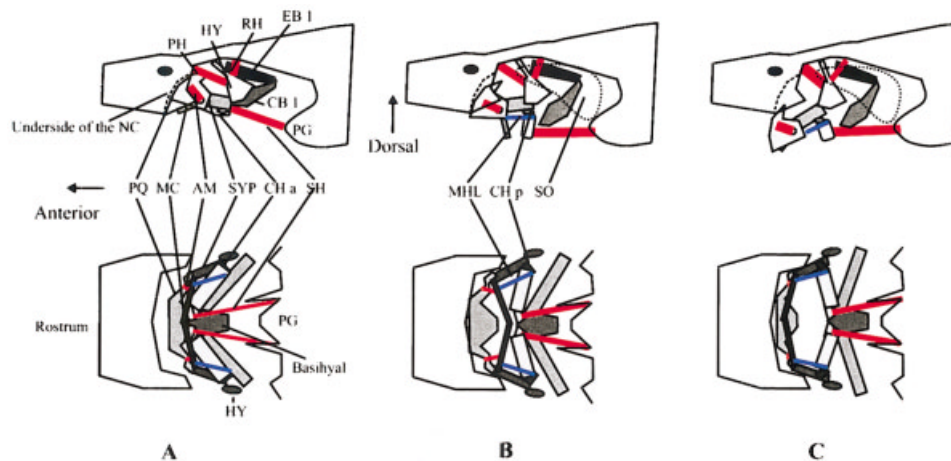


Fig. 9. Anatomical mechanisms. The positions of the major anatomical elements at 1) onset of the strike, 2) lower jaw fully depressed and jaws partially protruded, and 3) jaw closed and upper jaw protruded. Anatomical mechanisms are described in the text. Red is used to indicate muscles, blue to indicate ligaments. AM, adductor mandibulae; BM, branchiomandibularis; CB 1, 1st ceratobranchial; CH a, ceratohyal anterior; CH p, ceratohyal posterior; CV a, anterior constrictor ventralis; CV p, posterior constrictor ventralis; EB 1, 1st epibranchial; HH, hypohyal; HY, hyomandibula; LEP, lateral ethmoid process; MC, Meckel's cartilage; MHL, mandibulohyoid ligament; OM, opercular margin; PG, pectoral girdle; PH, protractor hyomandibularis; PQ, palatoquadrate; RH, retractor hyomandibularis; SH, sternohyoideus; SO, subopercle; SYP, symplectic.

tive for osteichthyes (Lauder, 1980a; Wilga et al., 2000).

Retraction of the hyoid causes the lower jaw to depress ventrally and caudally by tension through the mandibulohyoid ligament (MHL) (Figs. 3B, 9). The branchiomandibularis (BM) is in position to contribute to jaw opening as well; however, the extent of its role cannot be determined from our results. Jaw opening may be aided by the jaw joint protrusion occurring at the onset of the strike. Movement of the jaw joint forward during jaw opening would pull the lower jaw rostrally, away from the hyoid, and would be functionally equivalent to retraction of the hyoid. The adductor mandibulae (AM) is the only muscle in position to directly pull the upper and lower jaws together (Figs. 3, 9).

Movement of the hyoid is tied to movement of the lower jaw, but the hyoid continues to retract after the lower jaw has begun to move forward and stays retracted when the jaws close (Figs. 7, 8). This appears to present a paradox: if caudal rotation of the hyoid results in jaw opening, how can the jaws close while the hyoid is retracting? First, the lower jaw does not return to its original position during jaw closing because of the contribution of upper jaw protrusion to jaw closing, and because the lower jaw itself has been protruded (Figs. 5, 8). Second, the proximal ends of the anterior ceratohyal, to which the MHL is bound, are pulled rostrally by the hyomandibula as the jaws are protruded (Fig. 5), allowing the lower jaw to close while the MHL is of constant length (Fig. 9). These kinematic movements are similar to those described in the guitarfish *Rhinobatos lentiginosus* (Wilga and Motta, 1998b).

The hyoid appears to be returned to its prestrike position by action of both the interhyoideus muscles and by the anterior and posterior constrictor ventralis. Adduction of the proximal ceratohyals by these muscles would close the angle between the distal ceratohyals anterior and force the hypohyals into their resting position just below the upper jaw (Fig. 3B). The BM is in position to swing the hyoid and buccal floor rostrally after both jaws are closed and retracted. Whether the BM functions during jaw opening, hyoid retraction, or both cannot be determined from our results.

**Opercular abduction.** Abduction of the opercular margins is primarily a consequence of rostral movement of the anterior subopercle, which swings the opercular margin rostrally and laterally away from the pectoral girdle (Fig. 5). Rostral movement of the subopercle appears to be the result both of contraction of the opercularis muscle and rostral rotation of the proximal hyomandibulae to which the subopercles are bound. Contraction of the opercularis would also pull the dorsal edge of the subopercle rostrally and medially abducting its ventrocaudal edge. Opercular adduction is the result of caudal retraction of the hyomandibula and contraction of the posterior constrictor ventralis. Unlike the

teleosts and *Amia* (Lauder, 1980a), movement of the opercular series in sturgeon is not tied to jaw opening by any apparent connection.

Lateral expansion of the pharynx may also be due to anterior rotation of the first gill arch. When the hyomandibulae move forward, they pull the lateral edges of the first gill arch rostrally, causing it to rotate laterally (also described in Stengel, 1962). The subopercle is pushed laterally with the first gill arch, laterally expanding the pharynx.

**Neurocranial rotation.** Dorsal neurocranial rotation is the result of contraction of the epaxial muscles. Because of the independence of the neurocranium and the upper jaw in sturgeon, neurocranial rotation does not contribute to gape opening, as it does in other basal osteichthyes (Lauder, 1983; Bemis and Lauder, 1986) or in some sharks (Wilga and Motta, 2000), although neurocranial elevation may help expose the jaws to the prey. Unlike other basal actinopterygians, when the jaws of a sturgeon are protruded they can be closed independently of neurocranial angle. We observed strikes from *Acipenser medirostris* in which dorsal neurocranial rotation continued as the upper jaw translated ventrally and rotated caudally. This is a kinematic pattern that would not be anatomically available to other actinopterygians as they are described in the literature (Gregory, 1933; Edgeworth, 1935; Lauder, 1980a). A similar independence of the jaw and cranial kinematics is found in some sharks and rays (Wilga and Motta, 1998b).

**Jaw protrusion.** The sturgeon's jaw protrusion mechanism has been described by Stengel (1962), Tessarsky (1992), and Bemis et al. (1997). The primary actuator of jaw joint protrusion seems to be the protractor hyomandibularis (PH). Contraction of this muscle would result in rostral rotation of the ipsilateral hyomandibula (Figs. 3A, 9). Rostral rotation of the hyomandibula would push the symplectic rostrally and the symplectic would push the upper and lower jaws out of the orobranchial chamber. Rostral translation of the upper jaw is deflected ventrally as the palatal complex slides against the ventrally sloping underside of the neurocranium (Fig. 9). The lengths of the hyomandibula and symplectic are such that relatively slight rotation of the hyomandibula can result in considerable extension of the jaws. The AM may help protrude and rotate the upper jaw as the jaws are closed by pulling the upper jaw ventrally and caudally toward the depressed and protruded lower jaw (Figs. 8A, 9). The contribution of the AM may be especially important in the last phase of the strike, during which rostral movement of the hyomandibula is not always apparent beneath the skin of the cheek.

The acipenseriform mechanism for jaw protrusion is found in all sturgeon and in *Psephrus gladius*, the Chinese paddlefish, and has been modified into a four bar jaw opening mechanism in the American paddlefish, *Polyodon spathula* (Bemis, 1987; Grande

and Bemis, 1991). This mechanism is unique to the Acipenseriformes and the muscles that actuate it, the protractor and retractor hyomandibularis, are synapomorphies for the Acipenseriformes (Edgeworth, 1935; Bemis et al., 1997).

### Comparisons With Other Vertebrates

Sturgeon kinematics are similar to those of other anamniotic, suction-feeding vertebrates. *Scaphirhynchus albus* feed by opening their mouths and drawing water into their buccal cavity through lateral and ventral expansion. Dorsal expansion was observed in *Acipenser medirostris* sequences. Expansion is apparently the result of retraction of the hyoid and buccal floor, abduction of the suspensorium and operculum, and (in *A. medirostris*) dorsal rotation of the neurocranium. After prey entry the gape is closed and water is forced out the opercular openings as the skeletal elements are adducted and returned to near their original positions. The relative timing of kinematic events is consistent with that seen in other groups (Wilga and Motta, 1998a; Ferry-Graham and Lauder, 2001): retraction of the hyoid and buccal floor reach their maximum values after peak gape; maximum opercular expansion is after peak hyoid displacement, resulting in a rostral to caudal wave of expansion (Table 1, Figs. 5, 6).

Although sturgeon anatomy differs in many respects from that of other basal actinopterygians, the major anatomical elements, including the neurocranium, hyoid, jaws, branchial arches, and opercula, retain the key features of their primitive design and function. Sturgeon anatomy differs from other osteichthyes in the protrusability of the jaws and their independence from the neurocranium. Sturgeon prey capture differs from other osteichthyes in the kinematics of jaw protrusion and the kinematics of neurocranial elevation. Typically, *Scaphirhynchus albus* reached peak jaw protrusion as the jaws were closed; this pattern has not been reported in any other osteichthyan fish (see below). Neurocranial elevation is not part of the strike in *S. albus*, and *Acipenser medirostris* often showed a pattern of continued neurocranial elevation during jaw closing that would be anatomically impossible in other osteichthyes. It appears that, where sturgeon functional anatomy differs from the basal actinopterygian condition, those differences in anatomy have been accompanied by differences in prey-capture kinematics.

The formation of a circular mouth aperture is another aspect of convergence between sturgeon and other suction feeders. In many actinopterygians a roughly circular aperture is formed by rotation of the maxilla or, in more derived teleosts, the premaxilla (Alexander, 1966; Lauder, 1980b). Abduction of the labial cartilages in some suction-feeding sharks helps to create a circular mouth aperture (Motta and Wilga, 1999). In sturgeon the lips surrounding the

mouth create a circular aperture in an analogous mechanism to the labial cartilages of sharks or the maxilla and premaxilla of teleosts.

**Convergence with elasmobranchs.** Sturgeon cranial morphology shows remarkable convergence with elasmobranchs, including the presence of a rostrum and subterminal mouth and the independence of the upper and lower jaws from the neurocranium. Many features of the acipenseriform jaw protrusion mechanism are convergent with the mechanism hypothesized to be the ancestral condition for elasmobranchs (Wilga and Motta, 1998a,b, 2000). Both morphologies involve a process on the palatoquadrate that guides the protruding jaws, the orbital process in sharks, and the palatal complex in sturgeon. Both convert rostral motion of upper jaw into ventral motion by deflection of these processes against the neurocranium (Motta et al., 1997; Wilga and Motta, 1998a, 2000). Both groups take advantage of a rostrocaudally mobile hyomandibula to translate the jaws anteriorly. The two groups differ in that upper jaw protrusion in elasmobranchs is mediated by muscles, the preorbitalis, levator palatoquadrate, or the AM, that pull the upper jaw and hyomandibula forward (Motta and Wilga, 2001). In sturgeon the jaws are pushed forward by the hyomandibula and symplectic (Fig. 8). These bones are, in turn, are pulled forward by the protractor hyomandibularis muscle. The addition of a large mobile symplectic is itself an important part of the sturgeon anatomy not found in sharks.

**Convergence with other actinopterygians.** While most actinopterygians can only protrude their upper jaw (premaxilla), some groups of teleosts have evolved mechanisms for protrusion of the jaw joint that have convergent features with the acipenseriform jaw protrusion mechanism. Species of labrids (Westneat, 1991), cichlids (Thomas Waltzeck, pers. commun.) and cheatodontids (Ferry-Graham et al., 2001) have evolved a mobile jaw joint, analogous with that found in Acipenseriformes.

### Kinematics of Jaw Protrusion

The typical movement and timing of jaw protrusion in sturgeon bears more similarity to that reported for elasmobranchs than to that of other actinopterygians (Fig. 10). In teleosts peak protrusion is reached concurrently with peak gape (Gillis and Lauder, 1995; Ferry-Graham and Lauder, 2001). In elasmobranchs and in sturgeon the majority of ventral upper jaw protrusion occurs after the onset of jaw closing (Fig. 5; Motta et al., 1997; Wilga and Motta, 1998a,b, 2000).

One of the proposed functions of jaw protrusion in teleosts is to bring the mouth aperture near to a prey before or while it is sucked in (Alexander, 1966). The first phase of jaw protrusion in sturgeon serves a similar purpose. In this phase both jaws are pushed out from under the neurocranium and exposed to the

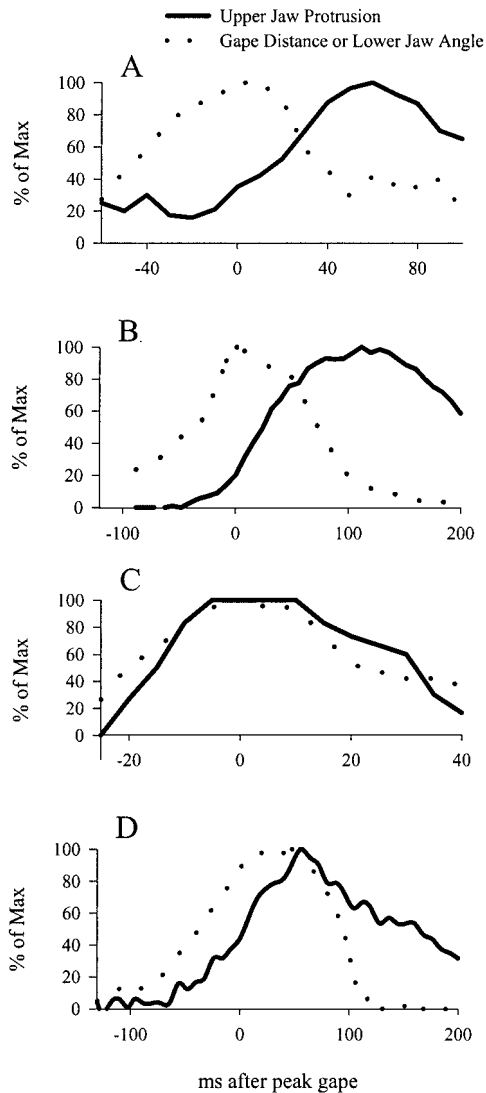


Fig. 10. Comparison of upper jaw protrusion and gape kinematics (expressed as percentage of maximum value) from (A) a leopard shark (*Triakis semifasciata*), (B) average *Scaphirhynchus albus* (data also shown in Fig. 6), (C) a teleost, the bluegill sunfish *Lepomis macrochirus*, (D) an atypical sequence from *S. albus* in which upper jaw protrusion peaks before jaw closure. In (A) and (B), upper jaw protrusion lags behind gape opening, while in (C) and (D) they are in phase. Although the kinematics of *S. albus* typically resemble those of chondrichthyes, individuals are anatomically capable of the teleost-like pattern. (A) is abstracted from Ferry-Graham (1998a); (C) is from Gillis and Lauder (1995).

prey as they are opened (Fig. 5). At the end of this phase the upper jaw is flush with or just below the underside of the neurocranium. The majority of ventral protrusion occurs after the jaws have begun to close.

One proposed function of jaw protrusion in elasmobranchs is to aid in jaw closing (Wilga and Motta, 1998a,b, 2000). In sturgeon the second phase of jaw protrusion likewise aids in closing the jaws (Fig. 8). This phase of jaw protrusion involves ventral displacement of the upper jaw towards the depressed

lower jaw by protrusion of the jaw joint and by rotation of the upper jaw around the jaw joint (Figs. 8, 9). The amplitudes of upper jaw and jaw joint protrusion can vary among strikes in sturgeon, as can the relationship between upper jaw rotation and jaw joint protrusion.

While the sturgeon's typical kinematic pattern (shown in Figs. 6, 10) resembles the elasmobranch condition (jaw protrusion during jaw closing), *Scaphirhynchus albus* individuals occasionally displayed a more teleost-like kinematic pattern (jaw protrusion during jaw opening) (Fig. 10). The sturgeon's typical kinematic pattern, therefore, is not the only one of which it is capable. The independence of the sturgeon's anatomical elements may translate into a flexible kinematic repertoire.

While this study furthers the experimental investigation of feeding in basal actinopterygian fishes as begun by Lauder (1980a), it is only the beginning of the study of Acipenseriform feeding. The activity patterns of sturgeon cranial muscles during prey capture need to be observed, both to test the mechanisms predicted here and to help complete the phylogenetic reconstruction of actinopterygian motor patterns.

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