

Evolution of the Feeding Mechanism in Primitive Actinopterygian Fishes: A Functional Anatomical Analysis of *Polypterus*, *Lepisosteus*, and *Amia*

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ABSTRACT The comparative functional anatomy of feeding in *Polypterus senegalus*, *Lepisosteus oculatus*, and *Amia calva*, three primitive actinopterygian fishes, was studied by high-speed cinematography (200 frames per second) synchronized with electromyographic recordings of cranial muscle activity. Several characters of the feeding mechanism have been identified as primitive for actinopterygian fishes: 1) Mandibular depression is mediated by the sternohyoideus muscle via the hyoid apparatus and mandibulohyoid ligament. 2) The obliquus inferioris and sternohyoideus muscles exhibit synchronous activity at the onset of the expansive phase of jaw movement. 3) Activity in the adductor operculi occurs in a double burst pattern—an initial burst at the onset of the expansive phase, followed by a burst after the jaws have closed. 4) A median septum divides the sternohyoideus muscle into right and left halves which are asymmetrically active during chewing and manipulation of prey. 5) Peak hyoid depression occurs only after peak gape has been reached and the hyoid apparatus remains depressed after the jaws have closed. 6) The neurocranium is elevated by the epaxial muscles during the expansive phase. 7) The adductor mandibulae complex is divided into three major sections—an anterior (suborbital) division, a medial division, and a posterolateral division.

In *Polypterus*, the initial strike lasts from 60 to 125 msec, and no temporal overlap in muscle activity occurs between muscles active at the onset of the expansive phase (sternohyoideus, obliquus superioris, epaxial muscles) and the jaw adductors of the compressive phase. In *Lepisosteus*, the strike is extremely rapid, often occurring in as little as 20 msec. All cranial muscles become active within 10 msec of each other, and there is extensive overlap in muscle activity periods.

Two biomechanically independent mechanisms mediate mandibular depression in *Amia*, and this duality in mouth-opening couplings is a shared feature of the halecostome fishes. Mandibular depression by hyoid retraction, and intermandibular musculature, consisting of an intermandibular posterior and interhyoideus, are hypothesized to be primitive for the Teleostomi.

The Actinopterygii or ray-finned fishes is by far the most diverse group of vertebrates; it includes more than 23,000 fossil and recent species. This tremendous diversity in number is mirrored by their extensive morphological and behavioral variations in prey-capture mechanisms and strategies. Diversity in jaw morphology is a hallmark of the actinopterygian radiation.

To date the major study of feeding mechanisms in primitive actinopterygian fishes is

that of Schaeffer and Rosen ('61). They examined the major adaptive levels in the evolution of the feeding mechanism of ray-finned fishes and proposed hypotheses of jaw function at each level. Their analysis was, of necessity, gradual.

Within the last decade, functional anatomists have begun to analyze experimentally the feeding mechanisms of fishes and to test the hypotheses of earlier investigators who had suggested possible patterns of jaw movement based on post mortem manipulations (e.g.,

Alexander, '66, '67; van Dobben, '35; Gunther and Deckert, '53; Holmquist, '10; Kampf, '61; Kirchhoff, '58; Tchernavin, '53). Experimental studies have involved high-speed cinematography (e.g., Dutta, '68; Liem, '67b; '70; Lauder, '79; Nyberg, '71), electromyographic analyses of cranial muscle activity (Ballintijn et al., '72; Elshoud-Oldenhave and Osse, '76; Lauder and Liem, '80; Liem, '73, '78; Liem and Osse, '75; Osse, '69), measurement of buccal cavity pressures (Alexander, '69; '70; Liem, '78), and strain gauge analysis (Lauder and Lanyon, in press). Almost all of these studies have focused on feeding in advanced teleost fishes, while primitive members of the Teleostei and other actinopterygian groups have been largely neglected.

An analysis of the functional anatomy of feeding in primitive ray-finned fishes is of particular importance in providing comparative data on fish feeding mechanisms and in aiding in morphological interpretations of fossil fishes. Such observations may support inference of function from structure in extinct taxa, and will allow a reinterpretation of the functional and phylogenetic significance of several features in the earliest ray-finned fishes. Examination of primitive taxa may reveal characters that corroborate (or refute) current hypotheses (Gardiner and Bartram, '77; Greenwood et al., '73; Liem and Lauder, in press; Patterson and Rosen, '77; Wiley, '79) of the systematic relationships of actinopterygians (see Table 1 for example).

This paper focuses on a comparative functional analysis of feeding in *Polypterus senegalus*, *Lepisosteus oculatus*, and *Amia calva*, three primitive living actinopterygian fishes. "Primitive actinopterygian" as used here refers loosely to all non-teleost actinopterygians. Although there has been some debate during the last century over the phylogenetic position of *Polypterus*, most of the recent evidence indicates that it is an actinopterygian (Gardiner, '73; Liem and Lauder, in press; Wiley, '79).

MATERIALS AND METHODS

All fishes studied experimentally were caught in the wild and obtained through commercial suppliers. Fish were acclimated to laboratory water and temperature (25°C) for several weeks before experimental work was begun; each fish was housed in a separate 80 liter tank.

Fine-wire bipolar electrodes (Evenohm S) were implanted in the cranial muscles using the technique of Basmajian and Stecko ('62).

The fishes were anesthetized during implantation with tricaine methane sulfonate, 200–400 mg/liter. Up to twelve pairs of electrodes were implanted at one time, although only five channels could be synchronously recorded during an experiment. This allowed multiple combinations of muscles to be investigated during any given recording session by simply changing leads at the connector. A dental drill was used to drill small (1 mm diameter) holes in the dermal bones overlying many of the cranial muscles (especially in *Lepisosteus* and *Amia*) to allow access to the muscle belly. The electrodes were glued together into a thin cable, color coded, and attached to a small plastic clamp (visible in Figs. 6, 10). The clamp either was anchored to a wire passing just dorsal to the epaxial musculature but ventral to the dorsal scales (*Lepisosteus*, *Polypterus*), or was screwed directly to the skull (*Amia*). Electrodes were implanted for up to three weeks and, although no deterioration in signal quality was noticed in this period, the electrodes usually worked loose after two weeks.

During recording sessions, the color-coded electrode leads were attached to a slip-ring, rotating connector, that was located just above the water surface and connected to Gould-Brush biomedical amplifiers. Electrical signals were stored on a Honeywell 5600 tape recorder at 37.5 cm/sec and played back for analysis at 4.7 cm/sec through a Gould 260 strip chart recorder.

High-speed films (200 frames per second) were synchronized with the electromyographic recordings by a special synchronization unit that counted pulses from the high-speed camera and placed a series of coded pulses (see Figs. 6, 10, 13: SYN) onto the tape recorder. The films were taken with a Photosonics 16-1PL camera on Kodak 4X Reversal and 4X Negative film. Three 600W Smith-Victor filming lights provided illumination for filming with a shutter speed of 1/1200 second. A short period of training (two weeks) was usually necessary to accustom the fishes to feed with the lights on.

More than 150 feeding sequences were examined for *Lepisosteus* (4 specimens, including MCZ 54289, 54291), 125 for *Amia* (2 specimens, including MCZ 54287), and 100 for *Polypterus* (2 specimens, including MCZ 54290), all taken over a two-year period. *Polypterus* was fed meal worms (*Tenebrio*), whereas *Amia* was fed pieces of smelt (*Osmerus*) and live (occasionally lightly anesthetized) goldfish (*Carassius auratus*). *Lepisosteus* was fed goldfish exclusively.

Comparative anatomical observations were

made on the following specimens: *Lepidosiren paradoxa*, U. S. National Museum 162504, one specimen; *Latimeria chalumnae*, American Museum of Natural History 32949, one cleared and stained embryo; five uncatalogued *Amia calva*, (MCZ); *Amia calva*, MCZ 8970, three specimens; *Lepisosteus oculatus*, MCZ 34650, two specimens; three uncatalogued *Lepisosteus oculatus* (MCZ); *Polypterus senegalus*, MCZ 48572, two specimens; *Polyodon spathula*, MCZ 40481, one specimen; *Acipenser huso*, MCZ 54269, one specimen.

Physiological properties of the jaw muscles are of considerable importance in interpreting the electromyographic data. However, only preliminary data are available for actinopterygian jaw muscles (Lauder and Hylander, unpublished). In the gar *Lepisosteus*, the twitch time to peak tension averages 34 msec in the adductor mandibulae and the latency between the stimulus and the onset of tension is 4 msec. Tetanic time to peak tension averaged 75 msec but the time to 50% response was 12 msec.

RESULTS

Anatomy

The cranial anatomy of *Polypterus* was described by Allis ('19a, '19b, '22), Luther ('13), Edgeworth ('35) and Nelson ('69). The cranial anatomy of *Amia* has been monographed by Allis (1897). The anatomy of *Lepisosteus* has not been well described. Allis ('20), Mayhew ('24), Patterson ('73), and Wiley ('76) partially described the cranial osteology, and Luther ('13), Edgeworth ('35) and Wiley ('76) provided brief accounts of the cranial myology.

Those aspects of the cephalic musculoskeletal system that are necessary for understanding the subsequent functional analysis are here emphasized, as are features inadequately described previously. The musculoskeletal couplings mediating jaw movements are discussed and organized within the *mechanical units* (Gans, '69) of the primitive actinopterygian skull, as follows: 1) neurocranium and premaxilla, 2) maxilla, 3) suspensory apparatus, 4) mandible, 5) opercular series, 6) hyoid apparatus, and 7) pectoral girdle.

Extensive synonymies for most muscles described below may be found in Winterbottom ('74) and Wiley ('79).

Neurocranium and premaxilla; maxilla

In primitive actinopterygians, the premaxilla forms part of the neurocranial mechanical unit and is firmly attached to the anterior

aspect of the neurocranium. In *Lepisosteus* and *Amia*, the premaxillae attach to the neurocranium by elongate "nasal processes" (Patterson, '73), whereas in *Polypterus*, the premaxillae are fixed to the neurocranium by internal connections to the parasphenoid and by small lateral bony processes extending dorsally on either side of the ethmoid region (ascending process of Allis, '22). These processes are not homologous to the ascending processes of the premaxillae in teleosts or to the "nasal processes" in *Lepisosteus* and *Amia*. Wiley ('76) suggested that these processes in *Lepisosteus* are not homologous to those in *Amia*.

The maxilla in *Polypterus* forms a rigid part of the upper jaw and is attached anteriorly to the premaxilla and lacrimal, and posteriorly to the ectopterygoid. Both the maxilla and ectopterygoid bear teeth. The maxilla of *Lepisosteus* is rudimentary (Wiley, '76) and a series of toothed infraorbital bones form the lateral toothed margin of the upper jaw. The maxilla of *Amia* (Fig. 3: MX) shares two features with the primitive teleost maxilla. 1) It attaches to the upper jaw by a medial, peglike process which fits into a socket formed by the vomer, ethmoid, and palatine. This articulation allows the maxilla to swing anteroposteriorly in the parasagittal plane (Lauder, '79). 2) Distally, the maxilla is connected to the coronoid process of the mandible by a flat maxillomandibular ligament. A thin sheet of connective tissue extends from the posterior edge of the maxilla to attach to the infraorbital bones and merges with the fascia covering the jaw adductor musculature laterally. A ligament from the apex of the coronoid process of the lower jaw (Fig. 3: MML) extends anteriorly to attach to the medial surface of the maxilla. A small supra-maxilla is present.

In *Amia*, *Polypterus*, and *Lepisosteus*, the epaxial muscles (Figs. 1, 3: EM) insert on the posterodorsal margin of the neurocranium. The obliquus superioris (Fig. 3: OBS) is a division of the hypaxialis and always extends anterodorsally to insert on the posterolateral margin of the skull.

Suspensory apparatus

The suspensory apparatus articulates with the neurocranium via two articular surfaces—the craniohyomandibular articulation posteriorly, and the articulation between the autopalatine (palatopterygoid in *Lepisosteus*) and the ethmovomerine region (premaxilla and vomer in *Lepisosteus*) anteriorly. The orientation of the axis of these two articulations is

nearly horizontal in *Lepisosteus*, but oblique in *Amia*; in *Polypterus* the suspensorial axis is steeply inclined in a posterodorsal to anteroventral direction. The suspensory apparatus pivots around the articular axis in a mediolateral direction. Lateral mobility increases in the series *Lepisosteus*, *Polypterus*, *Amia* as does the moment arm of the quadrate about the articular axis of the suspensorium with the neurocranium.

The suspensory apparatus supports the adductor musculature of the lower jaw. This muscle mass is subdivided into anterior, medial, and posterolateral parts (homologies are given in Table II, see Discussion).

Anterior divisions of the adductor mandibulae are absent in *Polypterus*. In *Lepisosteus*, the so-called palatomandibularis minor (Fig. 2: PMm) and palatomandibularis major (Edgeworth, '35; after Luther, '13) form the anterior adductor subdivision. The palatomandibularis minor originates from the dorso-lateral surface of the ectopterygoid and inserts on the surangular bone of the lower jaw. This muscle, actually separable into two well defined fiber bundles, wraps laterally around the anterior fibers of the preorbitalis muscles (Fig.

2: POs, POp). The palatomandibularis major extends from a wide origin on the ectopterygoid anterior to the origin of the palatomandibularis minor to insert on the surangular and articular.

Parts 3 and 4 of the levator maxillae superioris form the anterior adductor division in *Amia* (Fig. 3: LMS 3, LMS 4). Levator maxillae superioris 4 is cylindrical in shape and parallel-fibered. It originates on the antorbital and extends posteriorly to insert on the palatine (Fig. 3: PAL). A few of the more posterior fibers reach the ectopterygoid. Levator maxillae superioris 3 is a flat, parallel-fibered muscle that originates from the palatine and cartilage between the palatine and entopterygoid; it extends posteroventrally to join the tendon of the posterolateral division of the adductor mandibulae.

The medial division of the adductor mandibulae is represented in *Polypterus* by the so-called "pterygoideus" and "temporalis" muscles (Allis, '22) (Figs. 1, 4A: AMp, AMt). The "temporalis" originates from the sphenotic and frontal and extends posteroventrally where it contracts to a wide tendon which inserts medial to the coronoid process in the mandibular fossa.

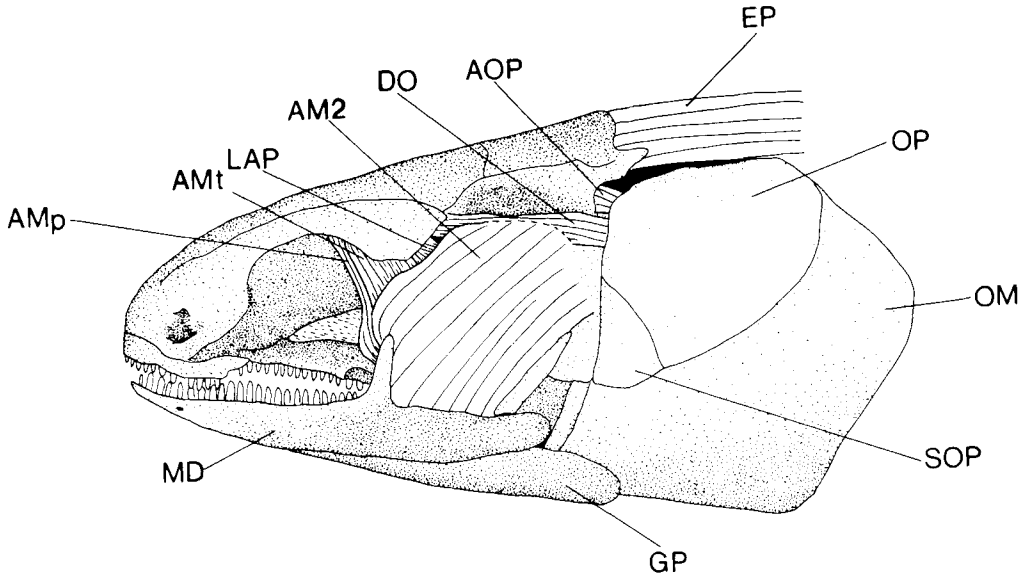
ABBREVIATIONS

AAM, anterior division of adductor mandibulae complex
 AAP, adductor arcus palatini
 AHY, adductor hyomandibulae
 AOP, adductor operculi
 AM, AM2, AM2', AM2'', posterolateral division of adductor mandibulae
 Amp, "pterygoideus" division of adductor mandibulae complex
 AMt, "temporalis" division of adductor mandibulae complex
 BB, basibranchial
 BC, buccal cavity
 BM, branchiomandibularis
 BML, branchiostego-mandibular ligament
 BSTG, branchiostegal ray(s)
 CB, ceratobranchial
 CC, cranial cavity
 CH, ceratohyal
 CL, cleithrum
 CLAV, clavicle
 CN, chondrocranium
 DO, dilator operculi
 EH, epihyal
 EM, EP, epaxial musculature
 GA, gill arch
 GF, gill filaments
 GP, gular plate
 HH, hypohyal

HHi, hyohyoideus inferioris
 HHS, hyohyoideus superioris
 HY, hypaxial muscles (= obliquus inferioris)
 HYm, hyomandibula
 IH, interhyoideus
 IHY, interhyal
 IML, interoperculomandibular ligament
 IMA, intermandibularis anterior
 IMP, intermandibularis posterior
 IOP, interoperculum
 LAP, levator arcus palatini
 LIM, interoperculomandibular ligament
 LMH, mandibulohyoid ligament
 LMS 1-4, levator maxillae superioris division of adductor mandibulae complex
 LOP, levator operculi
 LOPT, tendon of levator operculi
 MAM, medial division of the adductor mandibulae complex
 MD, mandible
 MHL, mandibulohyoid ligament
 MML, ligament from the coronoid process of the mandible to the maxilla
 MX, maxilla
 NC, neurocranium
 OBI, obliquus inferioris

OBS (r, l), obliquus superioris (right and left sides)
 OHY, operculohyomandibular articulation
 OM, operculo-gular membrane
 OP, operculum
 PA, parietal
 PAL, palatine
 PG, pectoral girdle
 PMm, palatomandibularis minor
 POP, preorbitalis profundus
 PS, parasphenoid
 Q, quadrate
 S, splenial
 SH (SHr, SHl), sternohyoideus (right and left halves)
 SHr (l) ant, SHr (l) post, anterior and posterior fibers of the right (left) halves of the sternohyoideus
 SHT, tendon of sternohyoideus
 SHS, median septum of the sternohyoideus
 SO, suborbital bone
 SOP, suboperculum
 SUS, suspensory apparatus
 SYN, synchronization pulse
 TAM, tendon of adductor mandibulae
 UBSTG, uppermost expanded branchiostegal ray

A



B

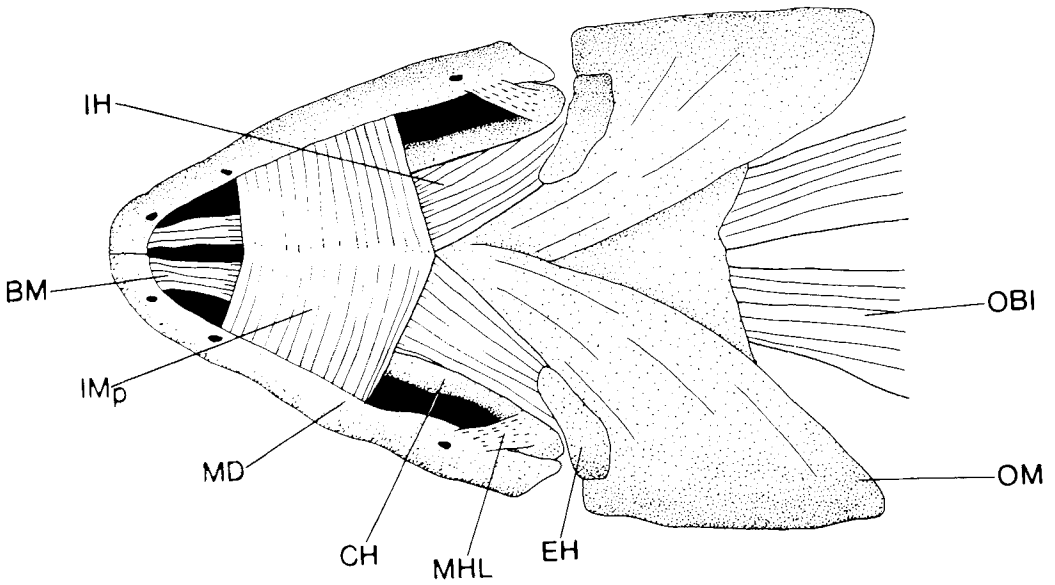
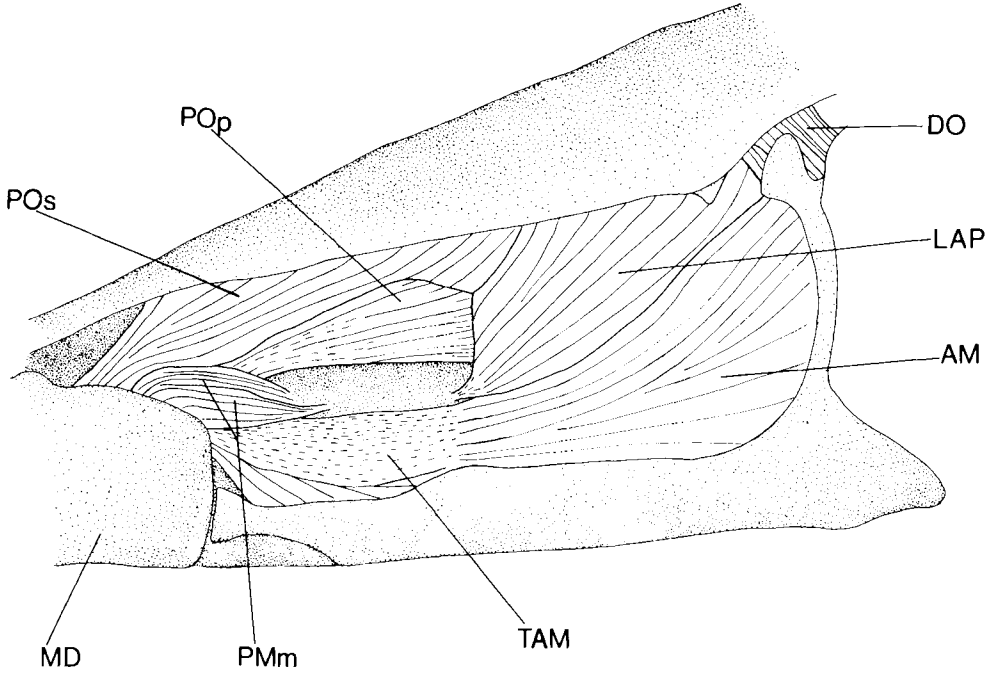


Fig. 1. *Polypterus senegalus*. Lateral view (A) and ventral view (B) of the head after removal of the eye, suborbital bones, gular plates, and maxilla.

A



B

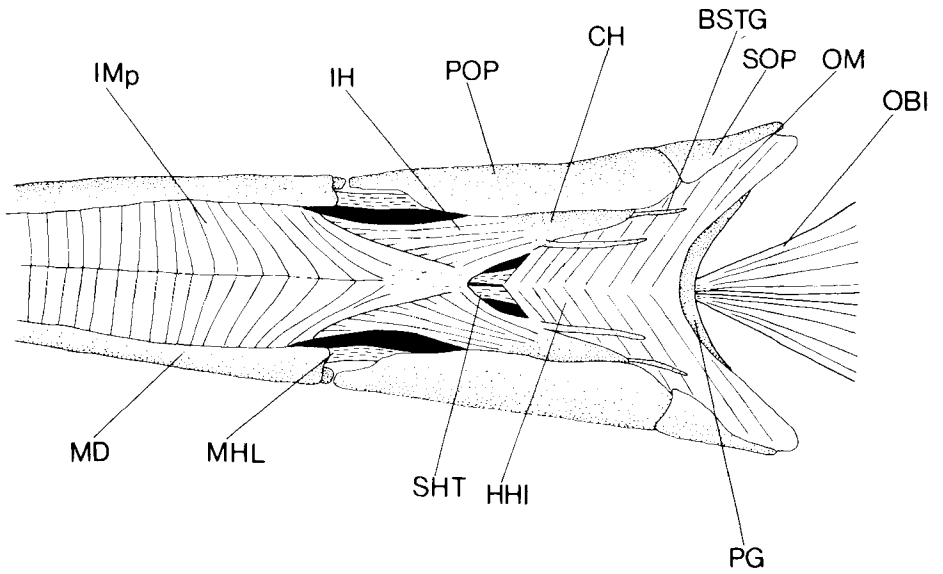


Fig. 2. *Lepisosteus oculatus*. Lateral view (A) and ventral view (B) after removal of the eye.

The "pterygoideus" originates from the parasphenoid and sphenoid (Allis, '22) and extends posteroventrally to insert on the medial surface of the wide "temporalis" tendon.

In *Lepisosteus*, the medial adductor division is represented by the preorbitalis superficialis and profundus muscles (Figs. 2, 4B: POP, POs). The preorbitalis superficialis originates from a wide area on the ventral surface of the frontal and dermosphenotic, and runs anteroventrally after passing above the orbit to insert muscously on the surangular and articular. The preorbitalis profundus originates medial to the levator arcus palatini on the lateral wall of the braincase and extends anteriorly, medial to the eye, before inserting on the articular and surangular deep to the palatomandibularis minor.

Parts 1 and 2 of the levator maxillae superioris (Figs. 3, 4C: LMS 1, 2) comprise the medial adductor division in *Amia*. These muscles arise from a common origin on the parasphenoid and anterior face of the hyomandibula and insert via separate tendons onto the tendinous insertions of the medial fibers of two of the posterolateral adductor divisions, AM2'' and AM2'''.

The posterolateral division of the adductor mandibulae in *Polypterus* has two components, a much larger lateral mass (Figs. 1, 4A: AM2) and a smaller medial one arising from the quadrate and inserting into the mandibular fossa. The lateral fibers (AM2) arise from the connective tissue medial to the suborbital bones, the hyomandibula, and connective tissue covering the lateral surface of the dilator operculi. The lateral fibers of this muscle run in a posterodorsal to anteroventral direction, but the medial fibers may extend more antero-posteriorly, especially along the ventral margin of the muscle. Insertion is onto the dermo-articular (Allis, '22) and lateral surface of the splenial.

Lateral movement of the suspensorium is mediated by the levator arcus palatini (Figs. 1-4: LAP). In *Polypterus*, this muscle arises from the postfrontal (Allis, '22) with the muscle fibers fanning out ventrally over the lateral face of the suspensory apparatus. The levator arcus palatini of *Lepisosteus* has a broad origin from the frontal and dermopterotic, and is pyramidal in shape with an apical insertion restricted to a narrow strip of the ectopterygoid and metapterygoid medial to the adductor mandibulae (Fig. 2: AM). Anteriorly, the insertion of this muscle becomes muscous. In *Amia* this muscle originates from the sphenotic (= postorbital ossification of Allis, '22) and inserts on the metapterygoid, both on the medial and

lateral faces of the ascending process (Fig. 4C: LAP).

Medial movement of the suspensory apparatus is accomplished by the adductor arcus palatini and adductor hyomandibulae (Fig. 5: AAP, AHY). *Polypterus* lacks an adductor arcus palatini (defined as fibers extending onto the suspensorium anterior to the hyomandibula) and, thus, medial suspensorial movement occurs via the adductor hyomandibulae alone. The latter originates on the opisthotic and extends laterally to insert on the medial surface of the hyomandibula. In *Lepisosteus*, the adductor arcus palatini and adductor hyomandibulae form a continuous sheet of parallel-fibered muscle that originates from the otic cartilage dorsal to the prootic and extends laterally to insert on the medial face of the hyomandibula, metapterygoid, and entopterygoid. The adductor arcus palatini is absent in *Amia*. The parallel-fibered adductor hyomandibulae is partially divided by a septum into anterior and posterior portions, both of which originate on the prootic and intercalar and insert on the medial surface of the hyomandibula.

Opercular series

The opercular series in *Polypterus* is composed of a large operculum and a small subopercular bone attached to the anteroventral margin of the operculum (Fig. 1: OP, SOP). A large opercular membrane (Fig. 1: OM) extends ventrally and anteriorly into the intermandibular region. Branchiostegal rays and a levator operculi muscle are absent.

The adductor operculi (Figs. 1, 5: AOP) is continuous with the adductor hyomandibulae and has a similar origin. Insertion of the adductor operculi is posterodorsal to the operculo-hyomandibular articulation along the medial edge of the dorsal opercular margin.

The dilator operculi is a long, parallel-fibered muscle (Figs. 1, 4A: DO) that originates on the postfrontal (Allis, '22) and stretches posterolaterally to attach to the anterodorsal margin of the operculum. The dilator operculi passes medial to the dorsal fibers of the adductor mandibulae and forms the lateral wall of the spiracular canal.

In *Lepisosteus*, the opercular series consists of an operculum and a suboperculum. Three elongate branchiostegal rays are present. The adductor operculi is continuous with the adductor hyomandibulae and adductor arcus palatini (Fig. 5B: AOP) and has a similar origin. Insertion is just posterodorsal to the articulation of the operculum with the hyoman-

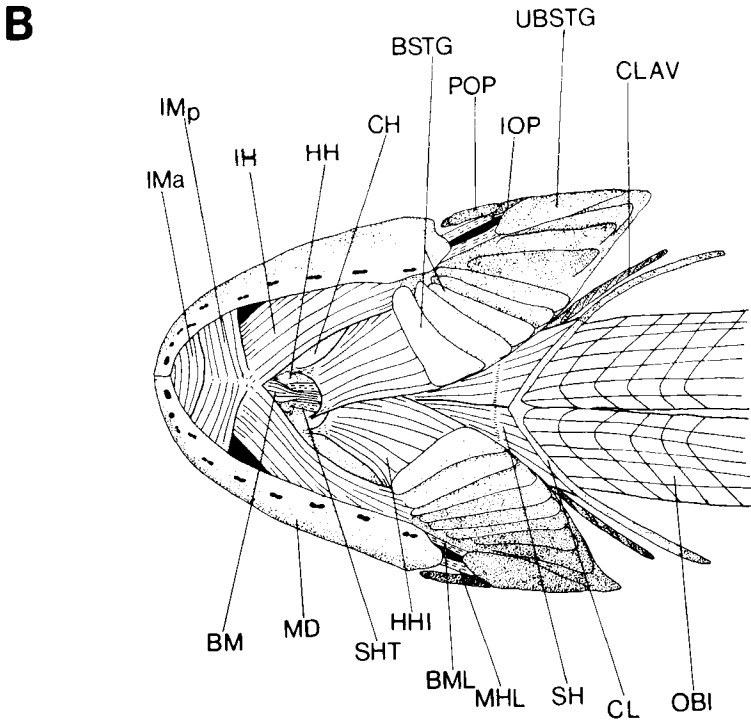
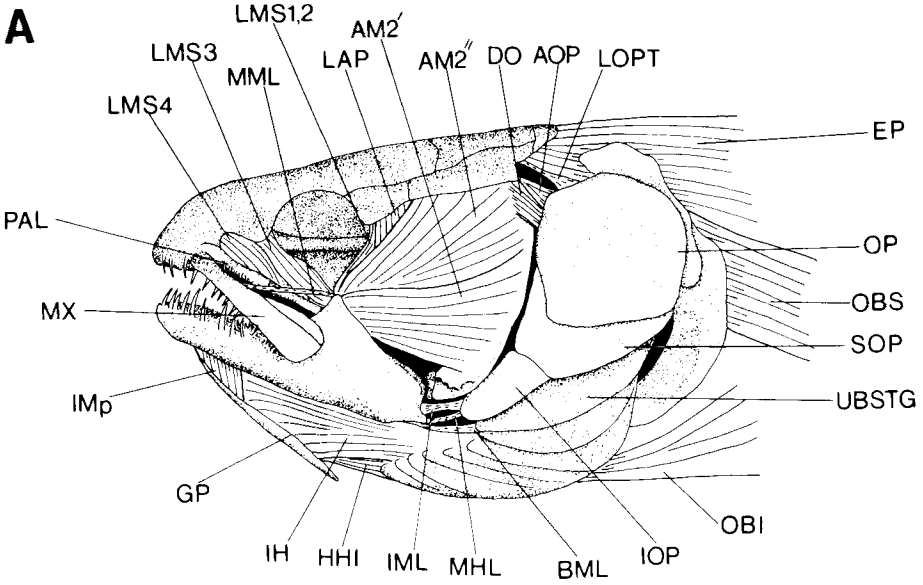


Fig. 3. *Amia calva*. Lateral view (A) and ventral view (B) after removal of the eye, dorsal aspect of the preoperculum, and gular plate.

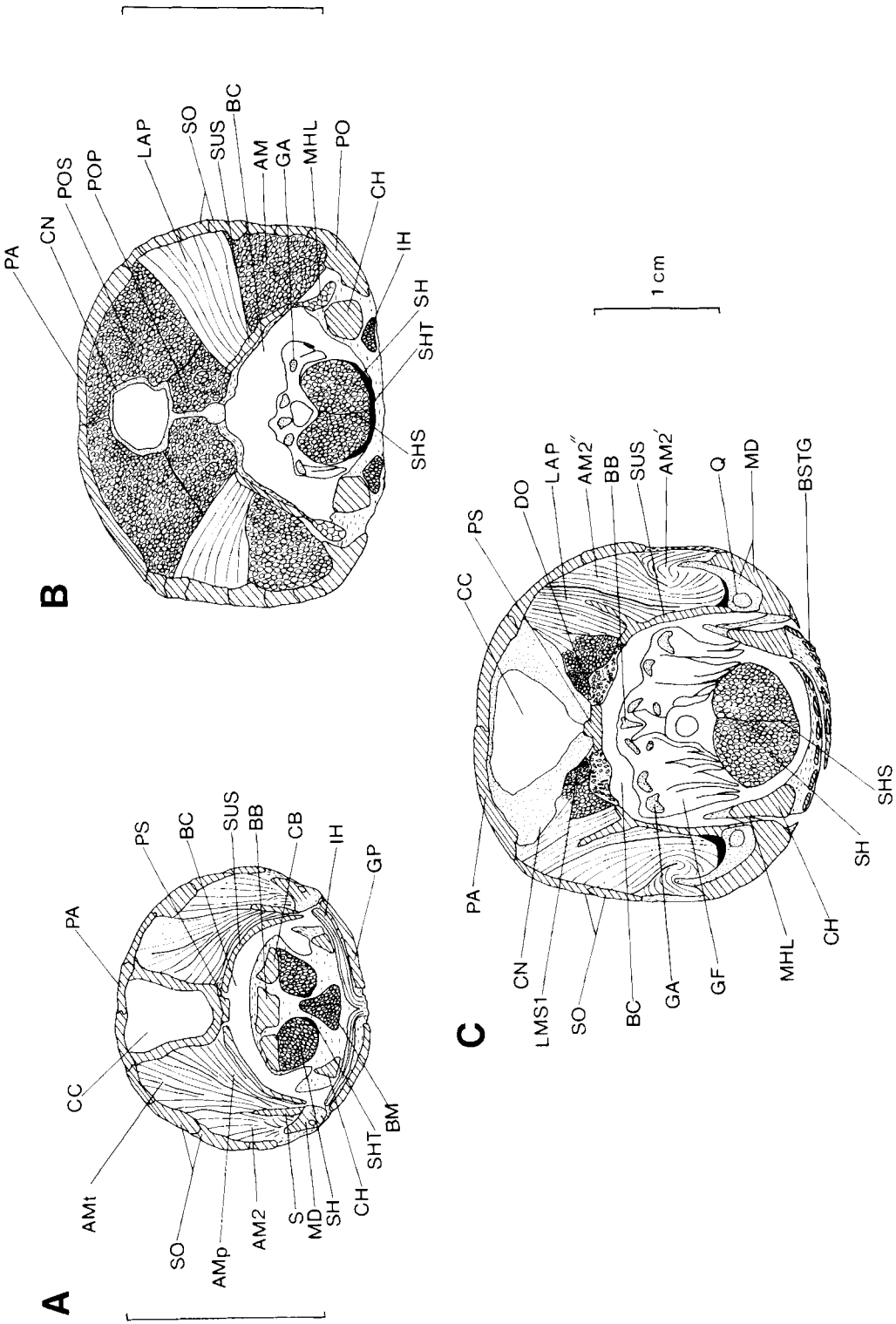


Fig. 4. Semi-diagrammatic cross-section through the head of (A) *Polypterus senegalus*, (B) *Lepisosteus oculatus*, and (C) *Amia calva*.

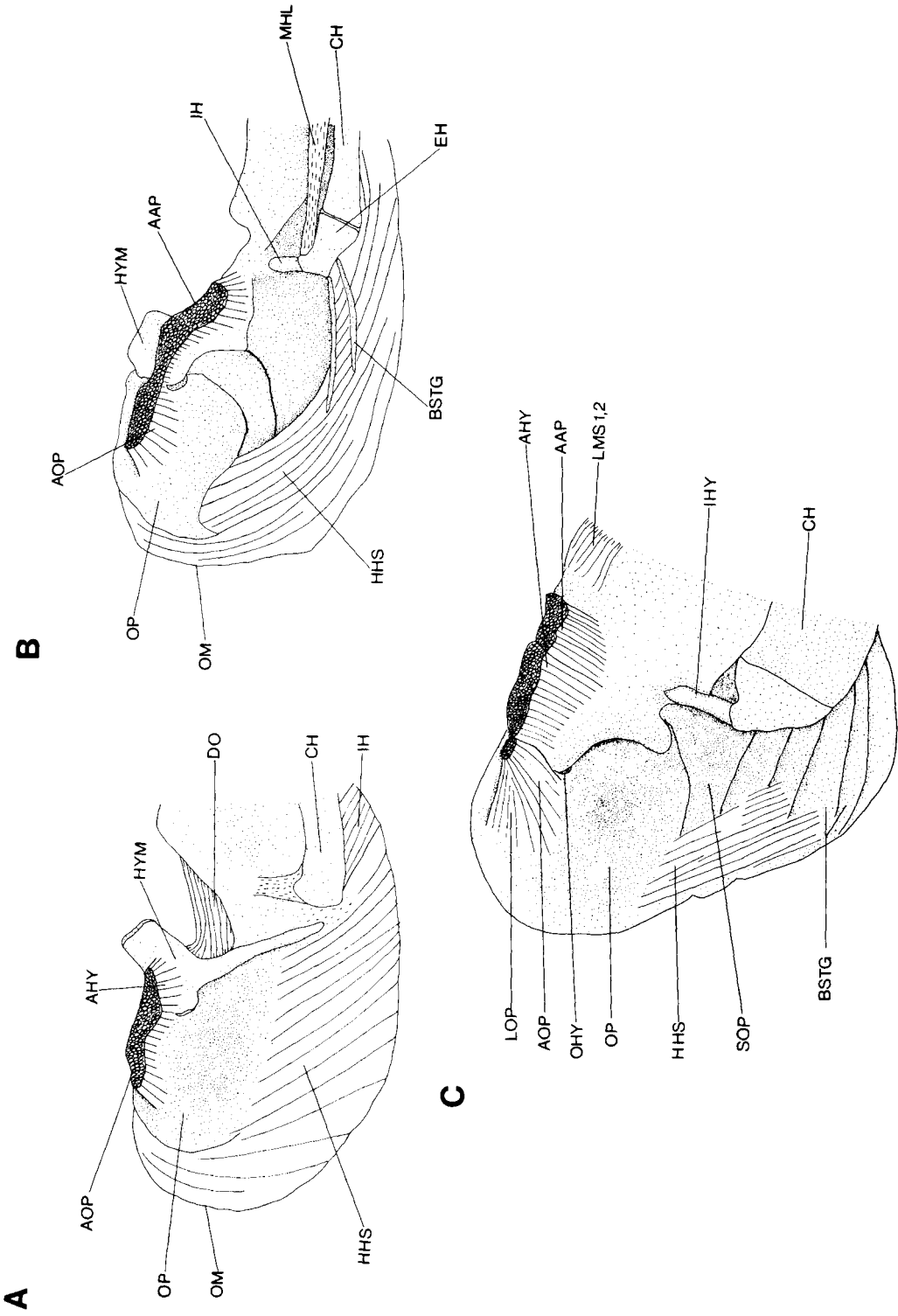


Fig. 5. Medial view of the posterior aspect of the suspensory apparatus of (A) *Polypterus senegalus*, (B) *Lepisosteus oculatus*, and (C) *Amia calva*. Note the relationships of the adductor operculi (AOP) to the adductor hyomandibulae (AHY) and the levator operculi (LOP; in *Amia* only).

dibula. The dilator operculi (Fig. 2: DO) originates on the sphenotic and is a short, parallel-fibered muscle inserting on the anterodorsal margin of the operculum. A levator operculi is absent.

The opercular series of *Amia* consists of the operculum, suboperculum, and interoperculum (Fig. 3: OP, SOP, IOP), as well as the expanded uppermost branchiostegal ray (Fig. 3: UBSTG), which is functionally a part of the opercular apparatus. This branchiostegal ray is attached to both the ceratohyal and opercular series by dense connective tissue. A ligament extends between the anteroventral aspect of the uppermost branchiostegal ray and the retroarticular process of the mandible (Fig. 3: BML), and a well-defined interoperculomandibular ligament connects the interoperculum to the retroarticular process (Fig. 3: IML).

The adductor operculi is completely separated from the adductor hyomandibulae (Fig. 5: AOP, AHY) and is continuous at its insertion on the operculum with the levator operculi (Fig. 5: LOP). Together, the insertion of these muscles occupies a broad area on the medial surface of the operculum. The origin of the adductor operculi is similar to that of the adductor hyomandibulae; both originate from the intercalar, whereas the levator operculi originates tendinously from the ventral surface of the posttemporal and posterior margin of the parietal (Fig. 3: LOPT).

The dilator operculi originates on the dermosphenotic and extends posterolaterally. It passes lateral to the hyomandibula, but medial to the dorsal margin of the preoperculum, to insert on the operculum.

Mandible

The mandible in *Polypterus*, *Lepisosteus*, and *Amia* is composed of a number of bony elements all of which are immovably joined (Figs. 1–4: MD); they form the mandibular mechanical unit. The intermandibularis posterior (Figs. 1–3: IMp) has a central median raphe and extends between the two mandibular rami. In *Amia* and *Polypterus*, the gular plate lies ventral to the intermandibularis posterior, but the muscle fibers do not insert onto the plate. A small intermandibularis anterior (Fig. 3: IMA) lies between the mandibular rami of *Amia*, anterior to the intermandibularis posterior.

The branchiomandibularis (= coracomandibularis, Wiley, '79) in *Polypterus* (Figs. 1, 4: BM) is paired throughout its length, originating near the mandibular symphysis on the

internal surface and extending posteriorly to insert on the third hypobranchials. In *Amia*, the branchiomandibularis (Fig. 3: BM) is paired at its origin, which is identical to that of *Polypterus*, but may merge into one median muscle mass before dividing again to insert on the third hypobranchials of each side.

Hyoid apparatus

The hyoid apparatus is composed of a ceratohyal, an epihyal, and a small styliiform interhyal which suspends the epihyal from the suspensory apparatus (Figs. 4, 5: CH, EH, IHY). In *Polypterus*, the interhyal is a small cartilaginous element covered medially by dense connective tissue between the ceratohyal and suspensorium.

The interhyoideus (Figs. 1–5: IH) arises from the ceratohyal and extends anteriorly ventral to the gular plate and intermandibularis posterior to meet its antimere in a median raphe. The lateral fibers fan out onto connective tissue dorsal to the intermandibularis posterior.

The hyohyoideus inferioris in *Polypterus* is represented by muscle fibers in the expanded opercular membrane. The hyohyoideus superioris (Fig. 5: HHS) originates on the medial surface of the operculum and runs ventrally in the opercular membrane, where the fibers merge with those of the hyohyoideus inferioris.

In *Lepisosteus*, the hyohyoideus superioris has a similar origin and also is continuous with the fibers of the hyohyoideus inferioris (Fig. 2: HHI) which meet in a median raphe ventrally. The hyohyoideus inferioris of *Amia* is a well developed muscle that inserts anteriorly on both the right and left hypohyals via small tendons (Fig. 3: HHI) and originates on the ceratohyal and inner surfaces of the anterior branchiostegal rays. The right and left tendons of insertion may be separate, or they may insert on the ventral hypohyal of each side in a common tendon.

A thick mandibulohyoid ligament extends between the hyoid arch (epihyal; ceratohyal in *Polypterus*) and the retroarticular process of the jaw (Figs. 1–5: MHL).

Pectoral girdle

The pectoral girdle of primitive actinopterygians can be treated as a mechanical unit that serves as the origin for the sternohyoideus and insertion for the obliquus inferioris. The sternohyoideus is divided into right and left halves by a median septum that completely divides the muscle (Fig. 4: SH, SHS). In *Polypterus*, the sternohyoideus shows three trans-

verse divisions by two transverse septa; the right and left halves of the muscle are completely separated for much of their course. The sternohyoideus inserts onto the hypohyals and a ventral tendinous thickening (Fig. 4A: SHT) extends anteriorly onto the ventral surface of the fleshy tongue. In *Amia*, the sternohyoideus is also divided transversely by two septa and inserts onto the hypohyals.

No transverse septa were found in the sternohyoideus of *Lepisosteus* and the sternohyoideus inserts onto the hypohyals by two stout tendons (Fig. 2: SHT). A thickened, tendinous expansion (Fig. 4: SHT) extends anteriorly onto the ventral surface of the basihyal tooth plates.

The obliquus inferioris, a division of the hypaxialis (Winterbottom, '74), is composed of fibers extending anteroventrally. These fibers insert on the pectoral girdle. There is no continuity between the obliquus inferioris and the sternohyoideus fibers.

FUNCTIONAL ANALYSIS OF PREY CAPTURE

Jaw movements during prey capture in fishes can be divided into three phases—a preparatory phase, an expansive phase, and a compressive phase. To date preparatory phases have only been observed in acanthopterygian teleosts. No preparatory phase was recorded in *Polypterus*, *Lepisosteus*, or *Amia*. The expansive phase is defined here as the time from the start of mouth opening to peak gape. The compressive phase extends from peak gape to complete closure of the jaws.

Polypterus senegalus

Expansive phase

The duration of this phase varies considerably from rapid (60 msec) to slow (125 msec) strikes and results in the creation of a flow of water into the mouth cavity, enabling prey to be sucked up off the bottom. The complete strike may take from 120 to 300 msec. The onset of the expansive phase is characterized by synchronous activity in the paired sternohyoideus muscles and obliquus inferioris (Fig. 6: SHr, l; HY). Activity in the epaxial muscles (Fig. 6: EP) begins 5 msec before the onset of activity in the sternohyoideus. The increase in

gape (Fig. 7A) occurs both by elevation of the cranium and by mandibular depression mediated by posterodorsal movement of the hyoid apparatus. This hyoid retraction, initiated by the sternohyoideus, is transmitted to the posteroventral aspect of the mandible by the mandibulohyoid ligament (Fig. 1: MHL) and results in mandibular depression. Hyoid depression reaches its maximum from 10 to 25 msec after peak gape (Fig. 7A). There is a consistent 15–25 msec delay between the onset of activity in the sternohyoideus and the initiation of mandibular depression (Fig. 6).

The adductor operculi becomes active 10 msec after the onset of activity in the sternohyoideus, and the adductor mandibulae (part two) frequently also displays low-level activity at this time (Fig. 6: AOP, AM2). Opercular adduction (Fig. 7A) is characteristic of the expansive phase, peak adduction usually occurring either synchronously with, or slightly before, peak gape. Late in the expansive phase the levator arcus palatini fires (Fig. 6: LAP), although suspensory abduction does not reach a maximum until 10 to 20 msec after peak gape.

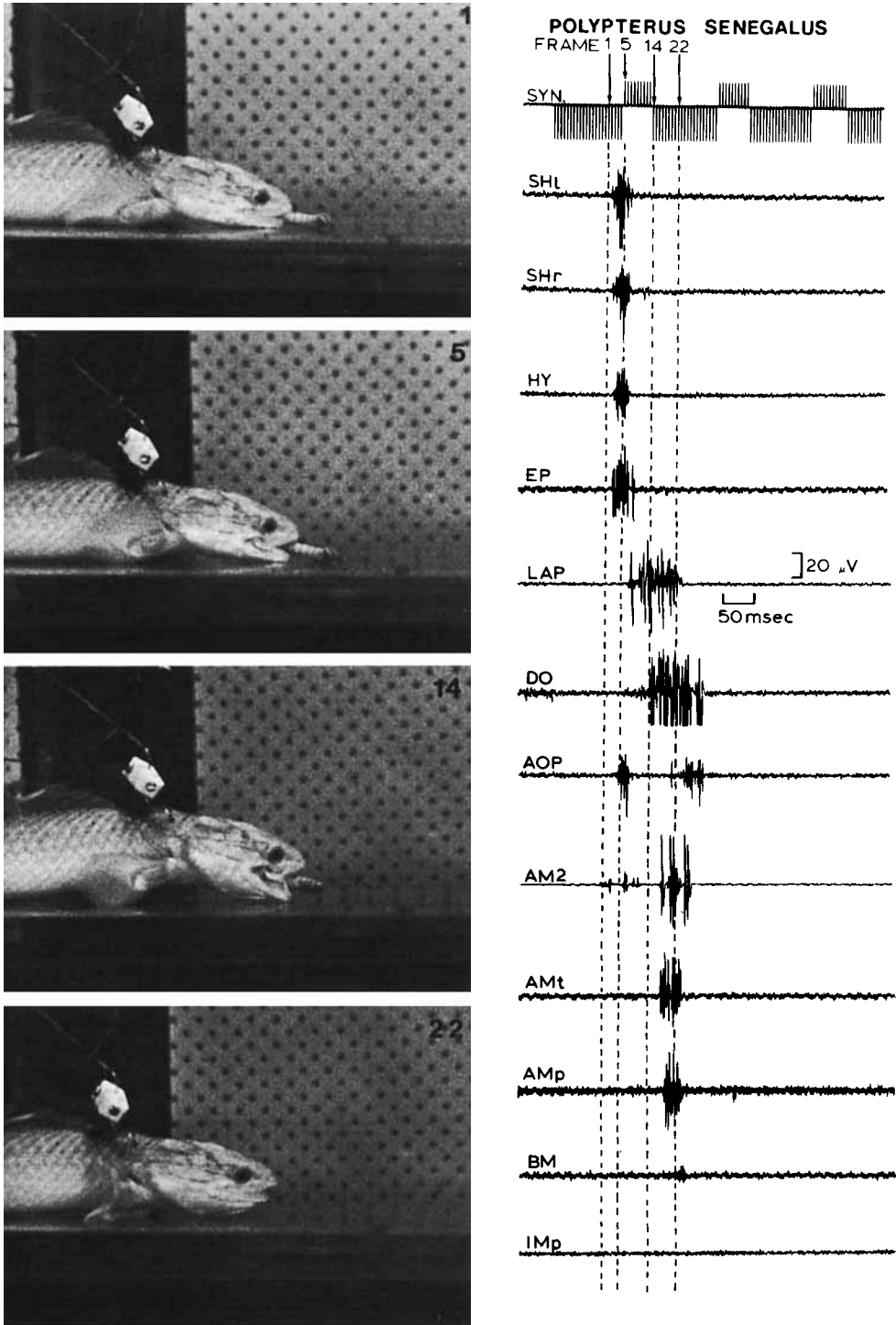
Activity in the hyohyoideus superioris is variable, but during vigorous strikes this muscle is active from 10 to 15 msec before activity in the sternohyoideus and remains active for up to 30 msec.

Compressive phase

The compressive phase is initiated by high-level activity in the dilator operculi (Fig. 6: DO, frame 14), which initiates opercular abduction (Fig. 7A: frames 12–22). Fifteen to twenty msec after the onset of the compressive phase, the adductor mandibulae part two becomes active (Fig. 6: AM2) and within 10 msec, a sharp burst of activity occurs in the other two divisions of the adductor complex, the "temporalis" and "pterygoideus" (Figs. 1, 6: AMp, AMt). In slow strikes, no activity in any adductor division is observed for nearly 100 msec after the onset of mouth opening and initial mouth closure appears to occur primarily by elastic recoil in the adductor mandibulae complex.

After the end of the compressive phase, a second burst of activity occurs in the adductor operculi and restores the operculum to its ini-

Fig. 6. *Polypterus senegalus*. Frames 1, 5, 14, and 22 (on left) from a high-speed (200 frames per second) film synchronized with electromyographic recordings of cranial muscle activity (on right). Shutter synchronization pulse (SYN) provided accurate correlation. Peak gape occurs in frame 14. Note the lack of overlap in activity between mouth opening muscles (SHr, l; HY; EP) and closing muscles (AM2, AMt, AMp).



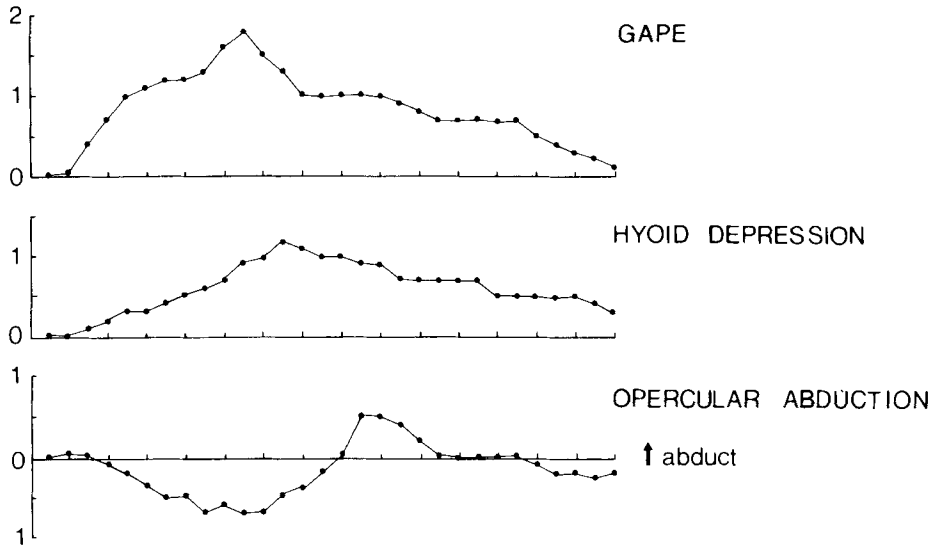
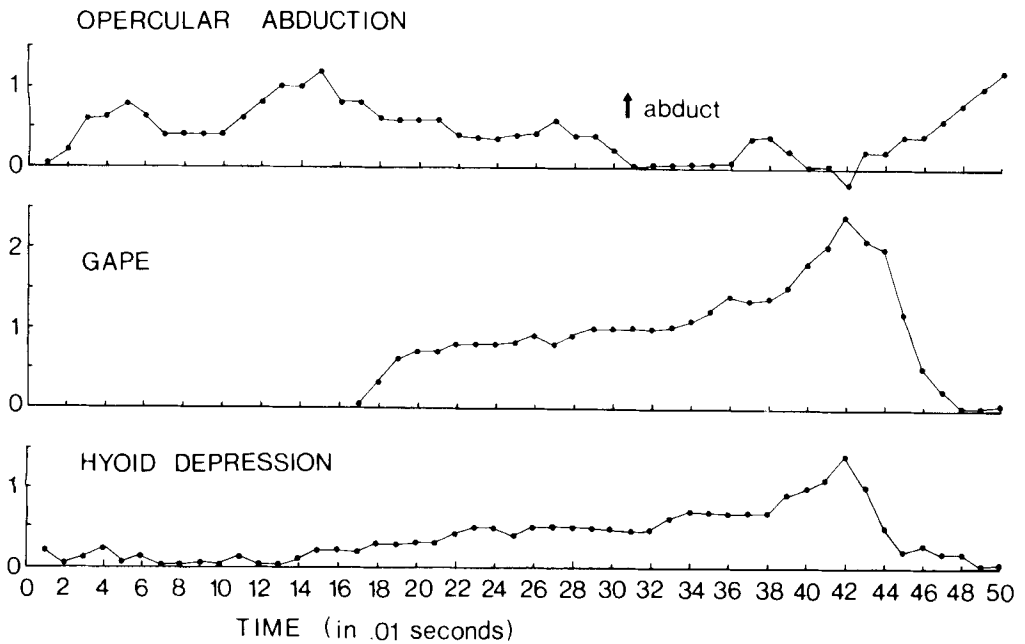
A**B**

Fig. 7. *Polypterus senegalus*. Graphic representation of gape, hyoid depression, and opercular abduction versus time during (A) the strike and (B) prey ejection during mastication (see text). Ordinate scale is relative. Note especially the changing pattern of opercular movement: adduct-abduct-adduct in the strike and abduct-adduct-abduct during prey ejection.

tial rest position (Figs. 6: AOP; 7A). Occasional low level activity is seen in the branchiomandibularis (Fig. 6: BM), whereas the intermandibularis posterior and interhyoideus are invariably silent.

Two main features characterize the strike in *Polypterus*— 1) the double burst pattern of activity in the adductor operculi, and 2) the complete lack of overlap between the early expansive phase muscles (the sternohyoideus, epaxial, and hypaxial muscles) and activity in the adductor complex.

Mastication and deglutition

The pattern of muscle activity and jawbone movement during mastication of the prey following capture may vary significantly from that seen during the strike. The usual pattern of prey manipulation involves a series of short "spitting out" movements, during each of which the prey is partially ejected from the buccal cavity and then crushed between the jaws. After a series of these ejection and crushing

movements, the prey is rapidly sucked back in to the buccal cavity (Fig. 8B) and the cycle started again.

During the ejection phase of mastication, the operculum abducts while the mouth is closed (Fig. 7B), then adducts as the mouth opens, forcing water out the mouth, and finally abducts again as the mouth closes. This is the reverse of the adduct-abduct-adduct pattern seen during the strike. Depression of the hyoid clearly is synchronized with gape (Fig. 7B).

Interspersed with prey ejection sequences are strong "crushing" and compressive movements. These involve high-level activity in the branchiomandibularis, intermandibularis posterior, interhyoideus, and adductor operculi (Fig. 8C), all compressive muscles. Crushing of prey also may occur with associated activity in the adductor mandibulae part two, levator arcus palatini, and dilator operculi, but no activity occurs in the sternohyoideus (Fig. 8A). Differential activity occurs between the adductor part two, and the "tem-

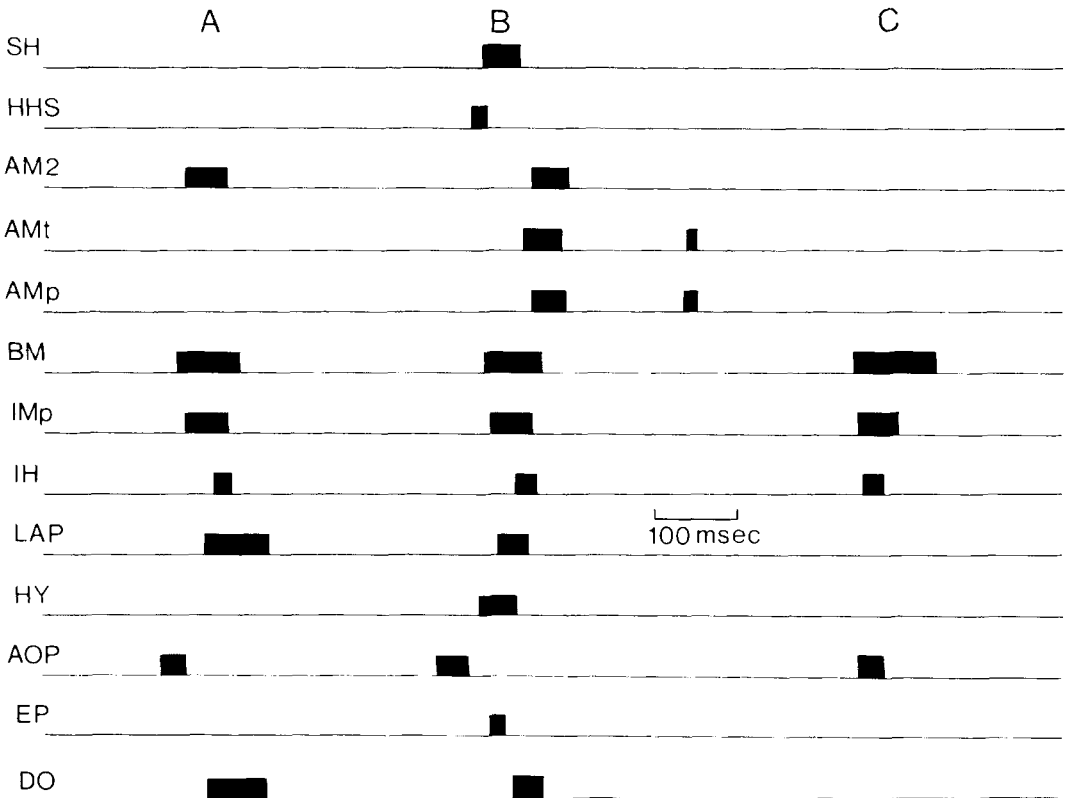


Fig. 8. *Polypterus senegalus*. Block diagram of three common patterns of cranial muscle activity occurring during mastication. Pattern B most closely corresponds to the pattern seen at the strike. See text for further explanation.

poralis" and "pterygoideus" divisions during mastication. These two divisions often show nearly synchronous isolated bursts of high-level activity (see Fig. 8B: AMp, AMt) independently from activity in AM2 (Fig. 8A).

During positioning of the prey in masticatory sequences, a distinct pattern of asymmetrical activity is often observed between the right and left halves of the sternohyoideus. Complete asymmetry occurs (Fig. 9B) in which both the anterior and posterior portions of one side are active simultaneously, while no activity is seen in the other half. Anteroposterior asymmetry also occurs in which the anterior portions of each side are active independently from the posterior fibers (Fig. 9C). Finally, asymmetries in timing are observed in which one side initiates activity 10–50 msec prior to activity in the opposite side (Fig. 9A). This asymmetrical activity could not be correlated with any obvious features of the pattern of jaw movement, although movements of the elements most likely to be affected by asymmetrical sternohyoideus activity—the hypohyals, ceratohyals, and basibranchials—could not be directly observed by light cinematography.

When the prey has reached the front of the jaws as a result of repeated cycles of ejection and crushing, it is rapidly sucked back into the buccal cavity by a sequence of events similar to those of the initial strike at the prey (Fig. 8B). The duration of the expansive and compressive phases is greater than at the strike, and activity is generally seen in the branchiomandibularis, intermandibularis posterior, and interhyoideus. The adductor operculi may become active up to 70 msec before activity in the

sternohyoideus, hyohyoideus superioris, dilator operculi, levator arcus palatini, and epaxial muscles, and all show nearly the same relative timing of activity as seen at the strike. Throughout the expansive and compressive phases, low-level activity occasionally is recorded in the branchiomandibularis.

Lepisosteus oculatus

Expansive phase

The initial strike at the prey by *Lepisosteus* is extremely rapid; the complete process of prey capture (from the start of mouth opening to closure of the jaws) often occurs in as little as 20 msec. There is remarkably little variation in the duration of the strike and all strikes occur within a time span of 20–35 msec. Thus, the expansive phase may last only one frame at filming speeds of up to 200 frames per second (e.g., Fig. 10).

Peak gape is rapidly achieved both by depression of the lower jaw and elevation of the cranium and upper jaw (Fig. 11). Mandibular depression is initiated by symmetrical activity in the paired sternohyoideus muscles (Fig. 10: SHr, l) which are active simultaneously with the obliquus inferioris (Fig. 10: HY). A delay of 5–10 msec occurs between the onset of activity in the sternohyoideus muscle and the start of mandibular depression. The epaxial muscles become active 5 msec after the onset of activity in the sternohyoideus (Fig. 10: EP).

Prey capture is effected by a lateral movement of the head towards the prey as the jaws open (see Fig. 10). This lateral movement is achieved by differential timing of activity between the right and left sides of the obliquus

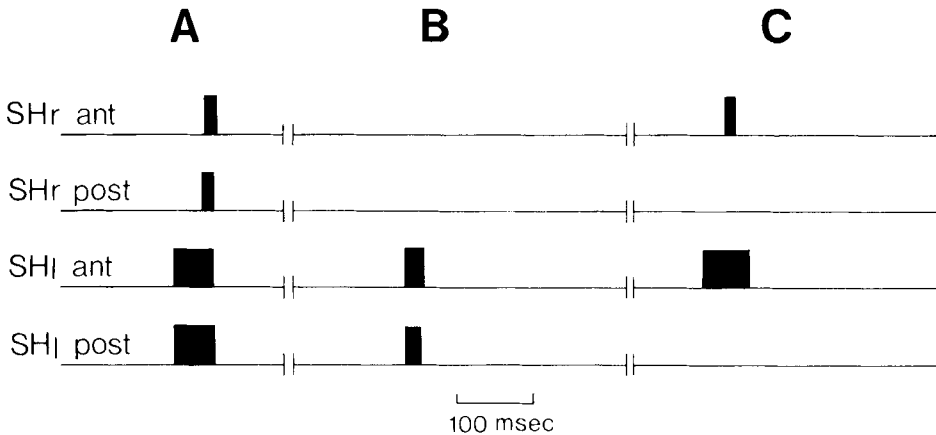


Fig. 9. *Polypterus senegalus*. Block diagram of three patterns of asymmetrical activity in the sternohyoideus occurring during mastication. Note both anteroposterior asymmetry and right-left asymmetry.

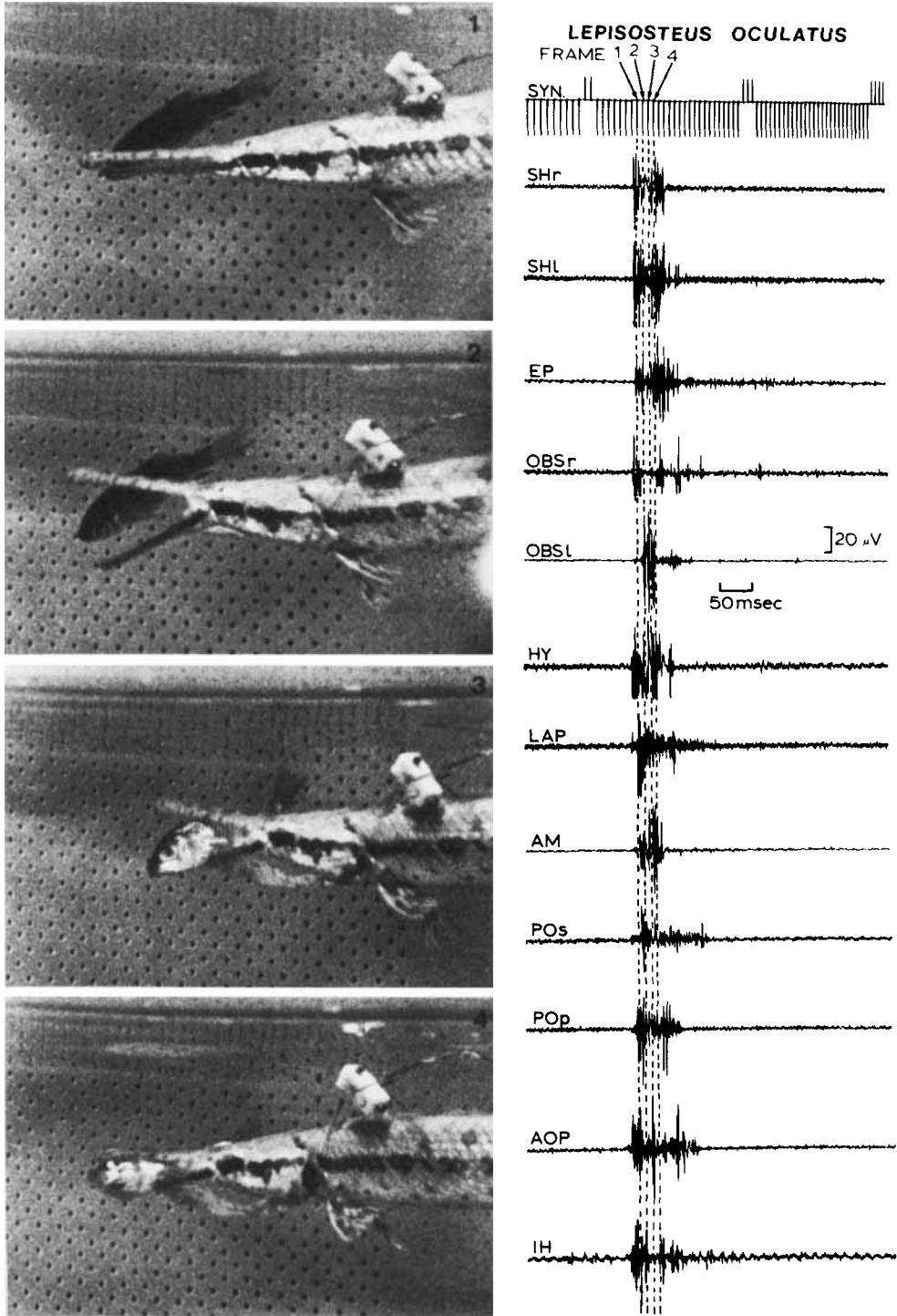


Fig. 10. *Lepisosteus oculatus*. Frames 1, 2, 3, and 4 (on left) from a high-speed (200 frames per second) film synchronized with electromyographic recordings of cranial muscle activity (on right). Peak gape occurs between frames 2 and 3. Note the extensive overlap in activity periods of the cranial muscles and the close synchrony in time of onset of activity.

superioris (Fig. 10: OBSr, l). This muscle is a division of the hypaxialis (Winterbottom, '74), and the fibers run anterodorsally to insert on the posterolateral area of the otic region (ptertotic); thus, they effect lateral bending of the head. In *Lepisosteus*, the obliquus superioris on the side of the head towards the prey is active 10–15 msec before the opposite side during strikes involving significant lateral head movement (Fig. 10). In strikes in which the prey is caught with little lateral head movement, the differences in timing between sides become small (< 2 msec).

The adductor operculi becomes active from up to 5 msec before activity in the sternohyoideus to 5 msec after (Fig. 10: AOP) and results in opercular adduction (Fig. 11) during mouth opening. Although the levator arcus palatini is active within 5 msec of the sternohyoideus (Fig. 10: LAP), suspensorial and opercular abduction

does not begin until 20 msec into the expansive phase (Fig. 11). The hyohyoideus superioris is also active at the onset of the expansive phase.

Because components of the adductor mandibulae complex become active during the expansive phase, it is impossible to distinguish opening from closing muscles on the basis of the time of electrical activity. The preorbitalis profundus is the first component of the adductor complex to become active; the adductor mandibulae and preorbitalis superficialis fire 5–10 msec later (Fig. 10: AM, PO_p, PO_s). The adductor mandibulae is consistently active 10 msec after the onset of activity in the sternohyoideus, and in spite of the rapidity of the strike, these two muscles are rarely active simultaneously. The interhyoideus (Fig. 10: IH) shows a short high-amplitude burst of activity within 5 msec of activity in the sternohyoideus.

Compressive phase

The compressive phase consists of depression of the upper jaw and mandibular adduction to trap the prey between the jaws (Fig. 10: frames 3 and 4; Fig. 11). All muscles active at this time were also active in the expansive phase.

Hyoid depression reaches a peak (Fig. 11) well after the jaws have begun to close and at peak gape only a small depression of the hyoid has occurred (Fig. 10: frame 2). Opercular abduction rises to a sharp peak during the compressive phase (Fig. 11) and the operculum slowly returns to its resting position due to a second burst of activity in the adductor operculi (Fig. 10: AOP). A double-burst pattern of activity also is seen in the interhyoideus, preorbitalis profundus, and also occasionally in the sternohyoideus resulting in the maintenance of a depressed hyoid after the mouth has closed.

In general, all muscles become active in the expansive phase and continue with at least low-level activity throughout the compressive phase.

Mastication and deglutition

Following initial capture of the prey, a complex pattern of manipulatory movements occurs. This orients the prey so that it may be swallowed head first. This process results in a number of asymmetrical activity patterns in the cephalic and anterior body muscles and will be treated in detail elsewhere (Lauder and Norton, in press).

In general, patterns of muscle activity during manipulation may be divided into two types. One pattern is very similar to that of the initial

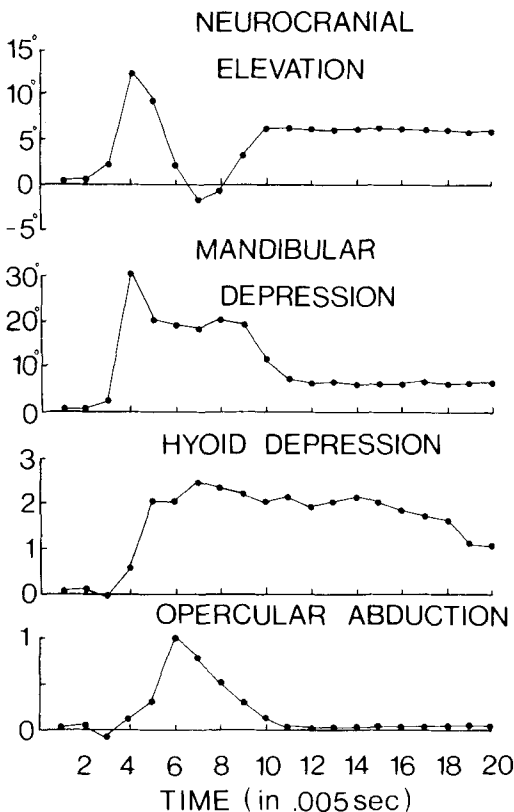


Fig. 11. *Lepisosteus oculatus*. Graphic representation of neurocranial elevation (in degrees), mandibular depression (in degrees), hyoid depression, and opercular abduction versus time during a strike. Ordinate scale is relative for hyoid depression and opercular abduction.

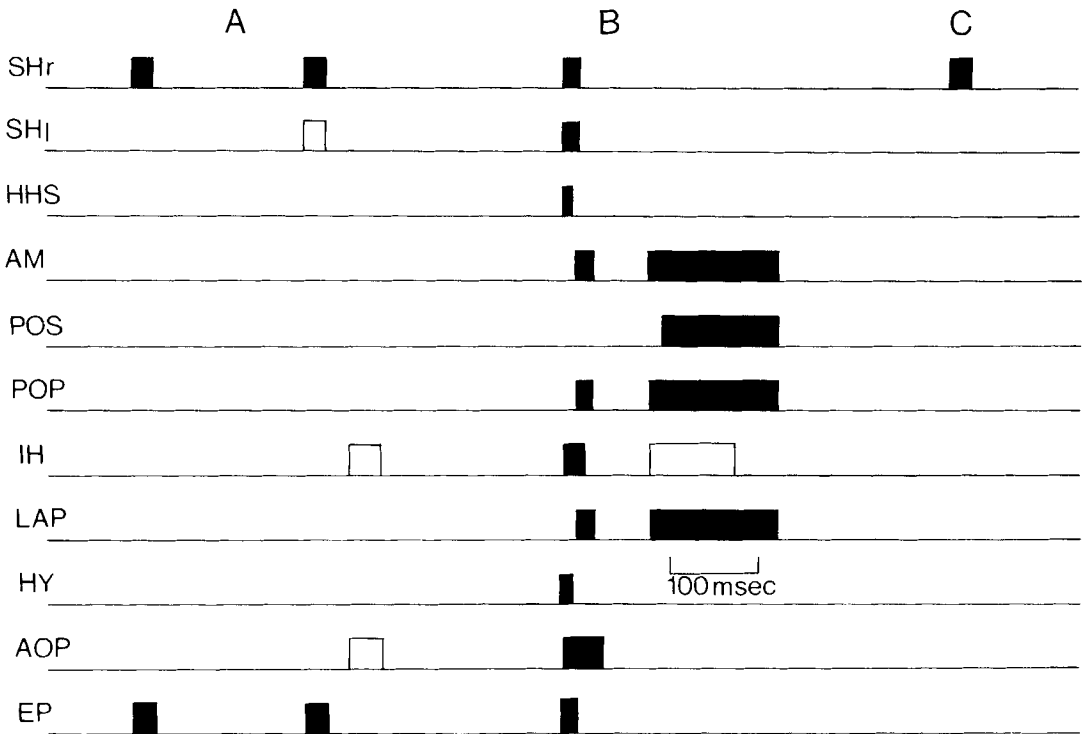


Fig. 12. *Lepisosteus oculatus*. Block diagram of three common patterns of muscle activity occurring during mastication. Pattern B most closely corresponds to the muscle activity pattern seen at the strike. Open bars represent occasional activity.

strike (Fig. 12B). Notable differences, however, include the generally continuous, uniphasic activity of the adductor operculi, a delay of up to 30 msec in initiation of activity in the levator arcus palatini, and the frequent lack of activity in the preorbitalis superficialis.

"Crushing" movements also occur during prey manipulation and correlate with high amplitude synchronous activity in the adductor mandibulae, preorbitalis superficialis and profundus, and the levator arcus palatini (Fig. 12: AM, POs, POp). Occasional activity also is seen in the interhyoideus at this time.

The second type of muscle activity pattern during manipulation involves mainly the epaxial muscles and sternohyoideus. Activity in both of these muscles (Fig. 12A) or activity in one side of the sternohyoideus only (Fig. 12C) is correlated with lateral bending of the head and slight mandibular depression (Lauder and Norton, in press). All patterns of sternohyoideus asymmetry found in *Polypterus* (Fig. 9) also occur in *Lepisosteus*. Activity in both sides of the sternohyoideus, interhyoideus, and

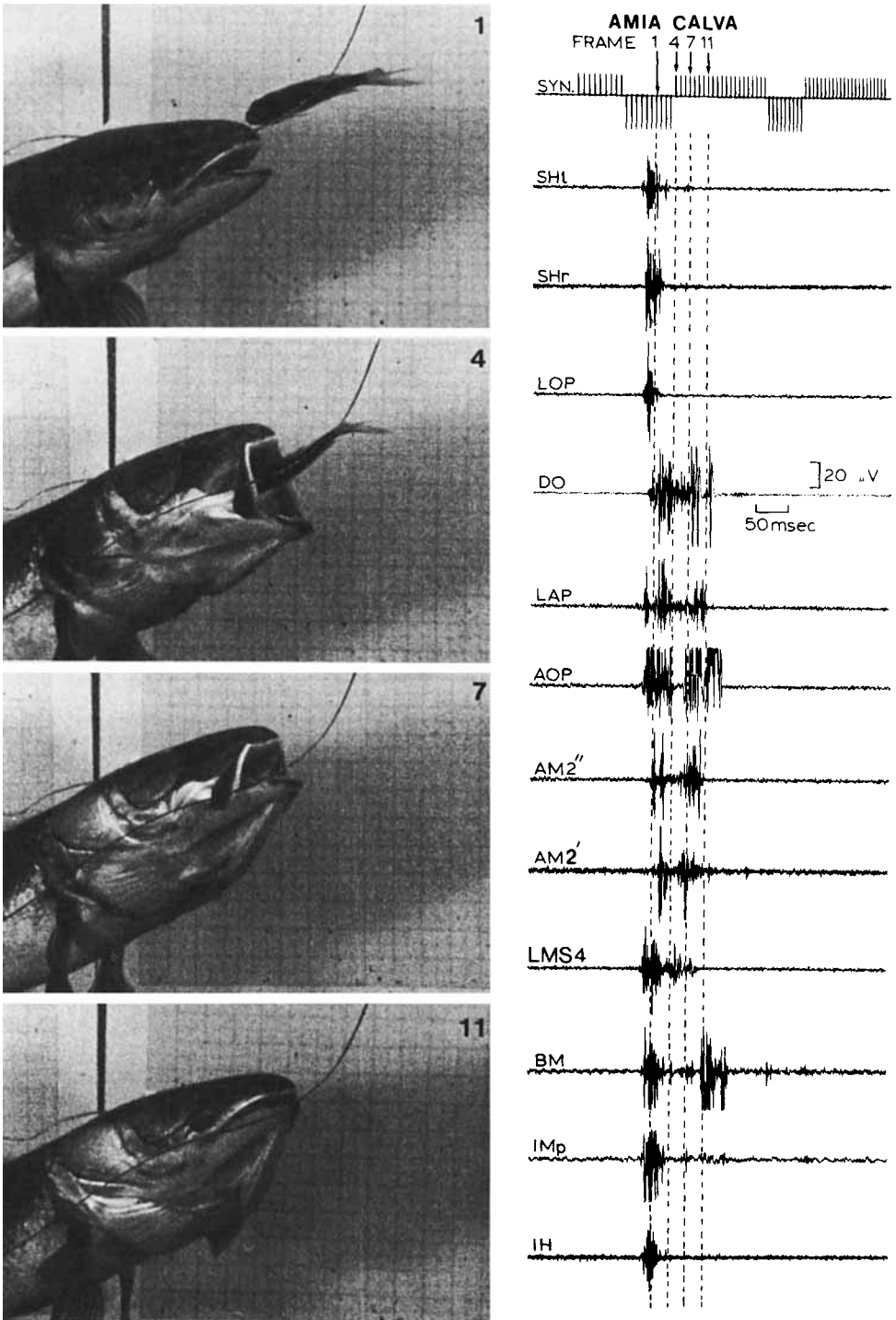
adductor operculi also may occur during these manipulations.

Manipulations of the second type typically last 50–100 msec.

Amia calva

Expansive phase

The complete strike in *Amia* usually lasts for 60–100 msec and is relatively invariant in length, although it is more variable than in *Lepisosteus*. The expansive phase is usually shorter than the compressive phase, lasting about 20–40 msec, and mandibular depression is initiated by synchronous high amplitude activity in the paired sternohyoideus muscles and activity in the levator operculi (Fig. 13: SHr, l, LOP). The sternohyoideus muscle causes hyoid retraction, a movement that is transmitted to the posteroventral aspect of the mandible by the mandibulohyoid ligament (Fig. 3: MHL). The obliquus inferioris is also active to stabilize the pectoral girdle at this time. Contraction of the levator operculi results in a dorsal rotation of the opercular series which is transmitted to



the mandible by the interoperculomandibular ligament (Fig. 3: IML). A delay of 15 msec occurs between activity in the levator operculi and the start of mouth opening.

Opercular adduction takes place during the expansive phase, and abduction of the operculum begins just before peak gape is reached (Fig. 14A, B; Fig. 15). Adduction results from the first burst of activity in the adductor operculi (Fig. 13: AOP) and occurs despite considerable overlap with activity in the dilator operculi and levator arcus palatini (Fig. 13: DO, LAP). The suspensory apparatus is only slightly abducted during the compressive phase (Fig. 15).

Both muscles dorsal to the gular plate—the intermandibularis posterior and interhyoideus—show a sharp, high-level initial burst of activity within 5 msec of the onset of activity in the sternohyoideus (Fig. 13: Imp, IH). The intermandibularis may contribute to the maintenance of suspensorial adduction during the expansive phase.

The branchiomandibularis also shows a sharp initial burst of activity within 10 msec of sternohyoideus activity (Fig. 13: BM).

All jaw muscles become active during the expansive phase as in *Lepisosteus*. The levator maxillae superioris (parts three and four) are the first adductor divisions to become active (Fig. 13: LMS 4); they initiate activity simultaneous with mouth opening muscles, the sternohyoideus and levator operculi. Ten milliseconds later, the adductor mandibulae (part 2'') is activated followed in 10 msec by AM2' (Fig. 13: AM2'', AM2'). These differences are relatively consistent between different feeding sequences, although occasionally AM2'' and AM2' are active simultaneously.

The most obvious feature of the movement pattern during the expansive phase is the extensive arc through which the maxilla swings (Fig. 13: frame 4). Maximally, it forms nearly a 90° angle to the body axis and effectively occludes the corners of the mouth opening by creating a nearly round tubular orifice. Although hyoid depression does not peak in the expansive phase, it does achieve nearly its

maximum value before peak gape (Fig. 15) and depression of the posterior margin of the gular plate results from ventral hyoid movement. During the expansive phase, the branchiostegal rays are tightly adducted by the hyo-hyoideus superioris (see Fig. 14A, B).

Compressive phase

Although activity in the adductor mandibulae complex starts in the expansive phase, it continues into the compressive phase and results in adduction of the jaws (Fig. 13: AM2'', AM2', LMS4; Fig. 15). The levator arcus palatini and dilator operculi remain active and result in a large lateral expansion of the orobranchial cavity (Fig. 14C, D; Fig. 15) as the mouth closes.

The second burst of activity in the adductor operculi occurs in the compressive phase and continues subsequent to complete jaw closure (Fig. 13: AOP). The branchiomandibularis also exhibits a strong burst of activity after the jaws have closed and may function to rapidly compress the buccal cavity by protracting the branchial basket.

During the compressive phase, the maxilla returns to its rest position, while the gular plate and hyoid remain depressed (Fig. 15). Branchiostegal expansion is maximal at this time.

Mastication and deglutition

Vigorous chewing movements follow prey capture in *Amia*, unless the prey has been sucked directly into the stomach during the strike. The manipulatory movements seem to be associated with positioning of the prey just anterior to the esophagus to facilitate deglutition.

Strong compressive movements of the buccal cavity walls occur frequently during "chewing," and activity is most commonly seen in the adductor operculi and branchiomandibularis (Fig. 16A: AOP, BM). These are the two muscles most frequently active during prey manipulation; often they display repeated simultaneous bursts for periods of up to several seconds. Occasionally the interhyoideus may be active

Fig. 13. *Amia calva*. Frames 1, 4, 7, and 11 (on left) from a high-speed (200 frames per second) film synchronized with electromyographic recordings of cranial muscle activity (on right). Peak gape occurs at frame 4. Note the extensive overlap in muscle activity periods and the relative movement of the predator and the prey during the strike.

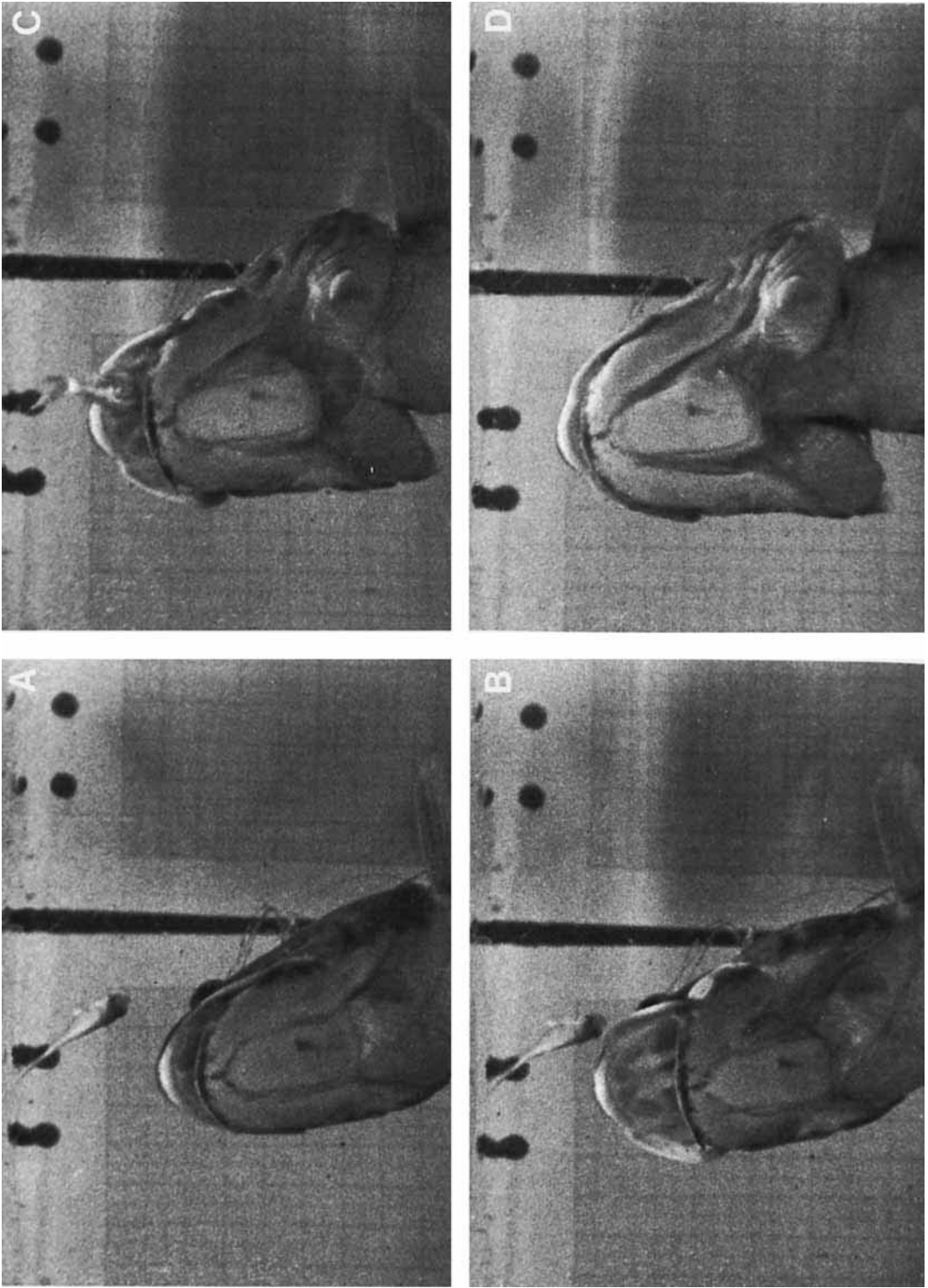


Fig. 14. *Amia calva*. Ventral view of the strike at a prey. Four representative frames from a high-speed (200 frames per second) film (A, B, C, D) correspond to the position of the jaw elements as seen in lateral view in the fourth frames of Figure 13. Note the opercular and suspensorial adduction as the mouth is opened.

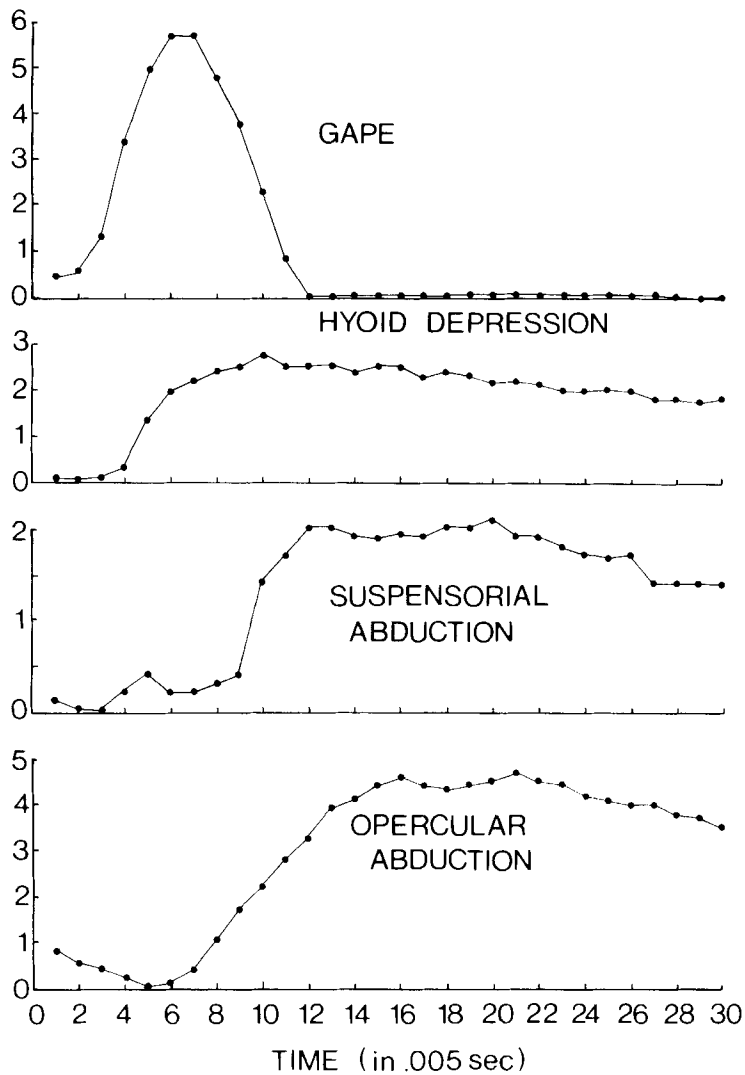


Fig. 15. *Amia calva*. Graphic representation of gape, hyoid depression, suspensorial abduction, and opercular abduction during the strike. Ordinate scale is relative.

during these bursts, and the levator maxillae superioris four (with the sternohyoideus and obliquus inferioris) may show alternating bursts of activity (Fig. 16A). This pattern also demonstrates differential activity between parts three and four of the levator maxillae superioris.

The patterns of right-left and anteroposterior asymmetry observed in the sternohyoideus of *Polypterus* and *Lepisosteus* also are found in *Amia* (Fig. 17). Sternohyoideus asymmetry

could not be clearly correlated with any specific movement pattern.

Other manipulatory activity patterns (Fig. 16C) demonstrate differential activity between the AM2'' and AM2' components of the adductor mandibulae complex as well as a double burst pattern of activity in the levator arcus palatini (Fig. 16C). No activity in the obliquus inferioris or epaxial muscles is observed.

Pattern B (Fig. 16) represents a manipulatory sequence with muscle activities similar

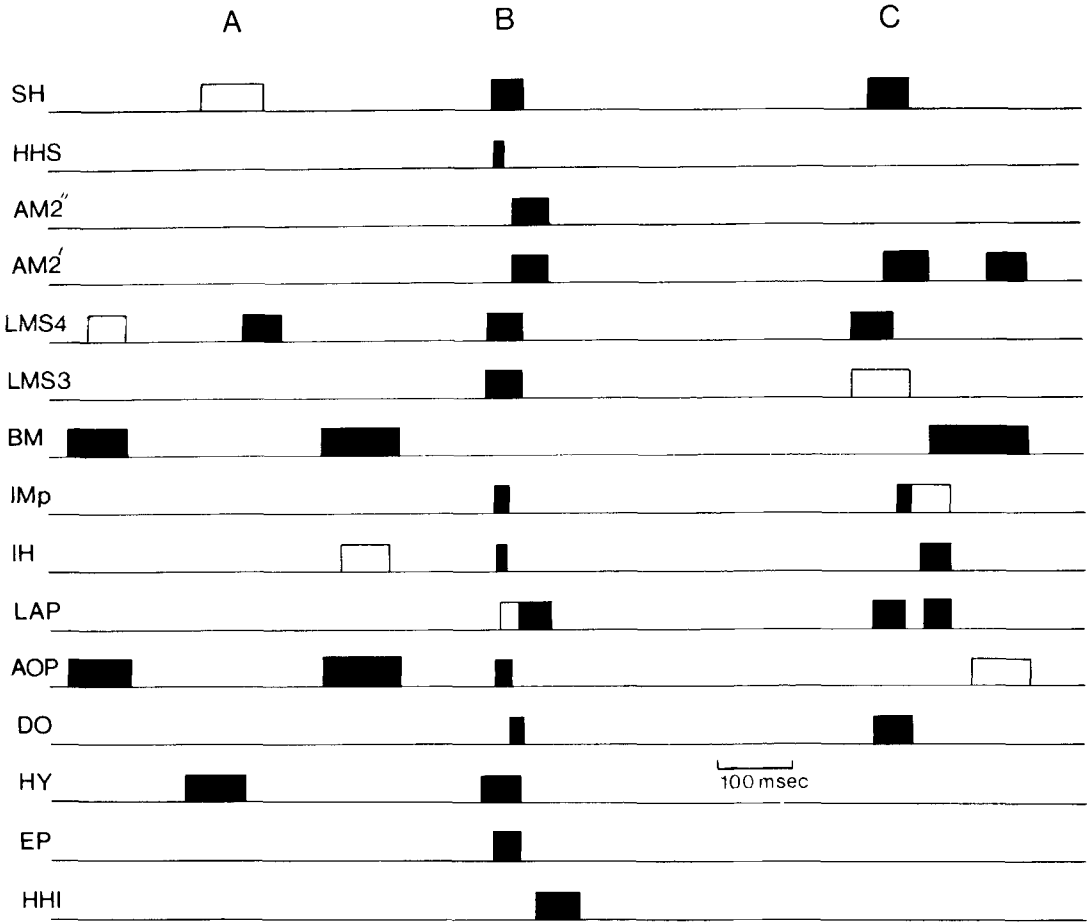


Fig. 16. *Amia calva*. Block diagram of three common patterns of muscle activity occurring during mastication. Pattern B most closely corresponds to the muscle activity pattern occurring at the strike. Open bars represent occasional activity.

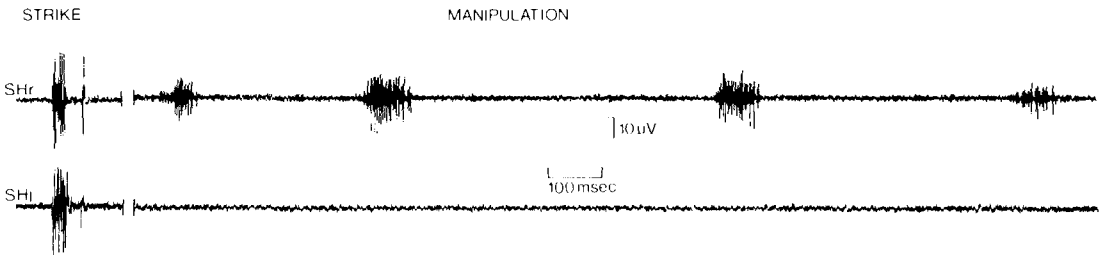


Fig. 17. *Amia calva*. Representative pattern of asymmetrical muscle activity in the sternohyoideus occurring during manipulation and mastication of prey. The symmetrical pattern of activity at the strike during the same experiment is shown to the left.

in timing to those seen at the initial strike. No activity is recorded in the branchiomandibularis. The levator maxillae superioris and adductor mandibulae divisions of the jaw adductor complex fire simultaneously. The relative timing of muscle activity is more variable during prey manipulation than during the strike.

DISCUSSION

Prey capture: comparisons and generalizations

Polypterus, *Lepisosteus*, and *Amia* all depress the mandible by contraction of the sternohyoideus muscle. Sternohyoideus activity results in a posteroventral rotation of the hyoid apparatus. This rotation pivots the interhyal bone (Fig. 5: IHY) which suspends the hyoid apparatus from the suspensorium. Rotation of the hyoid apparatus causes a posterodorsal force to be applied to the retroarticular process of the mandible via the mandibulohyoid ligament and causes mandibular depression because the force is applied ventral to the mandibular axis of rotation (see Fig. 18).

The ligamentous connection between the hyoid and mandible permits mandibular depression by hyoid retraction; the interhyal bone greatly increases the mechanical advantage of the hyoid retraction mechanism. If the hyoid articulated directly with the suspensory apparatus, contraction of the sternohyoideus would cause only a limited posterodorsal movement of the mandibulohyoid ligament because the origin of this ligament on the hyoid would have to move around the articulation of the hyoid with the suspensorium. Hyoid depression then could produce only a small posterior displacement of the ligamental origin.

The intercalation of an interhyal bone has two effects. It increases the effective moment arm of the origin of the mandibulohyoid ligament relative to the suspensorium, and it also introduces a second center of rotation (Fig. 18) that allows the hyoid to be retracted relative to the suspensorium. This greatly increases the excursion induced by the force resulting from sternohyoideus contraction—i.e., a given incremental hyoid retraction results in greater mandibular depression.

During contraction of the sternohyoideus, the pectoral girdle is stabilized by activity of the obliquus inferioris. In *Polypterus* and *Lepisosteus*, the obliquus inferioris shows a high amplitude burst of activity simultaneous with activity in the sternohyoideus (Figs. 6, 10:

HY, SH), whereas in *Amia* (Fig. 16), activity of the obliquus inferioris may slightly precede or occur simultaneously with that of the sternohyoideus. Relative stability of the pectoral girdle is important in providing a fixed origin for the sternohyoideus, allowing it to effect motion of the lower jaw, rather than protraction of the pectoral girdle.

Amia has an additional mechanism mediating mandibular depression. Contraction of the levator operculi causes a posterodorsal rotation of the operculum about the operculohyomandibular articulation. This rotation is transmitted to the mandible via the suboperculum, interoperculum, and the interoperculomandibular ligament and causes mandibular depression. The electromyographic data (Fig. 13: LOP, AOP, AM2') confirm the hypothesis (Lauder, '79) that *Amia* should have a levator operculi-opercular series-mandible coupling. This coupling in *Amia* is homologous to that of teleosts, and represents a previously unrecognized shared specialization of the halecostome fishes (Halecomorphi plus Teleostei; see Table 1).

Generally it is believed that the geniohyoideus muscle of teleosts (not homologous to the geniohyoideus of tetrapods) is formed by the fusion of the intermandibularis posterior and interhyoideus muscles of primitive actinopterygians (Winterbottom, '74). Primitively, then, two myosepta should occur in the teleost geniohyoideus: a longitudinal septum dividing the right and left sides of this muscle, and a transverse septum separating the "intermandibularis component" from the "interhyoideus component." The innervation of the anterior and posterior portions also differs; the intermandibularis component is trigeminal, whereas the interhyoideus is innervated by the facial nerve.

In *Amia*, both the intermandibularis posterior and interhyoideus are active at the onset of the expansive phase (Fig. 13: IMp, IH). In *Lepisosteus*, the interhyoideus is also active in the expansive phase (no data are available on the intermandibularis posterior), while in *Polypterus*, neither muscle is active during the strike (Fig. 6). The pattern of activity in *Polypterus* most closely resembles the timing of geniohyoideus activity in primitive teleosts (Lauder and Liem, '80). No activity occurs during the expansive or compressive phases and only following closure of the mouth does contraction of the geniohyoideus protract the hyoid arch. Both the intermandibularis pos-

terior and interhyoideus have important roles in compressing the buccal cavity during chewing (Fig. 8).

In *Amia*, activity of the intermandibularis posterior during the expansive phase may contribute to suspensorial adduction (Fig. 13: IMP; Fig. 15), but the significance of concomitant activity in the interhyoideus and branchiomandibularis is unclear. These muscles may directly contribute to mandibular depression by forming a "contractile link" between the hyoid, branchial basket, and mandible, or they may play a role in elevating the floor of the mouth during the early part of the strike. The branchiomandibularis is the main compressive muscle during chewing. The pattern of activity in the intermandibularis posterior and the interhyoideus of *Amia* does not correspond to known activity patterns in the geniohyoideus of primitive teleosts.

A differentiation in the timing of activity between the different components of the adductor mandibulae complex also has been observed. The medial adductor division may be active independent of the posterolateral division (*Polypterus*), or the anterior division may be active independent of the medial or posterolateral division (*Amia*). In *Amia*, the two components of the anterior division—the levator maxillae superioris parts three and four—also may be active independently. Only occasional independent adductor activity was found in *Lepisosteus*; activities of the adductor mandibulae, preorbitalis superficialis and profundus, and the levator arcus palatini usually overlap nearly completely during chewing sequences (Fig. 12).

The function of the levator maxillae superioris part four in *Amia* is obscure. The muscle extends from the antorbital to the palatine and ectopterygoid, and has relatively little moment arm about the axis of suspensorial movement. It may contribute slightly to suspensorial adduction.

In all three genera, asymmetrical activity was noted in the sternohyoideus muscle, and the anterior and posterior fibers also act at different times. Lauder and Norton (in press) correlated the activity in one side of the sternohyoideus with lateral bending of the head and slight mandibular depression in *Lepisosteus*. This asymmetry plays an important role by manipulating the prey into the preferred orientation for swallowing. In *Amia* and *Polypterus*, asymmetrical activity of the sternohyoideus may produce lateral movements of the tongue in the buccal cavity and aid in positioning and

manipulating prey prior to swallowing. Contraction of the right side of the sternohyoideus, for example, will exert a posterolateral force on the right hypohyal and the component of this force, acting perpendicular to the sagittal plane, will cause a lateral movement of the tongue and anterior portion of the hyoid apparatus. Asymmetrical activity was not observed in other cephalic muscles, although the obliquus superioris and epaxial muscles showed marked asymmetry during certain manipulatory patterns in *Lepisosteus* (Lauder and Norton, in press).

Suction feeding

In both *Polypterus* and *Amia*, prey capture occurs by an expansion of the buccal cavity that causes a pressure reduction and draws water in through the mouth. The unidirectional flow of fluid is the result of a precise control of the timing of jaw movements. The double-burst pattern of activity in the adductor operculi, for example, allows water to enter the buccal cavity only through the anterior mouth opening. The hyohyoideus superioris is also active at the start of the expansive phase and prevents water inflow from the posteroventral margin of the opercular cavity. This timing of activity by the adductor operculi and hyohyoideus superioris is maintained even in *Lepisosteus*. Hyoid depression always reaches its peak coincident with, or after, peak gape and the hyoid remains depressed well after the jaws have closed. A similar pattern is seen in suspensory abduction which peaks after the expansive phase has been completed. The delay in hyoid depression and suspensorial abduction may contribute to an unidirectional fluid flow through the orobranchial chamber. Water exits through the opercular cavity as the mouth closes and opercular dilation is maintained throughout the compressive phase.

An important characteristic of the suction-feeding mechanism is the creation of a circular orifice through which water is drawn (Lauder, '79; Osse, '69). In *Amia*, this is accomplished by the extreme anterior swing of the maxilla, which, along with the connective tissue extending posteriorly to the suborbital bones, serves to occlude the margin of the gape (Fig. 13: frame 4). Osse ('76) has measured buccal and opercular cavity pressures in *Amia* and found average values of -120 and -55 cm H_2O , respectively. In *Polypterus*, the corner of the mouth is occluded by the thickened connective tissues of the lip and cheek (Fig. 6: frame 14).

In a theoretical model of the suction feeding

mechanism, Elshoud-Oldenhave and Osse ('76) have proposed the following sequence for suction feeding in fishes: An initial *preparatory phase* in which the volume of both the buccal and opercular cavities is decreased; a *Phase I* in which the buccal and opercular cavities are expanded with the mouth closed; a *Phase II* when both chambers are rapidly enlarged; and a *Phase III* in which the mouth is closed and a positive pressure is generated in the buccal cavity forcing the water over the gills.

Although this model seems to apply to advanced teleosts, no preparatory phase has been observed in non-acanthopterygian teleosts and none was observed in *Amia*. In addition, lateral expansion of the suspensory apparatus does not begin until Phase II and reaches its peak in Phase III. Fishes for which this model does apply appear to be able to generate significantly greater negative buccal cavity pressures (-400 to -600 cmH₂O, Alexander, '70; Liem, '78) than *Amia*.

One salient feature of the suction feeding mechanism is the increasing overlap in antagonistic muscle complexes with increasing rapidity of the strike. In *Polypterus*, no overlap occurs between activity in the jaw opening muscles of the expansive phase (sternohyoideus, hypaxial, and epaxial muscles) and the jaw closing muscles (adductor mandibulae part 2, "temporalis", and "pterygoideus"). *Lepisosteus* and *Amia* both show extensive overlap in muscle activity and at least one component of the adductor mandibulae complex is active simultaneously with jaw-opening muscles. Although the electromyograms of expansive and compressive muscles may occur simultaneously, the forces generated by jaw opening and closing muscles probably peak at different times to generate the observed pattern of bone movement (jaw opening followed by closing).

Neural control of the strike

The rapidity of the strike in *Polypterus*, *Lepisosteus*, and *Amia* and the relatively invariant nature of the movement pattern and electromyographic profile suggests that the initial strike is governed by a preprogrammed output from the central nervous system that is not subject to peripheral feedback. In contrast to observations on piscivorous cichlid fishes (Liem, '78), no versatility was detected in the preprogrammed patterns elicited in response to different prey items. For example, strikes on prey completely immobilized by anesthesia occurred just as rapidly and with an identical pattern of muscle activation to those involving

the capture of elusive prey items. Visual input seems only to determine the time of onset of the programmed pattern.

Two hypotheses are consistent with the pattern of muscle activation observed during a preprogrammed strike, and either may account for the resulting movement pattern: 1) A precise neural program could activate the cranial muscles in the proper temporal sequence and with the appropriate preprogrammed patterns of force development. Under this hypothesis the mouth-opening muscles are activated nearly simultaneously with the closing muscles in *Lepisosteus*, but more motor units of the opening muscles are activated at a higher frequency of stimulation for the first 5–10 msec to cause mouth opening. Increasing stimulation rate and recruitment of motor units in the closing muscles then would result in jaw adduction.

2) A second hypothesis involves the near simultaneous activation of opening and closing muscles by a preprogrammed neural program at roughly equivalent frequencies and recruitment rates. The movement pattern (i.e., jaw-opening followed by closing) depends, however, on the mechanical characteristics of the peripheral jaw structures—i.e., the length-tension curves for the opening and closing muscles, mechanical advantage of the opening and closing lever systems, the length of the muscles at initial activation, and viscous and elastic properties of the joints and ligaments. This hypothesis has been advanced for the control of tongue function in the salamander *Bolitoglossa* (Thexton et al., '77) in which the protrusive and retrusive muscles are simultaneously activated, but the actual movement pattern of the tongue appears to be governed by differences in the initial length of the muscles relative to their length-tension curves.

The latter hypothesis involves the initial input of a preprogrammed oscillator, but obviates the need for precise preprogramming and rapid modification of recruitment rates and frequencies within an extremely short time span (20 msec in *Lepisosteus*). In the gar, both the sternohyoideus and adductor mandibulae could be activated simultaneously.

If the sternohyoideus is near its optimum length for force generation (control of pectoral girdle position would be important in regulating this parameter) and/or the mechanical advantage of the sternohyoideus is greater than that of the adductor mandibulae, mouth opening will result. As the mouth opens, the sternohyoideus will not remain at the same position on the length tension curve and the mechanical

advantage may decline, thus allowing the adductor mandibulae (which may now have been stretched to near its optimum length for force generation) to close the mouth. Testing of these two alternative hypotheses awaits accurate determination of length-tension curves and the mechanics of fish jaw muscles.

The primitive actinopterygian feeding mechanism: Jaw mechanics

Two key features of the mouth opening mechanism in *Polypterus*, *Lepisosteus*, and *Amia* are hypothesized to be primitive for actinopterygian fishes: 1) neurocranial elevation during the expansive phase by the epaxial muscles, and 2) mandibular depression mediated by contraction of the sternohyoideus muscle via the mandibulohyoid ligament.

Schaeffer and Rosen ('61) noted that elevation of the neurocranium seems to have been an important mechanism acting to increase the gape during feeding in palaeoniscoid fishes.

Neurocranial elevation also plays an important role during the expansive phase to increase the gape both in the fishes examined here and in teleosts (e.g., *Salvelinus*, Lauder and Liem, '80; *Hoplias*, Lauder, '79; *Lepomis*, Lauder and Lanyon, in press; *Perca*, Osse, '69; cichlids, Liem and Osse, '75). Thus, lifting of the head during the strike appears to be a fundamental characteristic of the feeding mechanism and has been retained throughout the radiation of the actinopterygian fishes.

Mandibular depression during the strike in palaeoniscoid fishes probably was accomplished by contraction of the obliquus inferioris, sternohyoideus, and possibly the branchiomandibularis. The occurrence of a mandibulohyoid ligament is hypothesized to be primitive not only for the Actinopterygii, but also for the Teleostomi as a whole (Table 1), and in palaeoniscoids this ligament served to transfer the posterodorsal hyoid movement to the mandible. Schaeffer and Rosen ('61:188) pro-

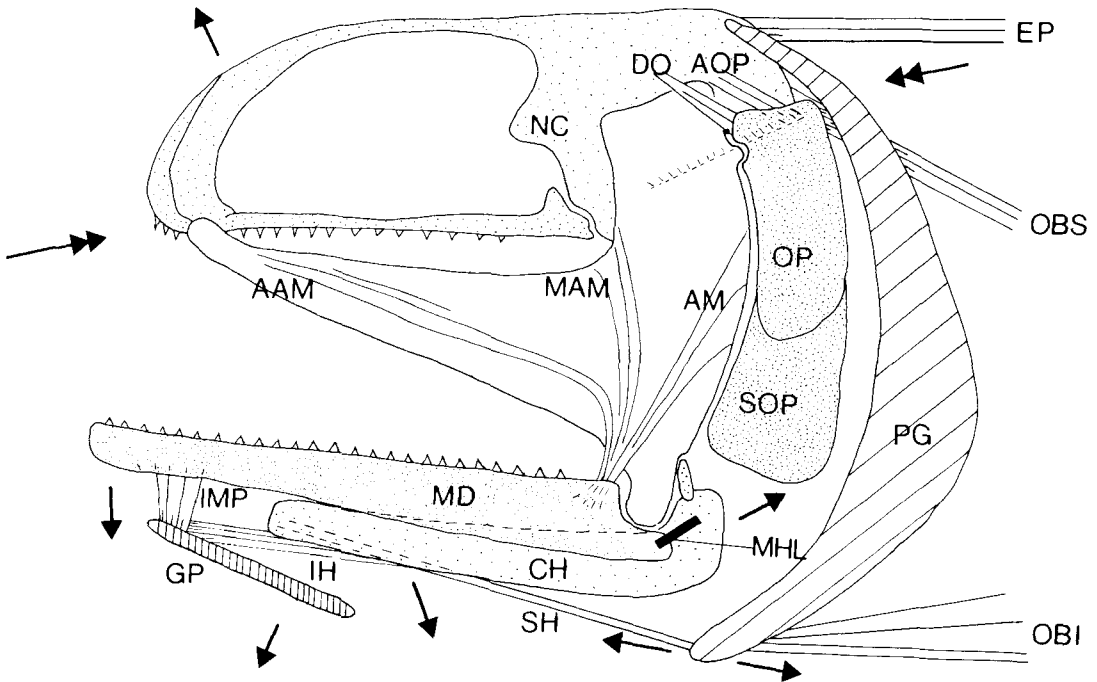


Fig. 18. Diagrammatic model of the feeding mechanism in a primitive actinopterygian fish (palaeoniscoid). Note the anteroventrally inclined axis of the suspensorium, the three divisions of the adductor mandibulae (see text) which are enclosed in a maxillary-palatoquadrate chamber, the presence of a mandibulohyoid ligament that transmits the force of sternohyoideus contraction to the retroarticular process of the lower jaw, the adductor operculi which is continuous anteriorly with the adductor hyomandibulae (dashed line on suspensorium), and the presence of intermandibularis posterior and interhyoideus muscles in the intermandibular region. Fibers of these muscles do not insert onto the gular plate (see text).

TABLE 1. *The distribution of certain anatomical and functional attributes of primitive fishes*

Character	Greatest level of generality at which character is hypothesized to be synapomorphic	Known character distribution: reference
1) Mandibular depression mediated by the sternohyoideus via the hyoid apparatus and mandibulohyoid ligament.	Teleostomi ¹	Actinistia: Lauder (80) Dipnoi: Lauder (unpublished data) Actinopterygii: this paper Actinopterygii: this paper
2) Double burst pattern of activity during the strike in the adductor operculi.	Actinopterygii	Actinopterygii: this paper
3) Adductor operculi continuous with adductor hyomandibulae. Lack of adductor arcus palatini.	Actinopterygii	Actinopterygii: this paper
4) Lack of a preparatory phase in the strike.	Actinopterygii	Actinopterygii: this paper
5) Sternohyoideus divided into two halves by a median septum or completely separated.	Teleostomi	Actinopterygii: this paper Actinistia: Millot and Anthony ('58) Dipnoi: Lauder (unpublished data) Teleostei: Winterbottom ('74)
6) Sternohyoideus <i>not</i> divided into two halves by a median septum.	Teleostei	Actinistia: Millot and Anthony ('58) Actinopterygii: this paper Choanata: Jarvik ('63)
7) Intermandibular musculature consisting of intermandibularis posterior and interhyoideus.	Teleostomi	Actinopterygii: this paper Actinistia: Millot and Anthony ('58) Choanata: Jarvik ('63)
8) Anterior division of the adductor mandibulae complex extending posteroventrally from the suborbital region to insert on lower jaw.	Elasmobranchiomorphi plus Teleostomi	Elasmobranchiomorphi: Lightoller ('39) Actinopterygii: this paper "Rhpidistia": Thomson ('67)
9) Presence of a levator operculi coupling mediating mandibular depression.	Halecostomi	Acanthodii: Lauder (unpublished) Halecomorphi: this paper Teleostei: Liem ('70)
10) Maxilla mobile and free from the cheek.	Halecostomi	Halecostomi: Patterson and Rosen ('77)

¹Teleostomi = Acanthodii + Actinopterygii + Dipnoi + Actinistia + Choanata

posed that the mandible was depressed by the geniohyoid muscles. Palaeoniscoids lacked a geniohyoideus because the primitive condition of the actinopterygian intermandibular musculature involves the presence of an intermandibularis posterior and an interhyoideus dorsal to the gular elements (Table 1; Fig. 18). These muscles may have been active during mouth opening (as in *Amia*) but could not have contributed to mandibular depression because of their line of action.

The mechanism of mandibular depression proposed here as primitive for actinopterygians also may be primitive at a much greater level of generality. Recently, I have reconsidered the feeding mechanism in the living coelacanth, *Latimeria*, (Lauder, '80) and proposed that mandibular depression is mediated by the sternohyoideus and ligamentous connections between the hyoid and mandible. All living lungfishes have mandibulohyoid ligaments. Although the structure of the hyoid arch is poorly known in acanthodian fishes, the occurrence of a small "accessory element" (= interhyal?) between the distal end of the hyomandibula and the ceratohyal (Miles, '73) suggests that hyoid retraction may have played a key role in mediating mandibular depression. This role of the sternohyoideus and hyoid apparatus in the feeding mechanism thus may be primitive for the Teleostomi (Table 1).

A comparative analysis of the structure of the jaw in primitive living actinopterygians, *Latimeria*, and lungfishes, suggests the following model for the feeding mechanism of palaeoniscoid fishes (Fig. 18): The suspensory apparatus possessed rather limited lateral mobility and the axis of rotation during mediolateral excursion was anteroventrally inclined (Fig. 18). Epaxial musculature inserting on the neurocranium was instrumental in increasing the gape during feeding, and lateral head movements were probably effected by the obliquus superioris (Fig. 18: OBS) division of the hypaxial muscles. The pectoral girdle remained nearly stationary during feeding as a result of antagonistic activity in the obliquus inferioris and sternohyoideus muscles, which controlled hyoid retraction and, indirectly, mandibular depression. The interhyal bone (Gardiner, '73) functioned to decouple movements of the hyoid from those of the suspensorium and increased the mechanical advantage of hyoid retraction. The gular elements and branchiostegal rays were relatively immobile and the intermandibular musculature did

not function to depress the mandible but rather to compress the buccal cavity during chewing following prey capture (interhyoideus), or to adduct the mandibular rami and suspensorium during the expansive phase (intermandibularis posterior).

Movement of the operculum and suboperculum was controlled by the dilator and adductor operculi which permitted limited control over opercular movements during feeding. Adduction of the operculum occurred in a bi-phasic pattern during the strike, the first phase occurring at the start of buccal expansion and the final phase following closure of the jaws.

Muscle homologies and comparative anatomy

The homologies of the divisions of the osteichthyan adductor mandibulae complex have not been considered since the earlier investigations of Edgeworth ('35), Souché ('32), Lightoller ('39), Luther ('13), and to some extent Allis (1897).

The adductor mandibulae complex of primitive living actinopterygians may be divided into three separate divisions: 1) an anterior (suborbital) division originating on the anterior of the palatoquadrate and extending posteroventrally to insert on the lower jaw; 2) a medial division that runs nearly dorsoventrally from the palatoquadrate to the mandible; and 3) a posterolateral division originating from the posterior aspect of the palatoquadrate (see Fig. 18). This partition is based on the topography of the adductor complex in the adult as well as on the embryology of the jaw adductor complex (Edgeworth, '35). The three adductor divisions in primitive actinopterygians represent a separation into discrete components of the primitively large fan-shaped adductor mandibulae of gnathostomes.

Within this scheme, the levator maxillae superioris of *Amia*, so-named by Allis (1897) because of its supposed homology with the levator maxillae superioris of selachians, is homologous to the suborbitalis of selachians (= levator labii superioris of Luther, '13; muscle preorbitaire of Souché, '32) as an anterior division of the adductor mandibulae. Thus, both the selachian suborbitalis and the levator maxillae superioris of *Amia* are derivatives of the anterior fibers of the primitive fan-shaped osteichthyan adductor mandibulae.

In *Lepisosteus*, the palatomandibularis minor and major (Luther, '13) correspond to the anterior adductor division (Table 2), whereas *Polypterus* lacks an anterior adductor compo-

TABLE 2. Homologies of the adductor mandibulae complex in actinopterygians

Genus	Adductor division: reference	Proposed homology
<i>Amia</i>	Levator maxillae superioris 3,4: Allis (1897) Levator maxillae superioris 1,2: Allis (1897) AM2', AM2'', AM2''', AM3: Allis (1897) A ₀ ', A ₀ '': Allis (1897) Palatmandibularis minor and major: Edgeworth ('35), Luther ('13)	Anterior adductor division Medial adductor division Posterolateral adductor division Intramandibular division Anterior adductor division
<i>Lepisosteus</i>	Preorbitalis superficialis and profundus: Edgeworth ('35), Luther ('13) AM: Edgeworth ('35), Luther ('13) AMp, AMr: Allis ('22) AM2, AM1: Allis ('22) AM3: Allis ('22)	Medial adductor division
<i>Polypterus</i>		Posterolateral adductor division Medial adductor division Posterolateral adductor division Intramandibular adductor division

ment. The homologies of the medial and posterolateral adductor components are indicated in Table 2.

The name "levator maxillae superioris" (LMS) was used by Rosen and Patterson ('69) to refer to certain divisions of the adductor mandibulae in paracanthopterygian fishes; Winterbottom ('74) pointed out that this muscle is not homologous to parts three and four of the LMS in *Amia*. Despite this, Nelson ('74) and Casinos ('78) continued to use "levator maxillae superioris" for paracanthopterygian muscles. The Osteoglossomorpha, Elopomorpha, Clupeomorpha, and basal euteleosteans lack any muscle comparable in origin, insertion, and ontogeny to the LMS of *Amia*. This renders any interpretation of paracanthopterygian muscles as LMS homologues highly unparisimonious. The anterior division of the primitive osteichthyian adductor complex to which the LMS of *Amia* is homologous (Table 2) has been lost in all teleost fishes.

The intermandibularis musculature of primitive, living actinopterygians consists of an intermandibularis posterior spanning the mandibular rami, and an interhyoideus muscle, extending anteriorly from the ceratohyal to insert dorsal to the gular plate (Figs. 1-3: IMP, IH). This condition is apparently primitive not only for the Actinopterygii (Fig. 18), but also for the Teleostomi (Table 1), because *Latimeria* (Millot and Anthony, '58; pers obs.) and choanates (Jarvik, '63) have intermandibular musculature nearly identical to that of actinopterygians. In none of these groups do the fibers of the intermandibularis posterior or interhyoideus actually insert on the gular plate (where this exists). Two groups of teleosts, the Osteoglossomorpha and Elopomorpha, retain identifiable intermandibularis and interhyoideus components of the geniohyoideus (Greenwood, '71; Liem, '67a). The presence of an intermandibularis anterior is an additional synapomorphy between *Amia* and teleosts.

The anatomy of the sternohyoideus muscle has been the subject of a number of recent investigations. Winterbottom ('74) and Greenwood ('77) commented on the difficulty of precisely defining the posterior limit of this muscle, because in teleosts, its posterior fibers are often continuous with those of the anterior obliquus inferioris. Commonly, teleosts have two transverse tendinous inscriptions in the sternohyoideus, and Winterbottom ('74) proposed that the posterior limit of this muscle be set, somewhat arbitrarily, at the third myosept.

The comparative anatomy of the sternohyoideus in *Polypterus*, *Lepisosteus*, and *Amia* suggests that the primitive actinopterygian sternohyoideus was paired (divided completely into right and left halves), originated from the anteroventral face of the pectoral girdle and had no fiber continuity with the obliquus inferioris, and was divided transversely by two myosepts. Winterbottom's ('74) proposal, thus, has some justification because the position of the third myosept may be expected to approximate the primitive attachment of the sternohyoideus to the pectoral girdle.

The paired condition of the sternohyoideus may be primitive for the Teleostomi (Table 1) because *Latimeria* and the living lungfishes also have a divided sternohyoideus. In teleost fishes, the sternohyoideus is consolidated into a single median muscle, although *Heterotis* still has a remnant of the primitive longitudinal sternohyoideus septum (Greenwood, '71:52).

The myology of primitive actinopterygians has remained remarkably conservative and relatively few differences in cephalic myology occur despite numerous (potentially disrupt-

ive) major osteological differences between the skulls of *Lepisosteus*, *Polypterus*, and *Amia*. The major variations in cranial myology occur in the adductor mandibulae complex, whereas all other jaw musculature is constant in position.

The origin and evolution of inertial suction feeding

The inertial suction strategy of prey capture involves the creation of a low pressure center in the buccal cavity by rapid mouth opening and expansion of the buccal floor. The pressure differential between the buccal and opercular cavities and the surrounding water results in a flow of water into the mouth. If the velocity of flow at the position of the prey is sufficiently great, the prey will be carried into the mouth with the flow of water. Forward body velocity of the predator may also be used in prey capture to varying degrees, some fishes relying exclusively on pursuit, whereas others remain essentially stationary and capture prey by suction feeding.

The features of the actinopterygian feeding

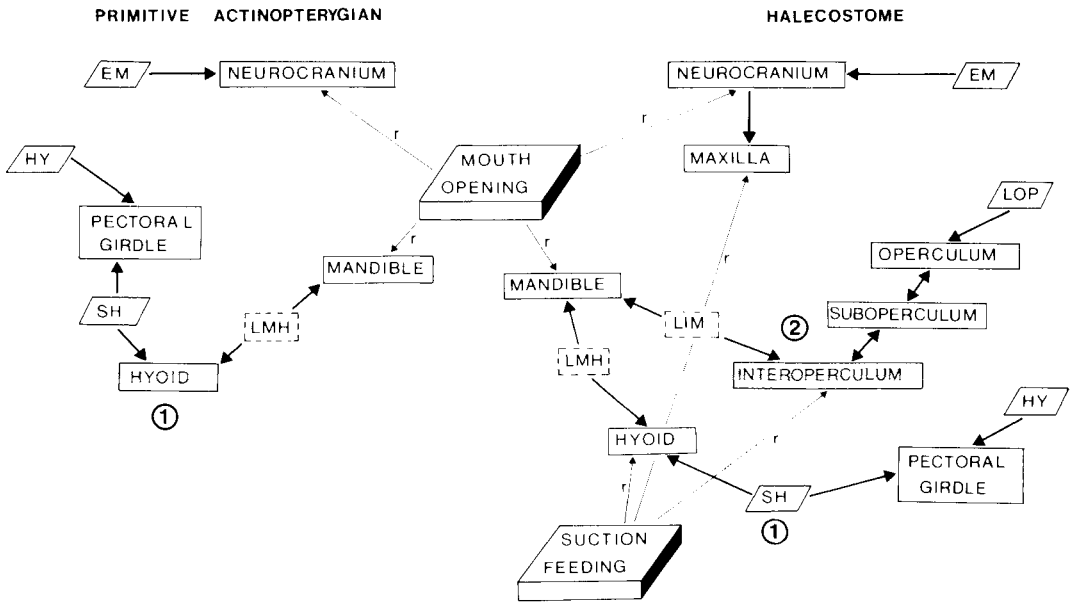


Fig. 19. Comparison of biomechanical pathways resulting in mandibular depression and neurocranial elevation in primitive actinopterygians (left) and halecostome fishes (right). Homologous pathways are similarly numbered; pathway two is a shared character of the Halecostomi. The occurrence of two new couplings in halecostomes, the epaxial muscles-neurocranium-maxilla and levator operculi-opercular series-mandible coupling, results in the realization (r) of a new function: suction feeding. Solid rectangles = bony elements; dashed rectangles = ligaments; parallelograms = muscles. Arrows run from the muscle to the bone of insertion; double-headed arrows indicate ligamentous connections between elements of a mechanical unit. Three-dimensional rectangles indicate major functions which are realized (r, arrows) by the biomechanical linkages depicted. The new function at the halecostome level, suction feeding, is realized by three independent musculoskeletal linkages acting synergistically.

mechanism, identified here as morphological correlates of an inertial suction feeding strategy of prey capture, complement the characters used by Patterson and Rosen ('77) in defining the halecostome fishes (= Halecomorphi plus Teleostei)—i.e., the free maxilla and interoperculum. The occurrence of a maxilla that is no longer immovably attached to the dermal cheek bones is a major feature of a suction feeding mechanism because maxillary swing prevents water inflow from the sides of the mouth and results in more anteroposteriorly oriented streamlines.

In addition, the halecostome fishes are the first to show a levator operculi-opercular series-mandible coupling that mediates mandibular depression (Table 1). The interopercular bone is a key element for transmitting the pull of the levator operculi to the mandible and this bone is absent in all nonhalecostome actinopterygians. The presence of a levator operculi coupling in addition to the primitive mechanism of mandibular depression (the sternohyoideus-hyoid apparatus-mandible coupling) allows the two couplings either to act synergistically to effect rapid mandibular depression or to function at different stages of the expansive phase. The presence of two independent mechanisms controlling mandibular depression (Fig. 19) is a shared feature of the halecostome fishes as is the inertial suction strategy of prey capture.

Verraes ('77) has shown in *Salmo* that the mandibulohyoid ligament is present at hatching, while the interoperculomandibular ligament develops during the late larval phase. The former is thus a more general character (sensu Nelson, '78) than the latter.

Hutchinson ('73) suggested that a group of "chondrosteans," the redfieldiiform fishes, were suction feeders. This conclusion was based on the suggestion that the buccal cavity could be expanded by posteroventral movement of the pectoral girdle and that "... considerable negative pressure in the buccal cavity could be achieved by independent abduction of the branchial basket." Abduction (ventral rotation) of the branchial basket can be achieved independently of mouth opening in all fishes, and is not a correlate of large negative pressures in the buccal cavity. Furthermore, posteroventral movement of the pectoral girdle will contribute little to a reduction of the pressure within the mouth cavity due to the small volume change. Hutchinson's observation that the sternohyoideus may have been a large muscle suggests that the pectoral girdle might actually have been protracted during feeding.

Redfieldiiform fishes also lack the morphological features identified here as correlates of a suction-feeding mechanism. The maxilla is fixed to the cheek, an interopercular bone is absent, and a single mechanism exists for mandibular depression.

The model of the palaeoniscoid feeding mechanism presented above suggests that redfieldiiform fishes used the primitive actinopterygian mechanism of mandibular depression mediated by the sternohyoideus via the mandibulohyoid ligament; the negative pressures within the buccal cavity were probably small (about 50 cm H₂O).

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