

# CHARRS

Salmonid Fishes of the Genus *Salvelinus*

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## The feeding mechanism and cephalic myology of *Salvelinus fontinalis*: form, function, and evolutionary significance

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### 10.1 Introduction

Studies on the feeding mechanics of teleosts have been focused primarily on the advanced teleostean groups (Alexander 1967a, 1967b, Anker 1974, Dutta 1968, 1975, Liem 1967, 1970, 1973, Nyberg 1971, Osse 1969), while relatively little attention has been paid to the more primitive fishes (Kirchhoff 1958, Tchernavin 1948, Vrba 1968). The salmoniforms in particular have been badly neglected; the major study of feeding in this group being that of Tchernavin (1953) who based his analysis on the manipulation of preserved specimens of *Salmo salar* and *Chauliodus sloani*. Ballintijn & Hughes (1966) recorded the activity pattern of respiratory muscles in *Salmo*; Günther & Deckert (1953, 1955) have studied the trophic structures in stomiatoids.

Salmoniform fishes are among the most primitive fishes of the cohort Euteleostei (Greenwood *et al.* 1966, Rosen 1973) and thus form an important link between the other basal teleostean groups (Osteoglossomorpha, Elopomorpha, Clupeomorpha) and higher euteleosteans. A detailed knowledge of the feeding mechanism in generalized salmoniform fishes is thus important, both for a comparative approach to teleostean functional anatomy, and as a major link in the evolution and adaptive radiation of the teleostean feeding apparatus.

The aim of this chapter is to provide a description of the cranial and branchial myology of brook charr, *Salvelinus fontinalis*, to analyze the feeding mechanism with special reference to musculoskeletal interactions within the head during prey capture, and to

discuss the form and function of the feeding mechanism in light of actinopterygian jaw evolution.

## 10.2 Materials and methods

The cranial and branchial myology was described from over twenty specimens of *Salvelinus fontinalis* (Museum of Comparative Zoology (MCZ) 52115; 28 specimens), *Salvelinus alpinus* (MCZ 52443; 3 specimens), *S. namaycush* (MCZ 52576, 52577; 6 specimens), and *S. malma* (MCZ 52445; 3 specimens) were also examined for comparative purposes.

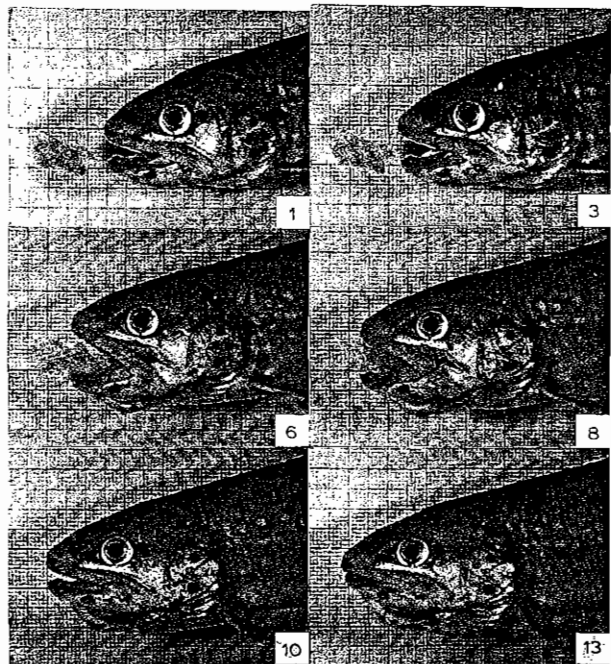


Fig. 1. High-speed cinematography ( $200\text{ frames sec}^{-1}$ ) of feeding *Salvelinus fontinalis* (17.8 cm SL; positive prints of frames 1, 3, 6, 8, 10 and 13 from a feeding sequence. Time between successive frames at  $200\text{ frames sec}^{-1}$  is 5 msec. Several of the markers used for cineradiography are visible.

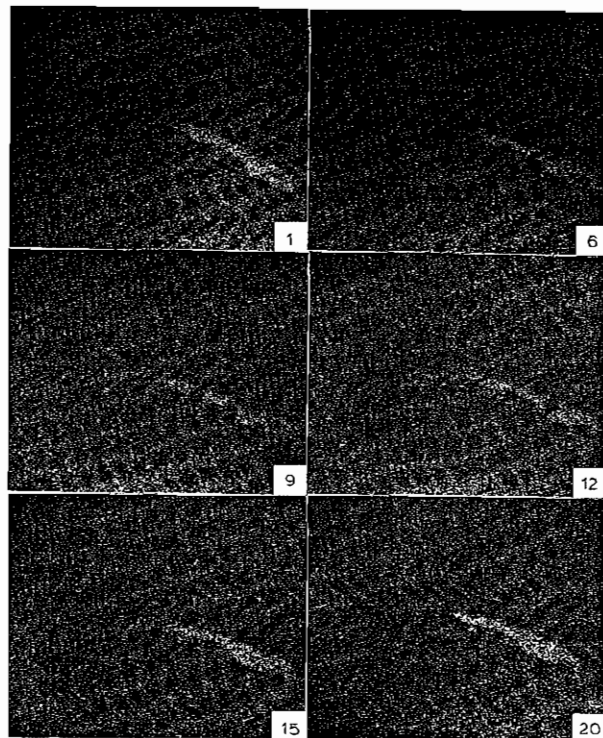


Fig. 2. High-speed cineradiography ( $200\text{ frames sec}^{-1}$ ) of feeding in *Salvelinus fontinalis*; frames 1, 6, 9, 12, 15 and 20 of a feeding sequence. The mouth has closed shortly before frame 15. Small steel screws, lead markers, and pieces of surgical wire have been unilaterally implanted in the bones allowing direct measurement of bone movement during feeding. For a key to the markers see Figure 15. Hyoid depression, maxillary swing, and mandibular depression are most easily seen; note the changing relationship between the maxillary and hyoid wires. The swimbladder is located to the right. The skull bones are not heavily ossified and are not clearly visible in cineradiographic films.

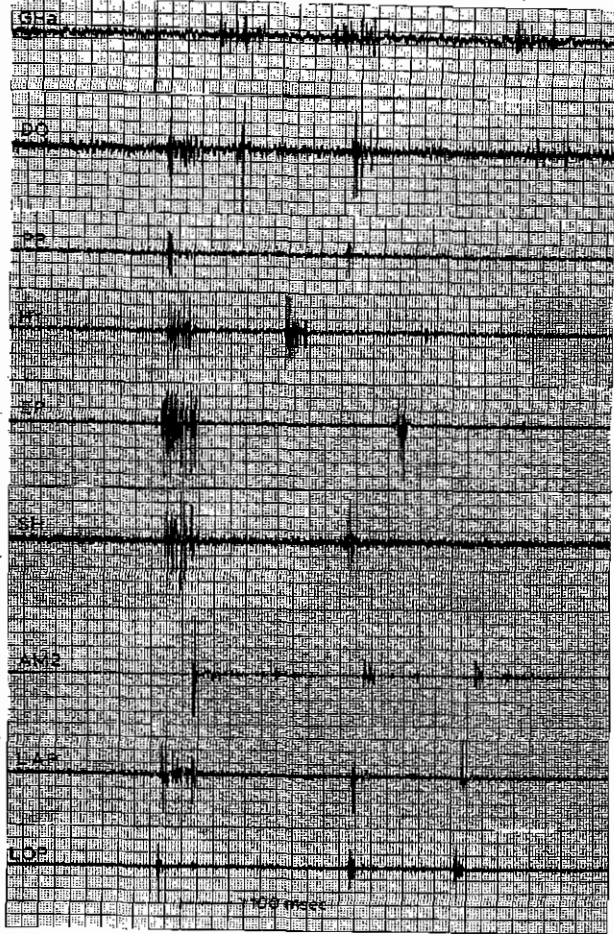


Fig. 3. Electromyograms of nine cranial muscles during feeding in *Salvelinus fontinalis*. The levator operculi and the epaxial muscles are the first muscles to contract during prey capture. Muscles: AM2, second division of the adductor mandibulae; DO, dilator operculi; EP, epaxial muscles; GHa, geniohyoideus anterior; HY, hypaxial muscles; LAP, levator arcus palatini; LOP, levator operculi; PP, obliquus superioris; SH, sternohyoideus.

High-speed cinematography at 200 frames  $\text{sec}^{-1}$  was used to establish the basic pattern of bone movements during feeding (Fig. 1). A Photosonics 16 mm-1 PL camera was used in conjunction with three 600 W Smith-Vector filming lights and Kodak 4X reversal film.

X-ray cinematography allowed direct measurement of bone movements. Siemens radiographic equipment with a Sirecon image intensifier and an Eclair GV-16 camera yielded cineradiographic film at 200 frames  $\text{sec}^{-1}$ . Kodak Plus-X reversal film was exposed at 120 mA and 38 and 40 kV. Small jeweler's screws (0.5–1 mm head diameter) and short pieces of surgical wire (0.4 mm in diameter) were implanted under anesthesia in the bones of the head and pectoral girdle several days before filming. The screws and wires appear clearly as points and lines on the film (Fig. 2) and permit the first direct measurement of bone movements during feeding in fishes. No adverse effects from the implantation were noted.

Positive prints of each frame of the feeding sequences were made from the 16 mm films, and the measurements taken from the prints with dial calipers.

Electromyography of the cranial muscles was used to determine the timing of muscle contraction during feeding (Fig. 3). A Brush High-Gain Biomedical Coupler (sensitivity  $1 \mu\text{V div.}^{-1}$ ) and a Brush 260 chart recorder were coupled to a revolving connector which allowed unrestrained movement of the fish. Fine wire electrodes were implanted in the muscles (Basmajian & Stecko 1962) and supported by a clamp attached to a loop of wire through the epaxial musculature. Electrical potentials were recorded at 37.5 cm  $\text{sec}^{-1}$  on a Honeywell 5600 tape recorder and played back at 4.7 cm  $\text{sec}^{-1}$  to facilitate analysis. Activity in five muscles was recorded simultaneously, and the consistently well defined and high amplitude contraction of the levator operculi at the start of the feeding sequence was used as a reference to compare the results of different experiments.

### 10.3 Myology of the feeding apparatus

The cephalic myology of *Salvelinus fontinalis* is described as a prelude to the functional analysis of the feeding mechanism. Our comparative studies have revealed only slight differences in the myology of the different species of *Salvelinus*. Chief interspecific differences in the cephalic myology are proportional ones coupled with only very slight differences in the insertion sites of certain muscles. Thus the description for *Salvelinus fontinalis* is representative for all members of the genus. Several authors have dealt with some aspects of the cephalic myology of *Salma* (Vetter 1878, Greene & Greene 1913, Van Dobben 1935, Ballintijn & Hughes 1965). In this topographical treatise, we will closely adhere to the nomenclature proposed by Winterbottom (1974).

#### 10.31 Muscles of the cheek

*Adductor mandibulae* (Fig. 4, 6, 10:am). As in most primitive teleosts, the adductor mandibulae muscle is divided into two parts:  $A_2A_3$  and  $A_w$ , both of which are innervated by branches of the ramus mandibularis of the trigeminal nerve. Part  $A_2A_3$  occupying the ventrolateral region of the cheek (Fig. 4:am) originates from the hyomandibular, preopercular, metapterygoid, symplectic and quadrate. Anteroventrally the fibers of the anterior part of  $A_2A_3$  pass medially to the coronoid process sharing a distinct myocomma with the posterior fibers of  $A_w$  (Fig. 6:am). Fibers of the posterior half of the  $A_2A_3$  complex converge on a well differentiated elongate tendon, which runs along the posterior edge of the  $A_w$  muscle to insert in the Meckelian fossa anterior to the quadratomandibular joint (Fig. 6). Thus the insertion of the  $A_2A_3$  complex is effectively in the Meckelian fossa via the  $A_w$  muscle and the elongate tendon.

The  $A_w$  part of the adductor mandibulae, often called the intramandibularis, attaches to the Meckelian fossa on the medial aspect of the mandible. The fibers of the  $A_w$  part arise from the myocomma of the  $A_2A_3$  complex and run from an anteroventral to a posterodorsal direction.

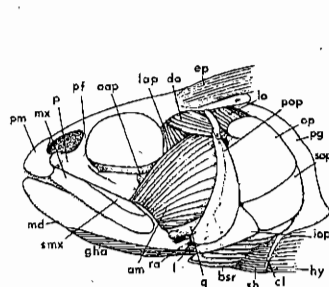


Fig. 4

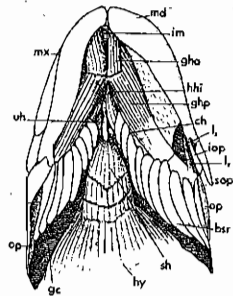


Fig. 5

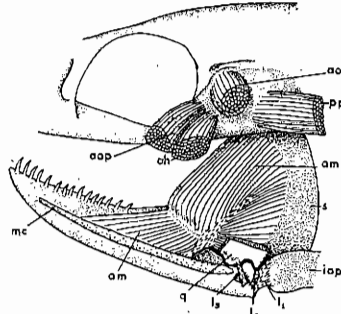


Fig. 6

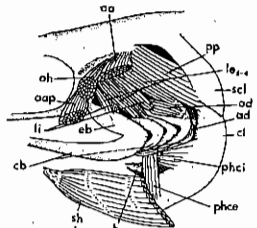


Fig. 7

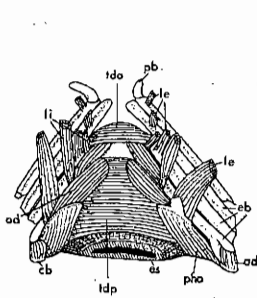


Fig. 8

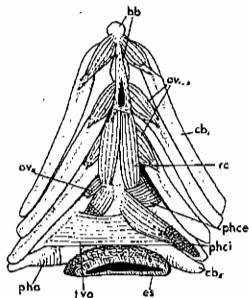


Fig. 9

*Levator arcus palatini* (Fig. 4, 10:lap). This muscle occupies the back part of the orbit between the skull and the suspensory apparatus and is innervated by the maxillo-mandibularis branch of the trigeminal nerve and by a major branch of the facial nerve (Meijer 1975). The muscle is conical, with the apex as its fleshy origin from the sphenotic. From this dorsalmost position, the fibers pass posteroventrally to insert muscicularly on the lateral aspects of the hyomandibular and metapterygoid. Common synonyms for this muscle are levator hyoidei, levator hyomandibulae et arcus palatini, and protractor hyomandibularis.

*Dilatator operculi* (Fig. 4, 10:do) lies posterior to the levator arcus palatini and is innervated by the maxillo-mandibularis branch of the trigeminal nerve and by a branch of the facial motor nerve (Meijer 1975). Although it is immediately adjacent to the levator arcus palatini, its fibers are clearly separated. From its fleshy origin within the shallow dilator fossa located in the sphenotic and frontal bones, the fibers run posteroventrally converging on a tendon of insertion, which is attached to an earlike process of the opercular (Fig. 4:op). A common synonym for the muscle is dilatator operculi.

*Levator operculi* (Fig. 4, 10:lo). Just behind the dilatator operculi, lies a clearly separated levator operculi muscle, which is innervated by the ramus hyomandibularis of the facial

Fig. 4. Left lateral view of superficial cephalic muscles of *Sabvelinus fontinalis*. Abbreviations: AAP, adductor arcus palatini; AM, adductor mandibulae A<sub>2</sub>A<sub>3</sub>; BSR, branchiostegal ray; CL, cleithrum; DO, dilatator operculi; EP, epaxial muscles; GHA, geniohyoideus anterior; IOP, interoperculari; HY, hypaxial muscles; L, interoperculomandibular ligament; LAP, levator arcus palatini; LO, levator operculi; MD, mandible; MX, maxilla; OP, opercular; P, palatine; PF, prefrontal; PG, pectoral girdle; PM, premaxilla; POP, preopercular; Q, quadrate; RA, retroarticular process; SH, sternohyoideus; SMX, supramaxilla; SOP, subopercular.

Fig. 5. Superficial aspect of ventral cephalic muscles of *Sabvelinus fontinalis*. Left side has been spread apart to reveal ligaments. Abbreviations: BSR, branchiostegal ray; CH, ceratohyal; GC, gill cavity; GHA, geniohyoideus anterior; GHP, geniohyoideus posterior; HHI, hyohyoideus inferior; HY, hypaxial muscles; IM, intermandibularis; IOP, interoperculari; L<sub>1</sub>, interoperculomandibular ligament; L<sub>2</sub>, mandibulohyoideum ligament; MD, mandible; MX, maxilla; OP, opercular; SH, sternohyoideus; SOP, subopercular; UH, urohyal.

Fig. 6. Medial aspect of right adductor mandibulae muscle complex after removal of the right palatopterygoid complex with intact right mandibular(s) and partially removed right quadrate (q). Neurocranium viewed from left lateral aspect with associated muscles. Abbreviations: AAP, adductor arcus palatini; AH, adductor hyomandibulae; AM, adductor mandibulae: upper part is A<sub>1,2</sub> and lower part is A<sub>3</sub>; AO, adductor operculi; IOP, interoperculari; L<sub>1</sub>, interoperculomandibular ligament; L<sub>2</sub>, mandibulohyoideum ligament; L<sub>3</sub>, medial collateral ligament; MC, Meckel's cartilage; PP, protractor pectoralis; Q, quadrate; S, suspensorium.

Fig. 7. Lateral view of the branchial muscles of *Sabvelinus fontinalis*, with other muscles associated with the neurocranium and pectoral girdle. Left opercular series, hyoid ramus, suspensory apparatus, gill filaments and gill rakers removed. Abbreviations: AAP, adductor arcus palatini; AD, adductor; AH, adductor hyomandibulae; AO, adductor operculi; cb, first ceratobranchial 1-5; CL, cleithrum; EB, first epibranchial; H, heart; LE 1-4, levatores externi 1-4; LI, levatores interni; OD, obliquus dorsalis; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PP, obliquus superioris; SCL, supraclithrum; SH, sternohyoideus.

Fig. 8. Dorsal view of the branchial basket and its musculature of *Sabvelinus fontinalis* after removal of gill filaments. Abbreviations: AD, adductor; CB, fifth ceratobranchial; EB, epibranchials 1-4; ES, esophagus; LE, levatores externi; LI, levatores interni; OD, obliquus dorsalis; PB, pharyngobranchial; PHA, obliquus posterior; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior.

Fig. 9. Ventral view of the branchial basket and associated muscles of *Sabvelinus fontinalis* after removal of gill filaments and the right pharyngocleithralis internus muscle. Abbreviations: BB, basihranchial; CB<sub>1</sub>, first ceratobranchial; CB<sub>5</sub>, fifth ceratobranchial; EB, epibranchials 1-4; ES, esophagus; OV<sub>1-3</sub>, obliqui ventrales 1-3; OV<sub>4</sub>, obliquus ventralis 4; PHA, obliquus posterior; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; RC, rectus communis; TVA, transversus ventralis.

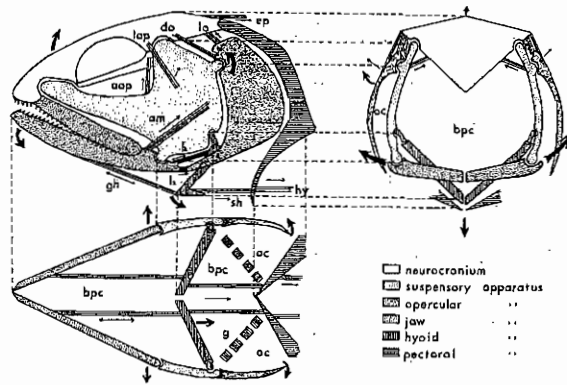


Fig. 10. Three-dimensional diagram of the major mechanical units, muscles and ligaments of the head of brook charr. Muscles and the principal direction of their forces are indicated respectively by light lines and light arrows. Heavy arrows depict major movements during the expansive phase of the feeding cycle. Ligaments ( $L_1$ , interoperculo-mandibular;  $L_2$ , mandibulo-hyoideum) are black. Abbreviations: AAP, adductor arcus palatini; AM, adductor mandibulae; BPC, buccopharyngeal cavity; DO, dilator operculi; EP, epaxial muscles; G, gills; HY, hypaxial muscles;  $L_1$ , interoperculo-mandibular ligament;  $L_2$ , mandibulo-hyoideum ligament; LAP, levator arcus palatini; LO, levator operculi; oc, opercular cavity; SH, sternohyoideus.

nerve. Ballintijn & Hughes (1965) claim that this muscle is not separate from the adductor operculi. Our observations on *Salvelinus* and *Salmo* show that the fibers of the levator operculi are distinctly discontinuous with those of the adductor operculi. Both the origin from the pterotic and insertion on the dorsal and dorsomedial face of the opercular are muscular. The straplike muscle is parallel fibered and not subdivided.

**Adductor arcus palatini** (Fig. 4, 6, 7, 10:aap). This conical muscle forms the posterior floor of the orbit between neurocranium and suspensorium. As is the case for all derivatives of the constrictor hyoideus dorsalis, this muscle is innervated by the ramus hyomandibularis of the facial nerve. Both the origin from the prootic and insertion on the metapterygoid and hyomandibular are muscular. As in all basal teleosts, the muscle is restricted to the posterior part of the orbital cavity, but its fibers are clearly separated from those of the adductor hyomandibulae and adductor operculi (Fig. 6:aap, ah, ao).

**Adductor hyomandibulae** (Fig. 6:ah). Closely associated with the adductor arcus palatini is the adductor hyomandibulae, which is also innervated by the ramus hyomandibularis of the facial nerve. Its topographical features seem to indicate that this muscle has separated from the posterior region of the adductor arcus palatini. Both muscles share a muscular origin from the prootic, but the fleshy insertion of the conical adductor hyomandibulae is restricted to the posterodorsomedial aspect of the hyomandibular. The muscle is more commonly known as the adductor hyomandibularis.

**Adductor operculi** (Fig. 6:ao). This short almost cylindrical muscle runs from the dorsomedial aspect of the opercular to the otic region of the neurocranium. It shares the same innervation, i.e. the ramus hyomandibularis of the facial nerve, with the adductor arcus palatini, adductor hyomandibulae and the levator operculi muscles. Both the origin from the prootic and pterotic, and the insertion on the medial aspect of the opercular just

behind the operculo-hyomandibular joint are muscular. The fiber pattern is essentially parallel.

### 10.32 Ventral muscles of the head

**Intermandibularis** (Fig. 5:im). This is the most anterior ventral cephalic muscle, innervated by the ramus mandibularis inferior of the trigeminal nerve. Its parallel fibers run transversely between the halves of the mandible. The muscle lies dorsal to the sites of attachments to the dentaries of the geniohyoideus anterior muscles.

**Geniohyoideus** (Fig. 4, 5:gha, ghp). This parallel-fibered muscle connects the mandible with the hyoid arch. Anteriorly, its left and right halves approximate one another very closely. At the point of approximation is a distinct myocomma. The geniohyoideus anterior (that part anterior to the bifurcation and myocomma) attaches to the inner side of the dentary near the symphysis ventral to the intermandibularis muscle. The geniohyoideus posterior (Fig. 5:ghp) bifurcates to attach to the lateral aspect of the ceratohyal. None of the fibers of the geniohyoideus attach to any branchiostegal ray. As shown by Meijer (1975) the geniohyoideus posterior possesses a double innervation, both by the trigeminal and facial nerves, while the geniohyoideus anterior is innervated by the ramus mandibularis inferior of the trigeminal nerve. The combined muscle complex of geniohyoideus anterior and posterior is more commonly called the protractor hyoidei or protractor hyoideus. We do not use the functional name, since protraction of the hyoid is only one of the functions of the muscle complex. Yet, the name geniohyoideus is not satisfactory either, since this muscle in teleosts is not homologous with the geniohyoideus of tetrapods.

**Hyohyoidei abductores** (Fig. 5:hh). These relatively small conical muscles are associated with the first branchiostegal rays. The fibers arise tendinously from the ventral hypohyal and are innervated by the ramus hyoideus of the facial nerve. The muscle is more commonly known as the hyohyoideus or the hyohyoideus inferior.

**Sternohyoideus** (Fig. 4, 5, 7, 10:sh). This cone-shaped muscle is thickened posteriorly and connects the hyoid arch to the pectoral girdle. Right and left halves are fused in the midline. Its innervation is derived from branches of the occipito-spinal nerves, although involvement of the vagus nerve is possible (Meijer 1975). The fibers originate musculously from the cleithrum and converge to insert on the urohyal. Three myocommata are clearly differentiated. It is customary to define the posterior limit of the muscle at the third myocomma. Frequently used synonyms are cleithrohyoideus and rectus cervicis.

### 10.33 Dorsal muscles of the branchial basket

Among this category we can recognize muscles having both sites of attachment on the branchial arches themselves (i.e. intrinsic) and those having one of the attachment sites on the neurocranium (i.e. extrinsic). Extrinsic muscles are the four external and two internal levators. As in most primitive teleosts the levator posterior and the retractor dorsalis are lacking. Intrinsic muscles are the obliquus posterior, obliquus dorsalis, transversus dorsalis anterior, transversus dorsalis posterior and the adductores.

**Levator externus** (Fig. 7, 8:le). Four levatores externi connect the neurocranium to the epibranchials and are innervated by posttrematic branches of the glossopharyngeal and vagus nerves. Fleshy origins of the parallel-fibered straplike muscles are from the prootic, while the tendinous insertions are on the dorsolateral aspects of the epibranchials of the first four arches. The tendon of the fourth levator externus inserts on the fourth epibranchial at a site posterior to the attachment of the fourth obliquus dorsalis. Synonyms for these muscles are levatores arcuum branchialium, levatores arcuum branchialium externi, and levator externus arcus branchialis.

**Levator internus** (Fig. 7, 8:li). Two relatively small levatores interni run between the prootic and the dorsal surfaces of the second and third infrapharyngobranchials. The

innervation is similar to that of the externi. The more anterior parallel-fibered straplike muscle passes in between the transversus dorsalis anterior and the anterolateral margin of the obliquus dorsalis III to insert tendinously on the dorsal aspect of the second infrapharyngobranchial. A hiatus between the posterior margin of the obliquus dorsalis III and the lateral margin of the obliquus dorsalis IV allows the tendon of the spindle-shaped posterior levator internus to attach to the dorsal aspect of the third infrapharyngobranchial. Synonyms for this muscle are levatores arcuum branchialium, levatores arcuum branchialium interni, and levatores interni arcuum branchialium.

**Obliquus dorsalis** (Fig. 7, 8:od). Two spindle-shaped obliqui dorsales III and IV run between the epi- and infrapharyngobranchials of respectively the third and fourth arches. Both muscles are innervated by branches of the vagus nerve. Origins and insertions are fleshy. Common synonyms include obliquus dorsalis inferior and obliquus dorsalis superior.

**Obliquus posterior** (Fig. 8:pha). A distinct obliquus posterior muscle connects the posteromedial margin of the fifth ceratobranchial to the extensive posteromedial aspect of the fourth epibranchial and is innervated by the vagus nerve. In contrast to other lower teleosts, the large, parallel-fibered muscle can be distinguished easily from the fifth adductor (Fig. 7:ad, pha). A commonly used synonym is the pharyngoarcualis.

**Adductor** (Fig. 7, 8:ad). The adductores are small muscles interconnecting the epibranchial and ceratobranchial. The fifth adductor is a short, but relatively stout muscle connecting the posterolateral corner of the epibranchial to the posterodorsal tip of the fifth ceratobranchial. The muscle is located just lateral to the obliquus posterior. A small fourth adductor lies on the medial aspect of the fourth arch, while adductores 1-3 are wanting. All adductores are innervated by the posttrematic branch of the vagus nerve serving the arch in question. The muscles are more commonly known as adductores arcuum branchialium and attractores arcuum branchialium.

**Transversi dorsales** (Fig. 8:tda, tdp). Two transversi dorsales are present, both of which are innervated by branches of the vagus nerve. Both muscles interconnect the dorsal elements of the branchial arches across the midline. The transversus dorsalis anterior (Fig. 8:tda) interconnects the epibranchials of the second arch, while the transversus dorsalis posterior (Fig. 8:tdp) interconnects the fourth epibranchials. Posteriorly the fibers of the transversus dorsalis posterior become continuous with those of the sphincter oesophagi.

### 10.34 Ventral muscles of the branchial basket

*Salvelinus* possesses four obliqui ventrales, transversi ventrales on the fourth and fifth arches, a rectus communis, and pharyngocleithralis externus and internus.

**Obliquus ventralis** (Fig. 9:ov). Spanning the joints between the ventral surfaces of the hypobranchial and ceratobranchial elements of the first four arches are the spindle-shaped obliqui ventrales muscles, innervated by the posttrematic branch of the vagus nerve. All obliqui ventrales muscles possess tendinous origins and insertions.

**Transversi ventrales** (Fig. 9:iv). Located posteriorly on the branchial basket are the transversi ventrales muscles, the fibers of which run uninterruptedly across the midline between the ceratobranchials. The attachment to the ceratobranchials is muscular. The major component runs between the fourth ceratobranchials, while a second part spans the gap between the fifth ceratobranchials.

**Rectus communis** (Fig. 9:rc). As in most basal teleosts, the rectus communis of *Salvelinus* connects the ventral aspect of the third hypobranchial to the anteromedial tip of the fifth ceratobranchial. It is a parallel-fibered, somewhat spindle-shaped muscle with tendinous attachments to the bones. Common synonyms are pharyngohyoideus, pharyngoarcualis and subarcualis rectus communis.

**Pharyngocleithralis externus** (Fig. 7, 9:pce). This muscle, originates from the lateral aspect of the anteroventral region of the cleithrum. Its parallel fibers run straight dorsally to insert on the anteroventral region of the fifth ceratobranchial. Its insertion is medial to

the rectus communis but lateral to the pharyngocleithralis internus muscle.

**Pharyngocleithralis internus** (Fig. 7, 9:pci). This muscle originates musculously from the anterior aspect of the cleithrum. Its fibers run anteriorly and converge to a tendinous insertion on the fifth ceratobranchial. Both the pharyngocleithralis internus as well as the externus are innervated by branches of the spinal nerves. These muscles are better known respectively as the pharyngocleithralis externus and internus.

### 10.35 Miscellaneous muscles

Under this admittedly inappropriate heading we present brief descriptions of two muscles which play an important role in the biomechanical and electromyographic profiles of the feeding function.

**Epaxial muscles** (Fig. 4, 10:ep). This muscle mass represents the dorsal complex of the body musculature. It passes anteriorly to insert musculously on the dorsal and posterior surfaces of the neurocranium. The more ventral parts of the muscle insert on the supraclithrum and cleithrum. Joining the epaxial muscles are fibers of the obliquus superioris component of the hypaxial body musculature. These fibers fuse with the ventral fibers of the epaxial muscle to insert on the posterolateral aspect of the otic region of the neurocranium.

**Hypaxial muscles** (Fig. 4, 5, 10:hy). Anteriorly the obliquus superioris and inferioris components of the hypaxial muscles insert on the posterior aspects of the cleithrum and coracoid. Ventrolaterally the superficial fibers pass lateral to the cleithrum and become continuous with the posterolateral part of the sternohyoideus.

### 10.4 Key ligaments

It is beyond the scope of this study to furnish a comprehensive review of the ligaments and arthrology. Instead we offer a brief account of just two ligaments that play a paramount role in the feeding mechanism.

**Mandibulohyoideum ligament** (Fig. 5, 6, 10:l). This ligament connects the medial aspect of the prominent retroarticular process of the mandible with the epiphyal of the hyoid arch. Its attachment to the posterodorsolateral aspect of the epiphyal just below the joint with the interhyal is quite a bit broader than the attachment to the retroarticular process. As the ligament passes anteriorly, its shape changes from a flat and broad profile, to a rounded one (Fig. 5, 6:l). Verraes (1977) has shown that the mandibulohyoideum ligament is present at hatching, and becomes functional at the onset of the cleutheroembryonic phase playing a key role in respiration and jaw opening.

**Interoperculomandibular ligament** (Fig. 5, 6, 10:l). This flat but stout ligament connects the anterior border of the interopercular with the posteroventral corner of the retroarticular process of the mandible. As shown by Verraes (1977) this ligament develops late during the period of active feeding. In contrast to the mandibulohyoideum ligament, the interoperculomandibular ligament is present in all adult teleosts.

### 10.5 Functional anatomy of feeding

#### 10.51 Basic model of the jaw apparatus

The head of teleost fishes may be divided into a series of mechanical units (Gans 1969), elements of the head which show little or no internal movement and act as a structural and kinetic unit. There are six such units in the head of charrs: (1) the neurocranium and premaxilla, (2) the maxilla, (3) the mandible, (4) the suspensorium, (5) the two hyoid

bars forming the hyoid arch, and (6) the opercular series. In addition, the pectoral girdle is composed of three units: (1) the posttemporal, (2) the supracleithrum, and (3) the cleithrum. The pectoral girdle is not considered as a single mechanical unit since each of the three bones is capable of some movement relative to the others. This proposal is corroborated by cineradiographic films of the pectoral girdle movement during feeding (see later).

These mechanical units are linked to each other by connective tissue or ligaments, and in conjunction with muscles and tendons form musculoskeletal couplings (Liem 1967, 1970) producing relatively well defined movements of the jaw apparatus.

In brook charr at least four major musculoskeletal couplings exist that are directly associated with feeding. The epaxial muscles-neurocranium coupling acts to raise the neurocranium dorsally during the feeding sequence. The lower jaw may be depressed through one or more of several couplings; the levator operculi-opercular series-mandible coupling (Fig. 10:1, 10), the sternohyoideus-hyoid apparatus-mandible coupling mediated by the mandibulohyoid ligament (Fig. 10:2) and a coupling involving the sternohyoideus-hyoid apparatus-geniohyoideus-mandible (= cleithrum-hyoid-mandible) and possibly connective tissue between the hyoid and lower jaw.

Other less complex couplings mediate movement of the suspensory apparatus and pectoral girdle. [Liem (1970) has considered the branchial musculoskeletal couplings.]

## 10.52 Movements of the jaw apparatus and electromyographic profile during feeding

### 10.521 General pattern

The pattern of muscle activity during feeding in *Salvelinus* shows significant variations within the general plan common to all feeding sequences observed. In certain muscles (Fig. 11:GHa, SH, AM2, LAP, LOP) two main patterns are distinguishable. The A-type feeding sequences involve feeding on food (usually one cm<sup>3</sup> piece of smelt) located on the bottom. The time sequence of events from the start of levator operculi contraction to the onset of adductor mandibulae activity is much longer (105 msec) than in B-type feeding (50 msec). B-type feeding is much more rapid and the time sequence is compressed producing more overlap in muscle activity. B-type patterns are produced when feeding occurs in mid-water on pieces of smelt or when feeding on live fish.

Mid-water feeding sequences are initiated by a well defined, high amplitude contraction of the levator operculi occurring nearly synchronously with hypaxial and epaxial muscle contraction (Fig. 11: LOP, EP, HY). Secondary bursts of activity in the levator operculi do not occur. About 5 msec after the start of levator contraction, the sternohyoideus and levator arcus palatini become synchronously active. The adductor mandibulae starts contracting 50 msec after the onset of activity in the levator operculi, immediately after cessation of sternohyoideus and levator arcus palatini contraction (Fig. 11: AM2, SH, LSP).

In sharp contrast, the A-type feeding sequences show a more variable pattern of muscle activity, the levator operculi and sternohyoideus in particular often showing multiple activity periods within the first 150 msec. Electrical activity in the jaw adductor is not observed until 55 msec later than in B-type feeding. At no time was any activity recorded in either the anterior or posterior portions of the geniohyoideus during the initial strike at the prey.

Although for certain muscles the general pattern and relative timing of activity remains relatively constant within each feeding category in spite of a compression of the time frame, other muscles show considerable variation in the activity period (Fig. 12:HY). This variation could not be correlated with the position of the food or the type of prey. There is relatively little variation in the timing of sternohyoideus contraction relative to the levator operculi but the hypaxial muscles vary greatly both in the onset and duration

of activity. In all cases, however, the initial contraction of the hypaxial muscles precedes that of the sternohyoideus (Fig. 12).

The epaxial musculature normally initiates a strong contraction exactly synchronously with the levator operculi but in some cases activity may slightly precede that of the levator

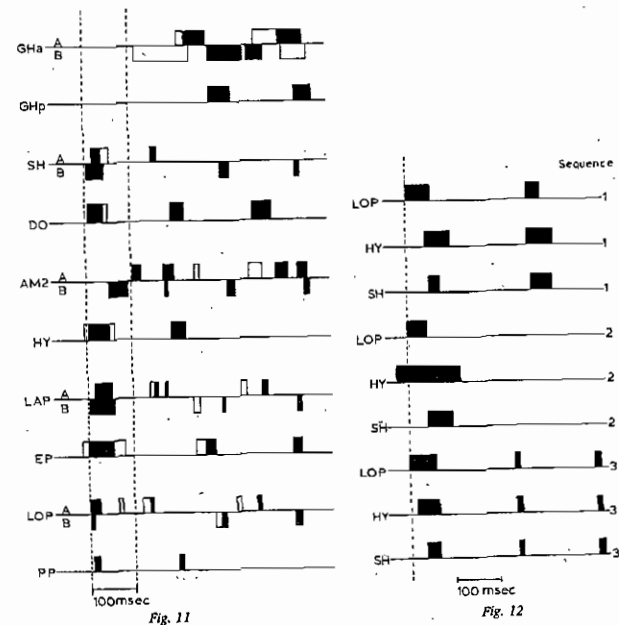


Fig. 11. Diagram of electromyographic (EMG) recordings of muscle activity in ten cranial muscles of *Salvelinus fontinalis* during the strike at the prey and the first stages of chewing and swallowing. Open blocks indicate frequent variations in the activity pattern. The double EMG record for five muscles, labeled A and B, indicates the two general patterns of muscle activity during feeding in these muscles. B-type activity occurred during rapid mid-water strikes while A-type activity occurred in feeding from the bottom. The first dashed line indicates the onset of levator operculi contraction. Muscles: AM2, second division of the adductor mandibulae; DO, dilator operculi; EP, epaxial muscles; GHa, and GHp, anterior and posterior divisions of the geniohyoideus; HY, hypaxial muscles; LAP, levator arcus palatini; LOP, levator operculi; PP, obliquus superioris; SH, sternohyoideus.

Fig. 12. Diagram of variations in the timing of hypaxial and sternohyoideus muscle activities relative to the levator operculi during the initial stages of feeding in *Salvelinus fontinalis*. The three muscles within each of the three feeding sequences were recorded simultaneously. The dashed line indicates the onset of levator operculi contraction.

operculi. The variability in epaxial muscle contraction time and duration is much less than that observed for the hypaxial muscles.

#### 10.522 Movement of the neurocranium, maxilla, and mandible

Elevation of the neurocranium during feeding is an extremely important aspect of the feeding mechanism and acts to increase the gape and the volume of the orobranchial chamber. Neurocranial elevation reaches a maximum 15 msec after the mouth has begun to open and is correlated temporally with peak maxillary swing and the maximum gape between the jaws (Fig. 11). At the end of the feeding sequence, the neurocranium remains in an elevated condition and the lower jaw is adducted against it. Thus, neurocranial movements contribute greatly to the increase in gape at the start of the feeding sequence, but rapid adduction of the lower jaw is primarily responsible for the decrease in mouth opening towards the end of the initial strike. The maxilla often does not return to its initial position by the time the mouth has closed due to continued neurocranial elevation (Fig. 13).

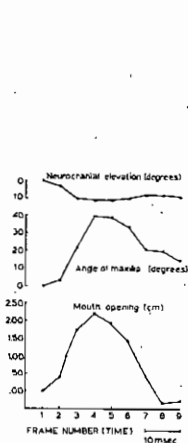


Fig. 13

Fig. 13. Graphic representation of neurocranial elevation, maxillary swing, and mouth opening during feeding in *Salvelinus fontinalis*. The initial value is set equal to zero, and all subsequent changes are recorded as a deviation from zero.

Fig. 14. Graphic representation of bone movements during feeding in *Salvelinus fontinalis* measured from successive frames of a cineradiographic film. Opercular dilation was measured by the change in distance between the interpercular point and the cleithral point (see Fig. 15). This distance increases as the operculum is abducted. Opercular levation was measured by the change in distance of a perpendicular line from the dorsal opercular point to the line representing the vertebral axis. All angles are measured relative to the vertebral axis. Changes in value were measured relative to the initial measurement which was set equal to zero. The dashed line represents the point of maximum gape.

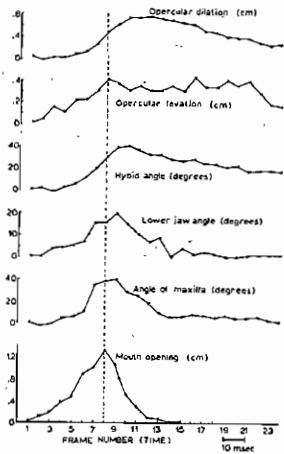


Fig. 14

Although the maxilla swings anteriorly through an angle of  $40^\circ$  and is temporally correlated with both mandibular depression and neurocranial elevation, experiments on *Salmo gairdneri* (Lauder 1979) in which the maxillomandibular ligament has been bilaterally removed suggest that the correlation with mandibular depression is spurious. Removal of the maxillomandibular ligament in *Salmo* resulted in an increased angular swing of the maxilla.

During feeding, the epaxial muscles show consistently large amplitude contractions, and electrical activity may be nearly continuous throughout the feeding sequence (Fig. 11:EP).

Mandibular depression may be initiated by one of several musculoskeletal couplings. The levator operculi is the first muscle to contract during feeding (Fig. 11:L.O.P.) (with the occasional exception of hypaxial and epaxial muscles) and mediates lower jaw depression by rotating the operculum around its articulation with the hyomandibular and transmitting a caudodorsal force via the opercular series and the interoperculomandibular ligament to the lower jaw. This force is applied ventral to the quadratomandibular articulation and causes the tip of the mandible to swing ventrally (Fig. 10).

Movements of the hyoid may also contribute to mandibular depression by exerting a posterodorsal force on the retroarticular through the mandibulohyoid ligament (Fig. 10:1). This ligament stretches from the epiphyal ventrally to the retroarticular and transmits a force produced by the sternohyoideus to the mandible. Since the contraction of the sternohyoideus consistently follows activity of the levator operculi, this coupling probably contributes to mandibular depression relatively late in the feeding sequence, shortly before maximum mouth opening is reached.

#### 10.523 Movements of the hyoid

Depression of the hyoid during feeding is an important mechanism to increase the volume of the orobranchial chamber. Contraction of the sternohyoideus exerts a posterodorsal force on the anterior of the hyoid arch (hypophyals) and exerts a moment around the interhyal-epiphyal articulation and the hyomandibular-interhyal articulation causing the hyoid to pivot ventrally.

The kinetic relationships between the hyoid arch, interhyal, and suspensorium are extremely complex. Osse (1969, Fig. 22) hypothesized that the working line of the sternohyoideus in *Perca* was raised dorsally during the feeding sequence. In *Salvelinus*, however, the opposite occurs.

High-speed cineradiography of brook charr has allowed the first direct measurements of bone movements during feeding in fishes. This technique is particularly useful for measurements of hyoid movement since a direct measurement is not possible from light films. Anker *et al.* (1967) have measured bone movements during respiration in the stickleback, but the experimental subject was held in a clamp and filming was only at 42 frames  $\text{sec}^{-1}$ .

Activity in the sternohyoideus starts 5–10 msec after the levator operculi and epaxial muscles have begun to contract, but activity in the epaxial muscles, although elevating the neurocranium does not also elevate the working line of the sternohyoideus as hypothesized by Osse (1969). In fact, the working line of the sternohyoideus has dropped due to retraction and subsequent ventral rotation of the hyoid (Fig. 15:A, B, C). Elevation of the neurocranium does carry the interhyal anterodorsally to a slight degree but the effect of this motion on the hyoid arch is minimal because of the posterior location of the interhyal-hyomandibular articulation on the suspensorium and the highly mobile nature of this joint. By the time the neurocranium has begun to rotate dorsally on the anterior vertebrae of the vertebral column, the hyoid has been partially retracted and pivoted ventrally. The net effect, shown by the angle of the hyoid and the position of the marker just ventral to the sternohyoideus (Fig. 15:B) is that the working line of the sternohyoideus is depressed ventrally and is never raised dorsally even early in the strike.

The force generated by the sternohyoideus during contraction may be resolved into two components acting at right angles to each other. One component, initially the smaller of



the two, is directed ventrally through the hypohyals and acts to depress the hyoid ventrally while the second component is directed posteriorly.

The effect of this component is to retract the hyoid posteriorly during the first half of the feeding sequence (Fig. 15: frames 1, 3, 6). Thus in addition to being carried dorsally by the neurocranium and pivoted ventrally by the ventral component of the sternohyoideus, the hyoid arch is also retracted.

Retraction and elevation of the epiphyal has important consequences for mandibular depression. As noted earlier, depression of the lower jaw may be due to one or more of several couplings. One of these, the sternohyoideus-hyoid-mandible coupling, can only be activated by a caudodorsal movement of the hyoid. The mandibulohyoid ligament, originating dorsally on the epiphyal will not transmit any force to the lower jaw as a result of hyoid depression alone. Retraction and dorsal movement of the epiphyal are essential for the creation of tension in the mandibulohyoid ligament and the transmission of a caudodorsal force to the retroarticular process of the lower jaw.

The mechanical dependence of the sternohyoideus-hyoid-mandible coupling on dorsal and caudal movements of the hyoid suggests an important functional role of the interhyal bone. Hyoid retraction and elevation would not be possible independently of suspensorial movements if the epiphyal articulated directly with the hyomandibular. In the first stages of a strike the suspensorium is carried anterodorsally and thus in a direction opposite to that needed for activation of the sternohyoideus-hyoid-mandible coupling. The interhyal thus permits movement of the hyoid in the opposite direction from that of the suspensorium during the early stages of the feeding sequence.

This analysis predicts that the interhyal will swing posteriorly during the first 50 msec of feeding and only later swing anteriorly as the hyoid moves ventrally or as the geniohyoideus protracts the hyoid.

Maximum ventral movement of the hyoid occurs 5–10 msec after maximum mouth opening has been achieved and corresponds well with sternohyoideus activity (Fig. 11:SH; 14). Hyoid depression is never synchronized with mouth opening and always reaches a maximum after the jaws have begun to close.

#### 10.524 Versatility in the cleithrum-hyoid-mandible coupling

Ekshoud-Oldenhave & Osse (1976) in *Gymnocephalus* and Lauder (1979) in *Hoplias* have suggested that a musculoskeletal coupling between the cleithrum, hyoid, and mandible mediated by the sternohyoideus, hypaxial muscles, and geniohyoideus can either adduct or abduct the mandible depending on the relative positions of the mechanical units. The hypothesized versatility of this coupling is due to a shift in the working line of the sternohyoideus and geniohyoideus muscles from below the quadratomandibular articulation during the middle of a strike to a position above the quadratomandibular articulation when the lower jaw is adducted at the end of the strike.

In *Salvelinus fontinalis*, such versatility in this coupling is highly unlikely, since the working line of the sternohyoideus never rises above the quadratomandibular joint. X-ray cinematography (Fig. 15) reveals that the hyoid remains depressed well after the jaws have closed (Fig. 14) and even in the initial rest position does not allow the working line of muscle action to pass dorsal to the jaw joint.

#### 10.525 Movement of the opercular series

The measurement of opercular series movement (Fig. 11:LOP; 14) is quite complex since high-speed films allow only a two-dimensional analysis while the actual motions take place in three dimensions. The two main motions of the opercular series are levation (dorsal rotation), and dilation (abduction).

Levation of the opercular series occurs in the first 15–20 msec of the feeding sequence. The consequence of levator operculi contraction is a rotation of the operculum around its articulation with the hyomandibular. In brook charr, the muscle fibers of the levator operculi run posteroventrally from the neurocranium to the inner anterodorsal margin of

the operculum (Fig. 4). As a consequence, the operculum is rotated by contraction of the levator operculi and the ventral margin moves posteriorly carrying with it the subopercular and interopercular. The posterior movement of the interopercular is transmitted to the lower jaw by the interoperculomandibular ligament causing jaw depression.

Dilation of the opercular series (Fig. 11:DO; 15) occurs relatively late in the feeding sequence. The maximum value of opercular dilation is reached 5 msec after hyoid depression reaches its maximum and is maintained for about 20 msec, slowly declining to its initial value long after the mouth has closed (Fig. 14). This presumably functions to permit the exit of water captured within the mouth during orobranchial expansion, and facilitates deglutition by allowing the continued flow of water to carry the prey towards the esophagus.

Electrical activity in the dilator operculi (Fig. 11:DO) generally precedes maximum dilation as measured from high-speed movies. Dilator activity begins nearly synchronously with contraction of the sternohyoideus and levator arcus palatini and may overlap the onset of activity in the adductor mandibulae.

The termination of dilator contraction is much more variable than the start; the first electrical activity in the dilator operculi consistently occurring 5–10 msec after the start of levator operculi activity, while the duration of activity depends on the rapidity of the strike and the size of the prey.

#### 10.526 Movements of the suspensorium

Abduction of the suspensorium contributes greatly to the expansion of the orobranchial chamber. Anteroposterior movement of the suspensorium is limited and thus lateral movement is restricted to an axis formed by the joint between the neurocranium and hyomandibular posteriorly and the palatine and neurocranium anteriorly. Lateral movement of the suspensorium is temporally correlated with hyoid depression, the levator arcus palatini firing nearly synchronously with the sternohyoideus (Fig. 11:SH, LAP).

Elevation of the neurocranium during the first 15 msec after the mouth begins to open carries the suspensorium anterodorsally. This results in the quadratomandibular articulation and the suspensorial articulation of the interhyal also being carried anterodorsally and facilitates depression of the lower jaw by increasing the mechanical advantage of the ventral head couplings.

Elevation of the neurocranium and depression of the lower jaw begin the feeding sequence, increasing the gape and initiating water flow into the mouth. This event is followed by a steady increase in hyoid depression and suspensorial abduction which reach their maximum excursion 5–10 msec after peak gape. Opercular dilation reaches a maximum value 10 msec after maximum hyoid depression (Fig. 14). The peak values of each of the major movements contributing to orobranchial expansion thus occur sequentially in a consistent anteroposterior direction and may function to move the low pressure center in the buccal cavity posteriorly. Nyberg (1971) has noted this same phenomenon in the bass (*Micropterus*).

#### 10.53 Movements of the pectoral girdle

The pectoral girdle has been generally ignored in studies of feeding in teleost fishes. Tchernavin (1953) has discussed the pectoral girdle and its contribution to the feeding mechanism of *Salmo salar* and *Chauliodus sloani*, but his analysis was based exclusively on the manipulation of preserved specimens. Similarly, Anker (1974) has suggested possible pectoral girdle movements in *Gasterosteus* and Osse (1969) has considered certain movements of the pectoral girdle of the perch.

High-speed X-ray cinematography of feeding in *Salvinus fontinalis* has allowed direct measurements of the pectoral girdle during feeding (Fig. 2, 15, 16). In general, the pectoral girdle moves considerably less than previous authors have predicted, and, surprisingly, the motion at the beginning of the strike is the opposite of published predictions.

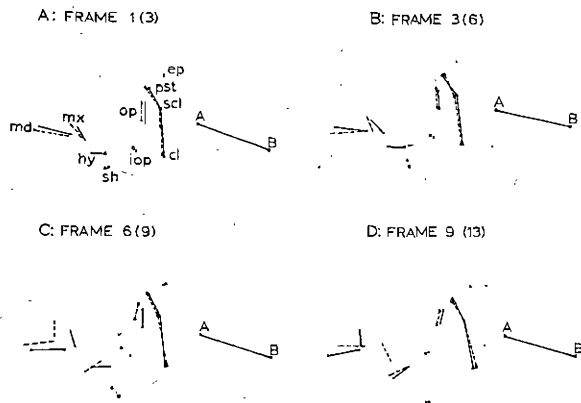


Fig. 15. Movement of the head during feeding in *Salvelinus fontinalis* as determined by high-speed (200 frames  $\text{sec}^{-1}$ ) cineradiography. The lines and the points represent the position of wires and screws implanted in the bones of the head (see Fig. 2). Each diagram shows the earlier position of the bones as solid lines and points, and the position at the later time (the frame number in parenthesis) as dotted lines or open circles. Note retraction of the hyoid between frames 3 and 6, hyoid depression between frames 6 and 9, and the motion of the pectoral girdle. Time between successive frames is 5 msec. Abbreviations: A-B, a line representing the vertebral axis; cl, a screw located in the cleithrum; ep, a lead marker located just dorsal to the epaxial muscle mass; hy, a wire located medially along the ceratohyal; iop, a screw located in the interopercular bone; md, the line formed by the two screws located in the lower jaw; mx, a wire located subcutaneously just lateral to the maxillary bone; op, a line between two screws in the opercular bone; pst, a screw in the post-temporal bone; scl, a screw in the supracleithrum; sh, a lead marker located just ventral to the sternohyoideus muscle mass.

The pectoral girdle is not a single mechanical unit, and since each of the three elements composing the pectoral girdle may exhibit movements at least partially independent of the other two units, the forces potentially influencing the motion of each of the three pectoral girdle bones will first be considered before the *in vivo* motions and patterns of muscle activity are described.

The post-temporal extends lateroventrally from its dorsal articulation with the neurocranium to the supracleithrum. As the neurocranium is elevated during feeding, the post-temporal may be carried dorsally and posteriorly since the point of post-temporal articulation with the neurocranium lies dorsal to the vertebral axis. The large protractor pectoralis (Fig. 7) will act to protract the post-temporal while the epaxial muscles will exert a posterior (retraction) force. Retraction is probably limited by Baudelot's ligament.

The supracleithrum is capable of some motion relative to the post-temporal, although a fairly stiff articulation exists ventrally with the cleithrum. The obliquus superioris protracts the supracleithrum while the epaxial and dorsal hypaxial muscles exert a posterior force.

The cleithrum is subject to the greatest variety of possible influences. The sternohyoideus, obliquus superioris, and the pharyngocleithralis internus and externus (see

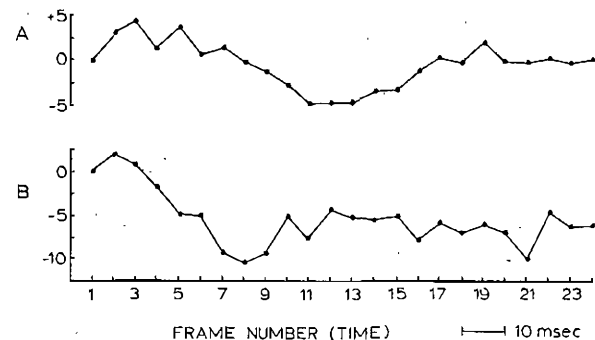


Fig. 16. Graphic representation of pectoral girdle movements during feeding based on measurements from high-speed (200 frames  $\text{sec}^{-1}$ ) cineradiography. A: the angle between the supracleithrum and cleithral markers and the vertebral column. B: the angle between the post-temporal and supracleithral markers and the vertebral column. Positive values indicate protraction, negative values indicate retraction.

Fig. 7) may all aid in protraction. The lateral and ventral hypaxial muscles may cause retraction during feeding. In addition, movements of the pectoral fin produce a constantly changing force on the cleithrum as the water pressure on the fin changes during feeding. The supracleithrum and cleithrum may also be lifted dorsally by elevation of the neurocranium.

The movements of the mechanical units in the pectoral girdle are thus the result of complex interactions between the four main muscles inserting on the girdle and their lever arms. Since all three mechanical units possess two mobile articulations, each unit will exhibit complex movements relative to the other units.

An integration of electromyographic evidence (Fig. 11:EP, SH, PP, HY) with cineradiographic data (Fig. 15, 16) reveals the following pattern of pectoral girdle movement during feeding.

In the early stages of the feeding sequence (Fig. 15:A), the entire pectoral girdle is raised dorsally due to the initial lifting of the neurocranium. Small anterodorsal movements of the two opercular points and the interopercular point corroborate this conclusion. At this stage the cleithrum is also slightly protracted (Fig. 11:PP, SH; Fig. 15).

Protraction of the cleithrum during the early stages of feeding is due to strong activity in the sternohyoideus and obliquus superioris which have just begun to contract. Nearly synchronous antagonistic contractions in the hypaxial musculature prevents large movements of the pectoral girdle and causes retraction of the cleithrum when sternohyoideus and obliquus superioris activity ceases (Fig. 15:D).

The discovery that protraction of the cleithrum occurs during the initial stages of feeding (the first 20 msec) is at complete variance with the suggestions of previous investigators. Both Tchernavin (1953) and Osse (1969) have illustrated the pectoral girdle as initially undergoing retraction as a result of hypaxial contraction. As shown here, the obliquus superioris and sternohyoideus cause protraction in spite of antagonistic activity in the epaxial and hypaxial muscles.

At a slightly later stage in the feeding sequence (Fig. 15:B), as the gape widens and the

prey passes into the orobranchial chamber, the supraclithrum is protracted, moving the post-temporal slightly posteriorly. The cleithrum stays in a relatively stable position until the later stages of feeding when the mouth has begun to close. The stable position of the cleithrum is important for the regulation of hyoid depression since the sternohyoideus will have only one mobile site of action – the hyoid. Fixation of the cleithrum by antagonistic contraction of the sternohyoideus and hypaxial muscles is similar to the fixation of the mandible by the adductor mandibulae while the geniohyoideus acts antagonistically to protract the hyoid.

Towards the end of the initial strike at the prey (Fig. 15:D), the cleithrum is retracted slightly while the post-temporal moves anteroventrally as a result of slight neurocranial depression.

Electromyography of the dorsal fibers of the hypaxial musculature which insert on the upper limb of the cleithrum above the pectoral fin showed very little activity during feeding, while motor units in the ventral midline between the pectoral fins showed consistently high amplitude contractions. The dorsal fibers of the hypaxial musculature are only active during strong swallowing motions. The mechanical advantage of these dorsal fibers is very small compared to that of the hypaxial fibers inserting on the tip of the cleithral symphysis.

Total angular swing of the pectoral girdle during feeding is quite small (Fig. 16). A line between the posttemporal and supraclithral markers only changes ten degrees in any given direction while the cleithral and supraclithral markers swing through only a five degree angle relative to the vertebral column during both protraction and retraction.

These measured movements are quite small compared to those suggested on the basis of anatomical work only. Tchernavin (1953:11–12) states that in *Salmo salar*, "the main ventral part of the shoulder-girdle (...) plays an important role in the process of expansion of the pharyngo-oral cavity, and serves for the insertion of the ventro-lateral and ventral muscles, which pull back the shoulder-girdle and turn it downwards (...). The result of this movement (...) is that the posterior wall of the pharyngo-oral cavity formed by the cleithra and partially by the coracoids, moves backwards and downwards and the pharyngo-oral cavity becomes extended in length and depth." The rather small movements of the pectoral girdle in *Salvelinus* do not agree with Tchernavin's anatomical hypothesis and suggest that the movement of the pectoral girdle has very little to do with expanding the orobranchial cavity directly.

Osse (1969) has hypothesized that in the perch, the angle between the supraclithrum and the cleithrum remains fixed as the pectoral girdle is retracted and that the articulation between the post-temporal and the supraclithrum is the pivot for retraction of the cleithrum-supraclithrum complex. This situation is not the case in *Salvelinus* where the cleithrum may be retracted while the supraclithrum and post-temporal are simultaneously protracted (Fig. 15:D).

### 10.54 Chewing and swallowing

The previous analysis has been exclusively devoted to the initial prey capture and subsequent processing of the food has not been considered. Once the food has been captured, however, it must be manipulated into a position allowing deglutition. In many cases, especially with relatively small prey (e.g. Fig. 1), the initial expansion of the orobranchial chamber apparently serves to bring the prey posteriorly to the opening of the esophagus where it is easily swallowed. In these cases, very little EMG activity or bone movements are observed after the strike. Presumably the prey has been captured and swallowed in essentially one motion.

In many cases, however, the initial strike does not result in complete ingestion of the prey, either because it is too large or the prey is not positioned properly for deglutition. As the prey is positioned and prepared prior to swallowing, jaw movements may occur that are completely different from those seen during feeding. Generally, the initial strike at the prey by brook charr reveals a relatively consistent pattern in which the amplitude

and time course of muscle contraction may change but the sequence of contraction and the basic pattern do not.

Chewing and swallowing motions exhibit an extremely variable pattern of muscle activity in which no single pattern is dominant.

Figure 17 illustrates the pattern of muscle activity during the chewing and swallowing of large prey. Sequence two is extremely similar to a feeding motion, both in duration of muscle activity, the sequence of contraction, and the overall duration (50 msec) of the sequence. The hypaxial muscles and the levator operculi contract almost simultaneously, closely followed by the epaxial muscles, levator arcus palatini, sternohyoideus, and dilator operculi (Fig. 17: HY, LOP, EP, LAP, SH, DO).

There are important differences between this movement of the jaws and the initial strike. The epaxial muscles during the initial strike consistently contract either synchronously with the levator operculi or begin contraction slightly before activity in the levator operculi. During chewing, contraction of the epaxial muscles (and thus neurocranial elevation) is often delayed and may follow activity in the adductor mandibulae (Fig. 17: EP, AM2), a condition that never occurs during the initial strike (Fig. 11: EP). Hypaxial contraction is also greatly abbreviated as compared with the initial strike (Fig. 17, 12: HY).

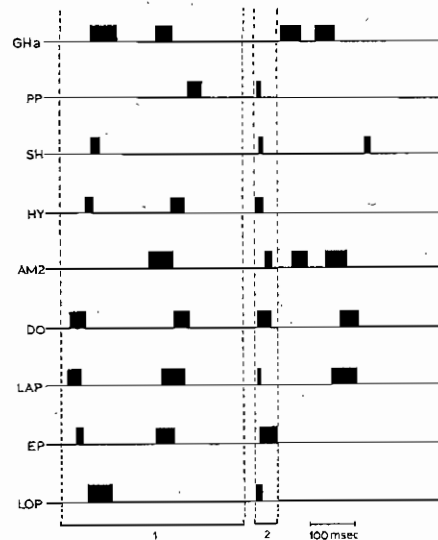


Fig. 17. Diagram of electromyographic recordings of muscle activity in nine cranial muscles during chewing and swallowing in *Salvelinus fontinalis*. The sequences labeled one and two represent patterns of activity respectively dissimilar and similar to EMG activity during feeding. Further discussion in the text. Muscles: AM2, second division of the adductor mandibulae; DO, dilator operculi; EP, epaxial muscles; GHa, anterior division of the geniohyoideus; HY, hypaxial muscles; LAP, levator arcus palatini; LOP, levator operculi; PP, protractor pectoralis; SH, sternohyoideus.

The rapid jaw movements just described are a common pattern during chewing and swallowing. The movements are generally similar to feeding and serve to draw the prey posteriorly and towards the esophagus.

In sharp contrast to these movements are other, less well defined, patterns of muscle activity (Fig. 17: sequence 1). Extreme variability in the sequence of muscle contraction is characteristic of these movements.

One musculoskeletal coupling possibly governing depression of the lower jaw is the cleithrum-hyoid-mandible coupling mediated by contraction of the sternohyoideus, geniohyoideus, and possibly also the hypaxial muscles. This coupling is not activated during feeding as noted earlier because the geniohyoideus shows no activity until after the jaws have closed. During chewing, however, this coupling is activated (Fig. 17: sequence 1: LOP, HY, SH, GHa). Activity in the levator operculi is slightly preceded by contraction of the epaxial and hypaxial musculature. A long period of levator operculi activity then occurs synchronously with contraction of both the sternohyoideus and geniohyoideus. This result conflicts with the conclusions of Ballintijn & Hughes (1966) who state that the geniohyoideus only protracts the hyoid.

The synchronous activity in the geniohyoideus, sternohyoideus, and levator operculi occurs in the absence of antagonistic activity by the adductor mandibulae, and thus it is highly unlikely that hyoid protraction is occurring. This simultaneous activity in the geniohyoideus and sternohyoideus only occurs during chewing and swallowing, never during feeding, and indicates the extreme plasticity of the interactions between the cranial muscles of brook charr during chewing.

The lack of antagonistic contraction in the adductor mandibulae during synchronous activity of the levator operculi, sternohyoideus, and geniohyoideus also illustrates the plasticity inherent in the interactions between the geniohyoideus and adductor mandibulae during chewing. Following the initial strike at the prey, there is often a characteristic double burst of activity that occurs synchronously with activity in the adductor mandibulae. Very similar patterns occur following snapping motions during swallowing (Fig. 17: GHa, AM2 - after sequence 2).

In this case, the geniohyoideus functions to protract the hyoid and return it to its initial position following depression by the sternohyoideus, and may aid in chewing by trapping the prey deep within the orobranchial chamber.

The geniohyoideus may also contract independently of the adductor mandibulae (Fig. 17: sequence 1) and large amplitude adductor activity may occur without corresponding geniohyoideus activity. The ability to separately control activity in these two muscles is entirely responsible for the functional versatility of the couplings between the hyoid and the mandible during chewing.

Several other patterns of muscle activity are distinguishable during chewing and show more regularity than interactions between the adductor mandibulae and the geniohyoideus. Often when chewing and swallowing elongate prey, the levator operculi, hypaxial muscles, and sternohyoideus show nearly synchronous bursts of activity at regular intervals. The time between bursts of activity in these three muscles varies from 200-300 msec but the pattern is generally repeated about every 250 msec for three or four seconds during prolonged swallowing attempts.

The obliquus superioris exhibits two main activity patterns during chewing and swallowing. One pattern is very similar to that seen during feeding (Fig. 17: PP-sequence 2). The other pattern is only observed in chewing and swallowing (Fig. 17: PP-sequence 1), and often alternates with the feeding pattern during prolonged swallowing motions. In the pattern occurring only during chewing, the obliquus superioris contracts almost in isolation, closely following activity in the dilator operculi and the hypaxial muscles. This relatively isolated contraction of the obliquus superioris may function to return the pectoral girdle to its initial position following retraction by the hypaxial muscles.

Osse (1969) in his study of the perch, noted a significant difference between activity in the two divisions of the geniohyoideus muscle. In brook charr, very little difference has been observed between contraction of the anterior and posterior divisions of the geniohyoideus.

## 10.6 Discussion

### 10.6.1 *The pattern of jaw movement in teleost fishes*

Throughout the course of actinopterygian evolution, the adaptive radiation in jaw morphology has been the main defining characteristic of the major levels of adaptation. The diversification of actinopterygians has been accompanied by an increasing complexity of the jaw apparatus with a concomitant increase in the mechanical independence of jaw elements.

In spite of the diversity and importance of the feeding mechanism, little is understood of variations in the basic patterns of jaw mechanics and feeding within the Teleostei. It is particularly important to compare the pattern of jaw movement in generalized primitive predators with that seen in generalized acanthopterygian fishes in order to establish how new functions are integrated into the existing feeding mechanism. The analysis of how a new complex feature is integrated into an existing character complex will provide a clearer understanding of the diversity of teleostean jaw morphology.

The pattern of muscle activity during feeding in brook charr is relatively consistent from one feeding sequence to the next, and the start of mouth opening is easily defined by the large amplitude contractions of the levator operculi, generally synchronous with high activity of the hypaxial and epaxial muscles. A consistent difference has been found between EMG patterns when food is taken from the bottom and from mid-water. In mid-water strikes, the sequence of events occurs more rapidly than in feeding from the bottom and consequently there is greater overlap in the periods of muscle activity. The sequence of muscle contraction is not, however, obscured.

Feeding in the perch (Osse 1969) is quite different from brook charr, particularly with regard to geniohyoideus activity and the events preparatory to and during the initial strike. In perch, a preparatory phase may occur in which the jaw adductors are activated prior to sudden orobranchial expansion at the strike, thus initially decreasing the volume of the buccal cavity. Brook charr never shows adductor activity prior to mouth opening. The sequence of muscle contraction is also different in the perch, where the levator arcus palatini contracts first, followed by the sternohyoideus, geniohyoideus, levator operculi, and then the epaxial and hypaxial muscles. The entire feeding cycle occupies 230 msec. Feeding in brook charr is much more rapid (45-70 msec), and the pattern of muscle activity better defined.

The ruffe, *Gymnocephalus cernuus*, exhibits a similar pattern of muscle activity to that of the perch (Elshoud-Oldenhave & Osse 1976). Feeding lasts 250 msec and the levator arcus palatini is again the first muscle to contract. Geniohyoideus contraction in the ruffe begins significantly before activity in the levator operculi.

Feeding movements in the generalized cichlid fish *Haplochromis burtoni* (Liem & Osse 1975) are highly variable and dependent on the type and location of the prey. A pronounced preparatory phase occurs during which the adductor mandibulae (part two) and both the geniohyoideus anterior and posterior are active. This phase is followed by expansion of the orobranchial chamber through contraction of the levator operculi, levator arcus palatini, and sternohyoideus. The geniohyoideus is not active during the initial phases of orobranchial expansion.

The main difference between the pattern of muscle activity recorded for brook charr and the data presented on percoids and cichlids lie in the preparation for the strike and the initial mouth opening. The brook charr is not primarily a suction feeder, although some suction can be created to draw prey off the bottom, and the EMG pattern reflects this. In *Haplochromis* and *Perca* the levator arcus palatini is strongly active before the levator operculi and the sternohyoideus contract to open the mouth, while in *Salvelinus*, the levator arcus palatini always follows the levator operculi. Early contraction of the levator arcus palatini in percoids may function to create a negative pressure in the buccal cavity prior to mouth opening and decrease the delay between the time the jaws open and the start of water flow into the mouth.

The presence of a preparatory phase and early levator arcus palatini activity in *Perca*,

and *Haplochromis* is related to the suction feeding mechanism. An inference between these fishes and *Salvelinus* is, however, not so easily charted: the geniohyoides is never active during the strike (Fig. 11:GH) as during chewing and swallowing. This is in sharp contrast to the (Osse 1969, Fig. 20) and *Gymnocephalus* (Elishoud-Oldenhave & Osse 1970, Fig. 20) and the geniohyoides actually precedes contraction of the second burst of activity.

Clearly a fundamental difference in jaw opening couplings exists between *Haplochromis* and *Salvelinus*. The geniohyoides in feeding is further complicated by our discovery that the interhyal bone is active during feeding, is active during suction feeding in *Salvelinus* (Fig. 17). The activation of this musculoskeletal coupling is dependent upon activity of the geniohyoides, however, but also upon the activity of the epipharyngeal muscles. In *Haplochromis burtoni* (Liem & Osse 1975, Fig. 8), these exhibit antagonistic contraction of the adductor mandibulae (part of the geniohyoides, while 200 msec later, during the second burst of activity, the adductor adductor contraction.

#### *g mechanics and the evolution of the actinopterygian jaw*

Important aspects of jaw evolution in actinopterygians is the increasing evidence of jaw opening couplings. Not only have multiple functional couplings been identified in the mouth, but these multiple solutions are capable of acting synergistically to increase the efficiency of lower jaw opening independently to regulate events involving the timing of suction feeding. The process through which functional solutions to mouth opening have been achieved is of paramount significance for an understanding of the evolutionary history of the actinopterygian adaptive radiation.

The evolution of the interpercular bone at the halecostome level allowed two distinct functional couplings to control lower jaw depression: the levator opercularis and the adductor opercularis. The levator opercularis and the adductor opercularis are series-mandible coupling and the cleithrum-hyoid-mandible coupling, respectively. The levator opercularis and the adductor opercularis are constrained to use only the ventral head muscles, perhaps in the hypaxial muscles to control lower jaw depression (Schaeffer & Liem 1975). The adductor opercularis is constrained to use the dorsal head muscles to control lower jaw depression (Schaeffer & Liem 1975). The differentiation of the interpercular released the functional constraints on the timing of hyoid depression during the feeding sequence.

The evolution of the interpercular bone at the halecostome and paleoniscoid feeding mechanism has been reevaluated in light of the functional relationships of the hyoid bone in *Amia*. In particular, the important role of the interhyal bone must be reevaluated in light of the functional relationships of the hyoid bone in *Amia*.

The evolution of the actinopterygian jaw. The evolution of the actinopterygian jaw is at least two main functions in the feeding mechanism of fishes. First, the jaw must be able to move in a dorsoventral plane with greater amplitude than otherwise possible. This is achieved by the addition of a link between the hyoid and the suspensorium. This increases the amplitude of the hyoid movement and by increasing the ventral swing of the hyoid (dorsal hyoid movement) and by increasing the ventral swing of the hyoid (dorsal hyoid movement). Secondly, the interhyal allows a posterodorsal movement of the hyoid bone during feeding, when the suspensorium is moving anterodorsally. The evolution of the interpercular bone at the halecostome level allowed two distinct functional couplings to control lower jaw depression: the levator opercularis and the adductor opercularis. The levator opercularis and the adductor opercularis are series-mandible coupling and the cleithrum-hyoid-mandible coupling, respectively. The levator opercularis and the adductor opercularis are constrained to use only the ventral head muscles, perhaps in the hypaxial muscles to control lower jaw depression (Schaeffer & Liem 1975). The adductor opercularis is constrained to use the dorsal head muscles to control lower jaw depression (Schaeffer & Liem 1975). The differentiation of the interpercular released the functional constraints on the timing of hyoid depression during the feeding sequence.

upper branchiostegal ray (e.g. *Amia*) would have served equally well to transmit the posterior hyoid movement to the lower jaw.

The first occurrence of this coupling in the fossil record is difficult to establish due to the small size of the interhyal bone and the lack of attention it is given in the literature. The interhyal is unknown in chondrosteans (Schaeffer 1969, Lehman 1966) and the genus *Opius*, a parasemionid fish of the Lower Triassic, apparently represents the earliest record of an interhyal with a comparable morphology to the interhyal of teleosts (Lehman 1966). A more careful examination of earlier fossils may reveal a similar interhyal in all halecostome fishes. The interhyal bone is an important adaptation for suction feeding since it increases the mechanical independence of musculoskeletal couplings and allows greater expansion of the orobranchial chamber.

The mandibulohyoid ligament, present in charr and many other teleosts (see Verreaux 1977 for a review), *Leptosteus* (Wiley 1976), and *Amia* (Alts 1897) provides a direct connection between the mandible and hyoid. In charr, this allows yet another coupling, the sternohyoideus-hyoid-mandible coupling, to aid in depression of the jaw. Verreaux (1977) has discussed the role of this ligament in respiration and feeding in rainbow trout cleithromyoblasts and alevins. In *Salmo* the mandibulohyoid ligament develops before the interpercular-mandibular ligament and controls respiration and feeding functions in the cleithromyoblasts and alevins.

The exact role of the mandibulohyoid ligament in the evolution of the actinopterygian jaw is unclear. This ligament may have played an important role in depression of the lower jaw in paleoniscoid fishes where a direct connection between the hyoid and the mandible would have greatly facilitated lower jaw depression by activation of the sternohyoideus-hyoid-mandible coupling. Alternatively, the mandibulohyoid ligament may be a primitive character for neopterygian fishes (having been lost in higher teleosts). The sternohyoideus muscle would then have been the prime mediator of lower jaw depression in early neopterygians.

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#### References cited

- Alexander, R. McN. 1967a. The functions and mechanisms of the protrusible jaws of some acanthopterygian fish. *Zool. J. Linn. Soc.* 67: 233-255.
- Alexander, R. McN. 1967b. Mechanisms of the jaws of some teleostiform fish. *J. Zool., Lond.* 151: 233-255.
- Alexander, R. McN. 1969. Mechanisms of the feeding action of a cyprinid fish. *J. Zool., Lond.* 159: 1-15.
- Alexander, R. McN. 1970. Mechanisms of the feeding action of various teleost fishes. *J. Zool., Lond.* 162: 145-156.
- Alts, E. F. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. *J. Morph.* 12: 487-808.
- Anker, G. CH. 1974. Morphology and kinematics of the head of the stickleback, *Gasterosteus aculeatus*. *Trans. Zool. Soc. Lond.* 32: 311-416.
- Amia, *Amia calva*. 1967. An apparatus for direct x-ray cinematography exemplified by anatomical studies of vertebrate joints in *Cor. J. Exp. Biol.* 23: 74-77.
- Ballalain, C. & G. M. Hughes. 1965. The musculature basis of the respiratory pumps in the trout. *J. exp. Biol.* 43: 349-362.
- Basmajian, J. V. & G. A. Stecko. 1962. A new bipolar indwelling electrode for electromyography. *J. Appl. Physiol.* 17: 849.

- Dutta, H. M. 1968. Functional morphology of the head of *Anabas testudineus* (Bloch). Ph.D. Thesis, Univ. Leiden. 146 pp.
- Dutta, H. M. 1975. The suspensorium of *Ctenopoma acutirostre*: a comparative functional analysis with *Anabas testudineus*. *J. Morph.* 146: 457-478.
- Elthoud-Oldenave, M. J. W. & J. W. M. Osse. 1976. Functional morphology of the feeding system in the ruff - *Gymnocephalus cernuus* (L. 1758) - (Teleostei, Percidae). *J. Morph.* 150: 399-422.
- Gans, C. 1969. Functional components versus mechanical units in descriptive morphology. *J. Morph.* 128: 365-368.
- Greene, C. W. & C. H. Greene. 1913. The skeletal musculature of the king salmon. *Bull. Bureau Fisheries* 33: 25-29.
- Greenwood, P. H., D. E. Rosen, S. H. Weitzman & G. S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bull. Am. Mus. Nat. Hist.* 131: 339-456.
- Günther, K. & K. Deckert. 1953. Morphologisch-anatomische und vergleichendökologische Untersuchungen über die Leistungen des Viscerocranial-Apparates bei Tiefseefischen der Gattung *Cyathophone* (Teleostei, Isospondyli). *Z. Morph. Ökol. Tiere.* 42: 1-66.
- Günther, K. & K. Deckert. 1955. Zweiter Versuch einer morphologisch-anatomischen Funktionsanalyse der Nahrungserwerbs- und Atmungsapparate von Tiefseefischen. *Zool. Beitr. (n.ser.)* 1:241-365.
- Kampf, W. 1961. Vergleichende funktionanalytische Untersuchungen an den Viscerocranien einiger raubfische lebender Knochenfische. *Zool. Beitr. (n.ser.)* 6: 391-496.
- Kirchhoff, H. 1958. Funktionell-anatomische Untersuchung des Visceralapparates von *Clupea harengus* L. *Zool. Jb. Anat.* 76: 461-540.
- Lauder, G. V. 1979. Feeding mechanics in primitive teleosts and in the halecomorph fish *Amio calva*. *J. Zool., Lond.* 187.
- Lehman, J.-P. 1966. Actinopterygii. pp. 1-242. In: J. Piveteau (ed.) *Traite de Paleontologie*, Vol. 4, part 3, Masson et Cie, Paris.
- Liem, K. F. 1967. Functional morphology of the head of the anabantoid teleost fish, *Helostoma temminckii*. *J. Morph.* 121: 135-158.
- Liem, K. F. 1970. Comparative functional anatomy of the Nandidae. *Feldiana*. Zool. 56: 1-166.
- Liem, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Zool.* 22: 425-441.
- Liem, K. F. & J. W. M. Osse. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. *Amer. Zool.* 15: 427-454.
- Meijer, N. W. 1975. Cranial motor nerves innervating superficial respiratory muscles in carp (*Cyprinus carpio* L.). *Netherlands J. Zool.* 25: 103-113.
- Nyberg, D. W. 1971. Prey capture in the largemouth bass. *Am. Midl. Nat.* 86: 128-144.
- Osse, J. W. M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.* 19: 289-392.
- Rosen, D. E. 1973. Interrelationships of higher euteleosteans. pp. 387-513. In: P. H. Greenwood, R. S. Miles & C. Patterson (ed.) *Interrelationships of fishes*, Academic Press, London.
- Schaeffer, B. 1969. The origin and basic radiation of the Osteichthyes. pp. 207-222. In: T. Orvig (ed.) *Current problems in lower vertebrate phylogeny*, Almqvist and Wiksell, Stockholm.
- Schaeffer, B. & D. E. Rosen. 1963. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Amer. Zool.* 1: 187-204.
- Tchernavin, V. V. 1948. On the mechanical working of the head of bony fishes. *Proc. Zool. Soc. Lond.* 118: 129-143.
- Tchernavin, V. V. 1953. The feeding mechanism of a deep sea fish *Chauliodus sloani* Schneider. *British Museum (Nat. Hist.)*, London. 99 pp.
- Van Dobben, W. H. 1935. Über den Kiefermechanismus der Knochenfische. *Arch. Neerl. Zool.* 2: 1-72.
- Verraes, W. 1977. Postembryonic ontogeny and functional anatomy of the ligamentum mandibulo-hyoideum and the ligamentum interoperculo-mandibulare, with notes on the opercular bones and some other cranial elements in *Salmo gairdneri* Richardson 1836 (Teleostei: Salmonidae). *J. Morph.* 151: 111-120.
- Vetter, B. 1878. Untersuchungen zur vergleichende Anatomie der Kiemen- und Kiefermuskulatur der Fische. II. *Jenaische Zeitschrift für Naturwissenschaft* 12: 431-550.
- Vrba, E. S. 1968. Contributions to the functional morphology of fishes, part V. The feeding mechanism of *Elops saurus* Linnaeus. *Zoologica Africana* 3: 211-236.
- Wiley, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *Univ. Kansas Mus. Nat. Hist. Misc. Pub.* 64: 1-111.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the teleostei. *Proc. Acad. Nat. Sci. Phil.* 125: 225-317.

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