

ASYMMETRICAL MUSCLE ACTIVITY DURING FEEDING IN THE GAR, *LEPISOSTEUS OCULATUS*

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(Received 20 March 1979)

SUMMARY

Prey capture in the spotted gar, *Lepisosteus oculatus*, was studied by high-speed cinematography synchronized with electromyographic recordings of cranial muscle activity. Muscle activity patterns were recorded during each of the three major phases of feeding: the initial strike at the prey, manipulation of the prey following capture, and swallowing. With one exception, the obliquus superioris, all muscles at the strike are active in a bilaterally symmetrical pattern. During the manipulation phase two distinct muscle activity patterns occur: one is characterized by symmetrical activity in the epaxial muscles and obliquus inferioris, the other by complete asymmetry between the right and left sternohyoideus, obliquus superioris, and epaxial muscles. Low-amplitude manipulatory movements are characterized by activity in one side of the sternohyoideus only, all other muscles being generally inactive. The adductor mandibulae and obliquus inferioris are always active symmetrically. Asymmetrical activity in the sternohyoideus, epaxial muscles, and obliquus superioris correlates with lateral head movements during feeding and acts to rotate prey into the preferred orientation for swallowing. The pattern of asymmetrical activity between right and left side muscles is discussed in relation to previous studies of feeding which utilized only unilateral muscle recordings.

INTRODUCTION

The experimental analysis of the feeding mechanism of fishes has focused increasingly in recent years on the definition of bone movements and associated muscle activity occurring during prey capture. While the important early studies of Alexander (1966, 1967*a, b*) primarily utilized manipulation of preserved specimens and cinematography to examine the mechanics of prey capture, recent investigators have turned to the use of electromyography to determine the timing of muscle electrical activity and its relationship to jaw bone movement (Ballintijn, van den Burg & Egberink, 1972; Elshoud-Oldenhavé & Osse, 1976; Lauder & Liem, 1979; Liem, 1978; Liem & Osse, 1975; Osse, 1969). Without exception these investigators have recorded muscle activity from one side of the head only, and assumed that the rapid (30-300 ms) prey-capture mechanism of fishes would result in bilaterally symmetrical muscle activity. To some extent this assumption is justified by evidence

that the initial strike at a prey is governed by a central nervous system oscillator which elicits a preprogrammed pattern of muscle activity during the strike (Liem, 1978).

The hypothesis that the preprogrammed motor output itself could be asymmetrical has not been considered and only within the last few years have the first bilateral recordings of cranial muscles been obtained (Sibbing, 1976; Liem, 1978; Lauder, 1980).

Liem (1980*a, b*) has recently discovered asymmetries between right and left side muscles in bottom-feeding cichlid fishes. Jaw movements during algae scraping are presumably subject to nearly continuous peripheral feedback and asymmetrical movements of the jaws may allow more efficient algae removal from uneven surfaces.

In this study we report asymmetrical patterns of cranial muscle activity during feeding in the primitive actinopterygian fish, *Lepisosteus oculatus*, the spotted gar. The recorded asymmetries involve not only differences between right and left side muscles, but also between the anterior and posterior portions of the sternohyoideus muscle. The observed asymmetrical activity is associated with specific patterns of prey manipulation prior to deglutition and graphically reveals the dangers of using unilateral muscle recordings to analyze the functional anatomy and mechanics of feeding in fishes.

The generally symmetrical muscle activity pattern at the strike will be considered elsewhere (Lauder, 1980), where a complete electromyographic profile of 13 cranial muscles will be compared with the strike in other primitive actinopterygians (*Amia* and *Polypterus*). We will focus here on the pronounced asymmetrical activity in certain muscles and its functional significance during feeding.

MATERIALS AND METHODS

Fish

Four commercially obtained spotted gars ranging in length from 20 to 30 cm in total length were used for electromyographic and cinematographic studies. All individuals showed the same patterns of asymmetrical muscle activity. Representative specimens have been deposited in the Fish Department of the Museum of Comparative Zoology (MCZ 54289; 54291).

Each fish was confined in a separate 80 l tank and acclimated to laboratory water and temperature (25 °C) over a period of several weeks. All gars were fed live goldfish (*Carassius auratus*) exclusively and food was withheld for up to a week before an experiment.

Electromyography

Fine-wire tin-copper bipolar electrodes (Evanohm S, 0.051 mm diameter, W. B. Driver, Newark, N.J., U.S.A.) were implanted in the cranial and anterior body musculature using the technique of Basmajian & Stecko (1962). Due to the large rhomboid scales and thick layers of dermal bone covering many of the muscles, small (1 mm diameter) holes were drilled through the bone with a dental drill to allow easy access to the muscle surface for electrode implantation. The electrode pairs were colour-coded, glued together, and attached to a small plastic clamp

(visible in Fig. 2), following the procedure of Liem (1978) and Lauder (1980). During implantation the fish were anaesthetized with tricaine methane sulphonate.

For recording sessions the electrode leads were attached to a slip-ring rotating connector located just above the water surface. Electrical signals from the muscles were processed by Gould-Brush high-gain biomedical couplers (sensitivity $1 \mu\text{V}$ per division) and recorded on a Honeywell 5600 tape recorder at 37.5 cm s^{-1} . To facilitate analysis the signals were played back at 4.7 cm s^{-1} – a reduction factor of 8.

A maximum of ten pairs of electrodes were implanted at any one time although only five could be synchronously recorded during an experiment. Within any given experimental session different, but overlapping, sets of muscles could thus be obtained simply by changing leads at the connector. Electrodes were implanted for up to 3 weeks and no deterioration of signal quality over this period was noted.

Cinematography

High-speed film ($200 \text{ frames s}^{-1}$) was synchronized with electromyographic recordings by a special synchronization unit that provided a digital readout and automatic counting of camera frames (see Fig. 2: SYN). A Photosonics 16-1PL high-speed camera and Kodak 4X Reversal and 4X Negative film were used in conjunction with three 600 W Smith-Victor filming lights. More than 100 feeding sequences were analyzed with synchronous electromyograms and high-speed films, while an additional 50 feedings were studied by electromyography alone.

RESULTS

Anatomy

The cranial anatomy of *Lepisosteus* will be described in detail elsewhere (Lauder, 1980), and only the salient features relevant to understanding the functional significance of asymmetrical muscle activity patterns will be considered here. The cranial osteology of *Lepisosteus* has been examined by Mayhew (1924), Patterson (1973) and Wiley (1976), and the most recent accounts of cranial myology are those of Luther (1913) and Edgeworth (1935).

The anterior body muscles are of major importance in asymmetrical movements of the head. The obliquus inferioris (Fig. 1: OBI) consists of hypaxial muscle fibres extending anteroventrally (Winterbottom, 1974) to attach to the cleithrum near its symphysis. There is no fibre continuity between the ventral portion of the obliquus inferioris and the sternohyoideus: these two muscles are completely separated by the pectoral girdle (Fig. 1B: SH, OBI). The obliquus superioris fibres (Fig. 1: OBS) run in a posteroventral to anterodorsal direction and attach to the posterolateral margin of the skull (pterotoc). These muscles effect lateral movements of the head.

The epaxial muscles in *Lepisosteus* attach to the posterodorsal margin of the skull and possess a well-developed tendon on each side (Fig. 1: EPT) which inserts on the skull near the articulation between the supracleithrum and dermopterotoc. There is a median septum dividing the right and left sides of this muscle.

The sternohyoideus originates musculously from the cleithrum and inserts anteriorly on the hypophyals of the hyoid arch. A well-developed internal connective tissue septum divides the entire muscle completely into right and left halves (Fig. 1:

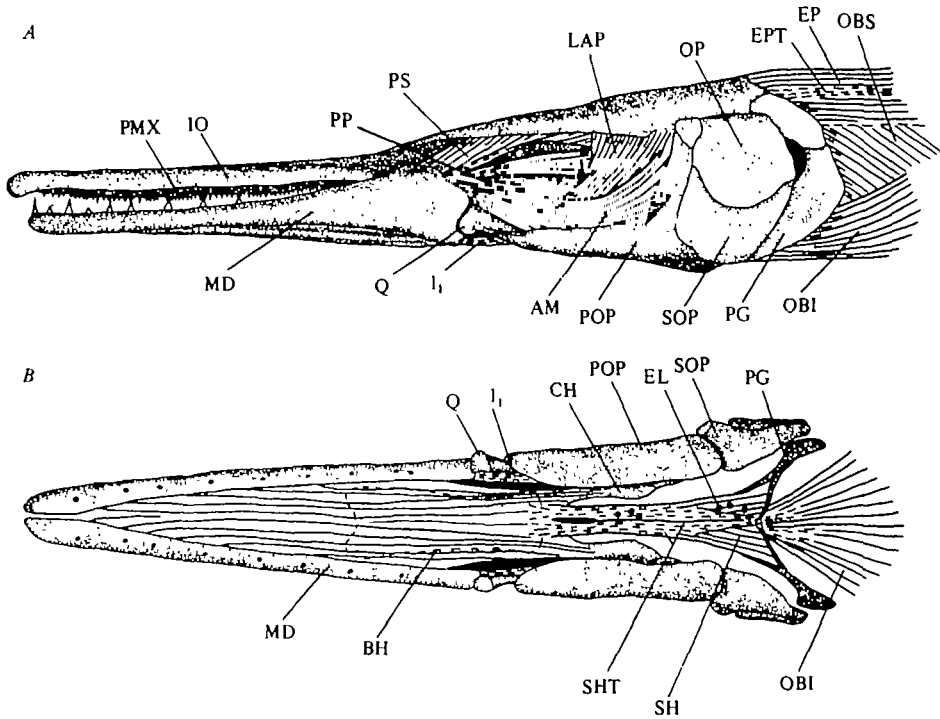


Fig. 1. (A) lateral view and (B) ventral view of the head of *Lepisosteus oculatus*, the spotted gar, after removal of the skin, eye and suborbital bones. Abbreviations: AM, adductor mandibulae; BH, outline of the basihyal; CH, ceratohyal; EL, position of the sternohyoideus electrodes in the anterior and posterior areas of the muscle; EP, epaxial muscles; EPT, lateral tendon of the epaxial muscles; IO, infraorbital bones; I_1 , mandibulohyoid ligament; LAP, levator arcus palatini; MD, mandible; OBI, obliquus inferioris; OBS, obliquus superioris; OP, operculum; PG, pectoral girdle; PMX, premaxilla; POP, preoperculum; PP, PS, so-called preorbitalis profundus and superficialis divisions of the adductor mandibulae (Luther, 1913); Q, quadrate; SH, sternohyoideus; SHT, median vertical septum dividing the right and left halves of the sternohyoideus muscle and the ventral flat horizontal tendon covering the anterior portion of the muscle; SOP, suboperculum.

SH, SHT). Ventrally, the median septum extends over the surface of the muscle in a thick tendinous expansion that runs anteriorly, dividing into two separate fan-shaped insertions on the basihyal. In cross-section the septum and tendon of the sternohyoideus are T-shaped with the ventral median septum extending dorsally.

The adductor mandibulae, the final muscle to be considered here, originates on the posterior aspect of the suspensory apparatus (Fig. 1 A: AM). It extends antero-ventrally, merging into a thin flat tendinous sheath that passes anterodorsally and inserts on the lower jaw dorsal to the quadratomandibular articulation.

Mandibular depression in the gar is initiated by posterodorsal movement of the hyoid apparatus (Fig. 1 B: CH), which exerts a posterior force on the retroarticular process of the lower jaw via the mandibulohyoid ligament (Fig. 1: I_1). Since this force is applied ventral to the quadratomandibular articulation, the mandibular symphysis will rotate ventrally around an axis passing through the quadratomandibular joints. A levator operculi muscle is absent as is the interopercular bone, and thus posterodorsal rotation of the operculum cannot mediate mandibular depression as in teleosts (Liem, 1970; Osse, 1969) and *Amia* (Lauder, 1979).

Table 1. *Bilateral muscle activity patterns during feeding in the gar, Lepisosteus oculatus*

Phase	Muscle	Pattern of activity	Variations	
Strike	Sternohyoideus	Symmetrical*	—	
	Obliquus superioris	Asymmetry in timing	—	
	Obliquus inferioris	Symmetrical	—	
	Epaxial muscles	Symmetrical	—	
	Adductor mandibulae	Symmetrical	—	
Manipulation	Type I	Sternohyoideus	Asymmetry in timing	—
		Obliquus superioris	Asymmetrical†	Asymmetry in timing
		Obliquus inferioris	Symmetrical	—
		Epaxial muscles	Symmetrical	—
		Adductor mandibulae	Symmetrical	—
	Type II a	Sternohyoideus	Asymmetrical	Ipsilateral side activity and/or antero-posterior asymmetry
		Obliquus superioris	Asymmetrical	Ipsilateral side activity
		Obliquus inferioris	No activity	—
		Epaxial muscles	Asymmetrical	Ipsilateral side activity
		Adductor mandibulae	No activity	Low-level activity
Type II b	Sternohyoideus	Asymmetrical	Ipsilateral side activity and/or antero-posterior asymmetry	
	Obliquus superioris	No activity	—	
	Obliquus inferioris	No activity	—	
	Epaxial muscles	No activity	Low-level activity	
	Adductor mandibulae	No activity	Low-level activity	
Swallowing	Sternohyoideus	Symmetrical	Asymmetry	
	Obliquus superioris	No activity	Low-level activity	
	Obliquus inferioris	Symmetrical	—	
	Epaxial muscles	No activity	Low level activity	
	Adductor mandibulae	No activity	—	

* Symmetrical = muscle active bilaterally symmetrically (within 5 ms).

† Asymmetrical = only one side active.

Prey capture

The process of feeding in the gar may be divided into three general phases: the initial strike at the prey, the manipulation of the prey following capture, and the actual swallowing of the prey. Table 1 summarizes the muscle activity patterns during feeding in each of these three phases.

The initial strike at the prey is accomplished by a lateral movement of the head and the simultaneous elevation of the cranium and upper jaw and depression of the mandible. The strike may be extremely rapid (25–30 ms) and all muscles are active in a bilaterally symmetrical pattern with the exception of the obliquus superioris. The obliquus superioris on the side of the head toward the prey is active from 5 to 15 ms prior to its antimere. This asymmetry in timing results in the lateral movement of the head to the appropriate side.

A successful strike results in the prey being held perpendicular to the long axis of the elongate upper and lower jaws (see Figs. 2, 7). Since scale rows in fishes are orientated with the free scale margin facing posteriorly, prey are preferentially swallowed head-first (to reduce resistance from the scales). The posterior inclination of fin rays and spines also necessitates head-first swallowing. In order to be swallowed head-first, the prey must be rotated 90° in either a clockwise or counter-clockwise

direction (in dorsal view). Movements of the head effecting this rotation occur during the manipulatory phase of the feeding sequence and involve complex patterns of muscle asymmetry. In order to simplify the description of manipulatory events, the muscles on the same side of the gar as the head of the prey will be referred to as ipsilateral while muscles on the opposite side will be called contralateral.

Manipulation

Following prey capture a complex series of manipulatory activities occur which are primarily designed to position the head of the prey at the opening to the buccal cavity so that the prey may be swallowed head first. Two distinct movement patterns may be defined in the manipulatory phase with very little overlap between the two.

A Type I movement pattern (Table 1; Figs. 2, 3) involves large-amplitude motions of the jaws and hyoid apparatus and results in large changes in prey location. Type I manipulatory patterns are initiated by contralateral sternohyoideus activity (Fig. 2: SHr) that moves both the jaws and the prey to the contralateral side. Approximately 25 ms later as the head nears the limit of its contralateral swing the jaws begin to open (Fig. 2: frame 5). Mouth opening occurs with synchronous activity in both right and left halves of the sternohyoideus muscle and the obliquus inferioris. As the mouth opens, the head of the gar swings ipsilaterally due to strong asymmetrical activity in the ipsilateral obliquus superioris (Fig. 2: OBS l). Occasionally activity is seen in the contralateral side (Table 1), although it is always delayed until well after the onset of activity in the ipsilateral muscle. The gape is also increased through lifting of the head and upper jaw by the epaxial muscles (Fig. 2: EPr, l). As the mouth opens, the jaws lose contact with the prey (Fig. 2: frame 7) which continues freely in a contralateral direction due to momentum imparted by the initial contralateral head swing. The jaws close on the prey nearer to the head than they were before the onset of mouth opening (Fig. 2: frames 1 and 10). Note that there is a delay of 20–30 ms between the onset of contralateral sternohyoideus activity and the start of mouth opening. This delay is significantly greater than that which occurs during the initial strike (5–10 ms).

The relationship between hyoid depression and gape in a Type I manipulatory pattern (Fig. 3) is similar to that seen during the strike (Lauder, 1980). The hyoid initially undergoes a posterodorsal movement (reflected in vertical measurements of hyoid depression as a small elevation, Fig. 3) which correlates with the onset of mouth opening. Peak depression of the hyoid apparatus occurs after peak gape and the hyoid remains depressed long after the mouth has closed.

If the prey is initially captured near its tail, then several repeated Type I manipulations may be necessary to manoeuvre the head of the prey between the jaws. Generally, however, several (5–10) cycles of the Type II manipulatory pattern occur between Type I movements. Type I manipulatory movements may be defined by the consistent presence of symmetrical activity in the epaxial muscles, symmetrical activity in the obliquus inferioris, and activity in both sides of the sternohyoideus.

In sharp contrast, Type II jaw movements are characterized by nearly complete asymmetry between right and left sides of the sternohyoideus and by the absence of obliquus inferioris activity (Table 1). Two subdivisions of the Type II pattern will be discussed. Type II a manipulations involve asymmetrical activity in the

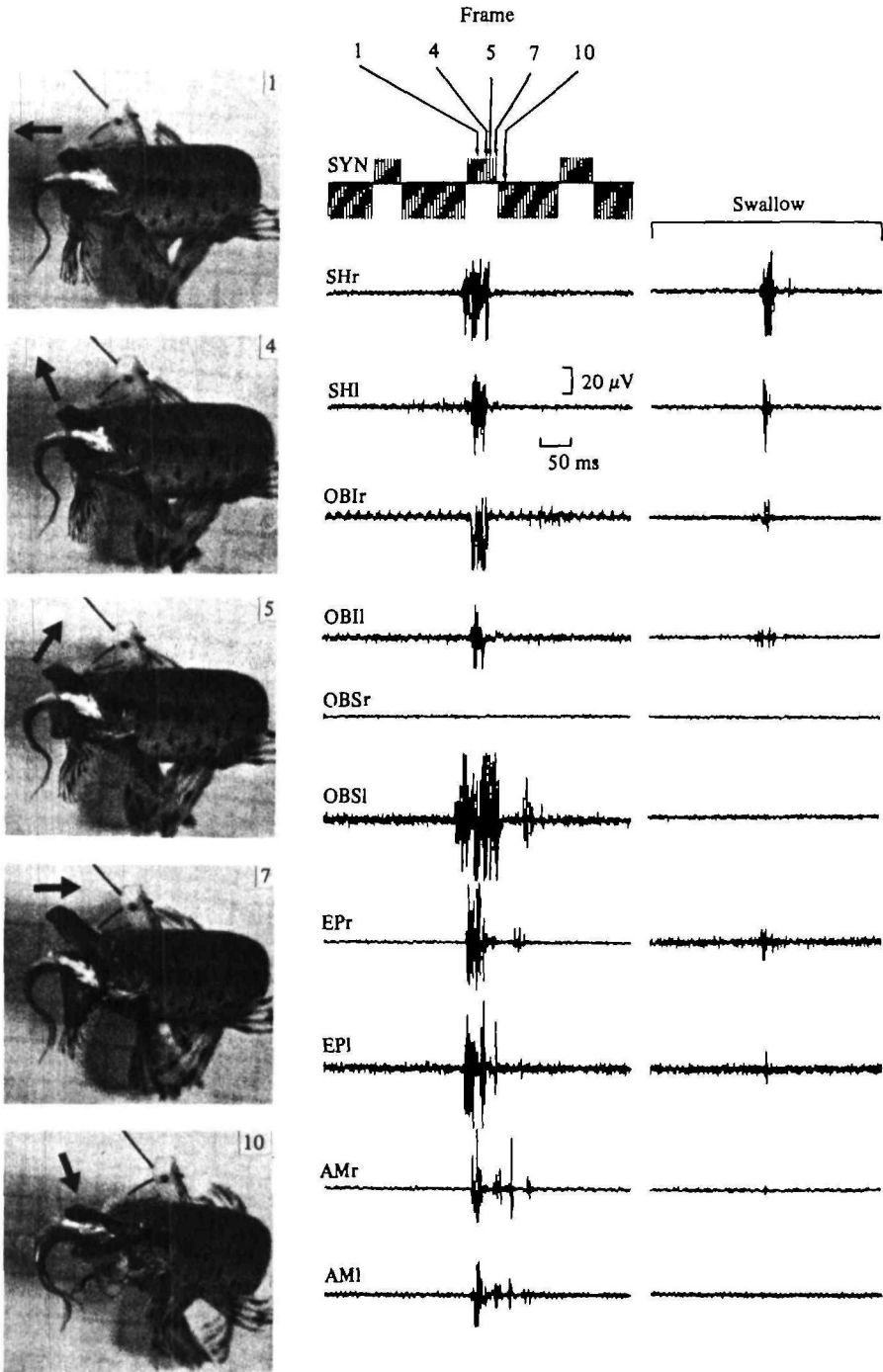


Fig. 2. Pattern of jaw movement and bilateral muscle activity during a Type 1 manipulatory sequence (on the left) and the electromyographic pattern during the swallowing phase (on the right). Synchronization pulses (SYN) provide an exact correlation between the movie frames and electromyograms. r and l indicate muscles on the right and left sides respectively. Arrows indicate the direction of upper jaw movement. Note the asymmetrical activity in the obliquus superioris and the difference in timing (15 ms) between the onset of activity in the right and left halves of the sternohyoideus. For other abbreviations see Fig. 1.

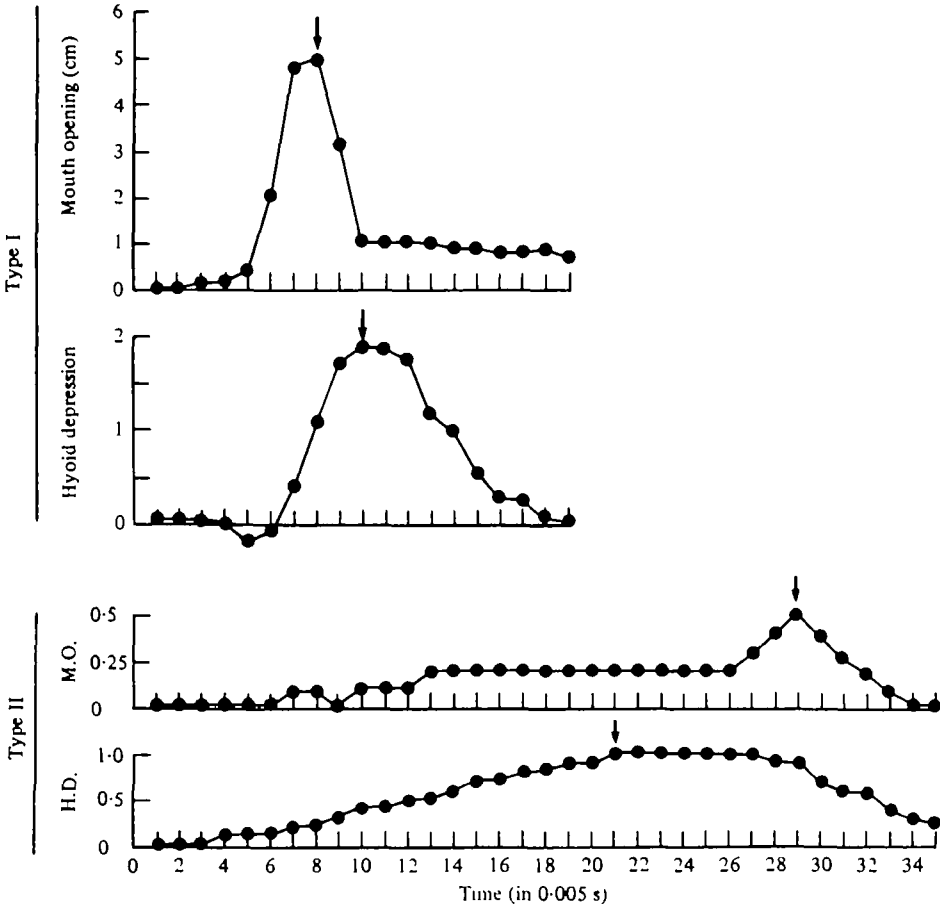


Fig. 3. Graphic representation of the change in gape and hyoid depression with respect to time in Type I and Type II manipulatory patterns. Arrows indicate the position of peak excursion. Note the change in relative timing of peak gape and hyoid depression in Type I and II patterns and the different amplitude and pattern of jaw movement. Scale on the ordinate is relative and does not represent actual excursion.

sternohyoideus, obliquus superioris, and epaxial muscles while in Type IIb all muscles except for one side of the sternohyoideus are generally inactive.

The key feature of Type II activity patterns is the remarkable asymmetry of the two halves of the sternohyoideus muscle. This asymmetry is correlated with the direction in which the prey is rotated from its initial position perpendicular to the jaws.

The general pattern of sternohyoideus asymmetry is shown in Fig. 4. The two sets of experiments, A and B, were conducted within minutes of each other. The only difference between the two is the orientation of the prey in the jaws. Note that in each case the contralateral sternohyoideus is active during manipulation of the prey. Often the ipsilateral sternohyoideus, completely silent at the onset of manipulation, exhibits increasingly strong bursts of activity with each Type II cycle and by the end of the manipulatory phase the sternohyoideus is often symmetrical. The presence of symmetrical activity during the strike and swallowing phases rules out electrode malfunction as a possible source of this pattern.

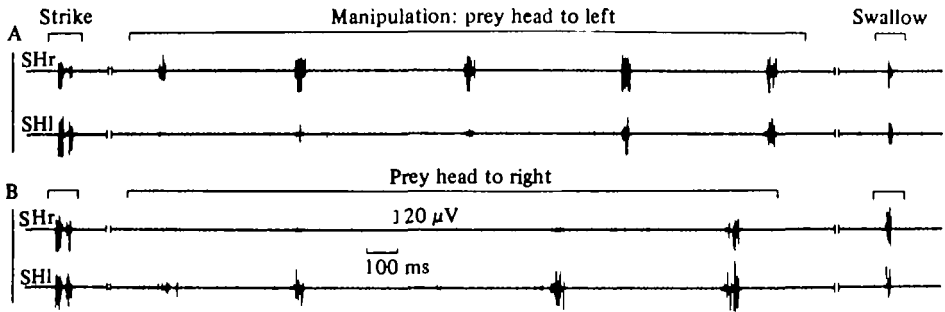


Fig. 4. Asymmetrical activity in the right and left halves of the sternohyoideus muscle during manipulation. Note the symmetrical pattern of activity during the initial strike and during swallowing. Experiments A and B were conducted within minutes of each other under identical experimental conditions. In each case the contralateral half of the sternohyoideus is active (see text).

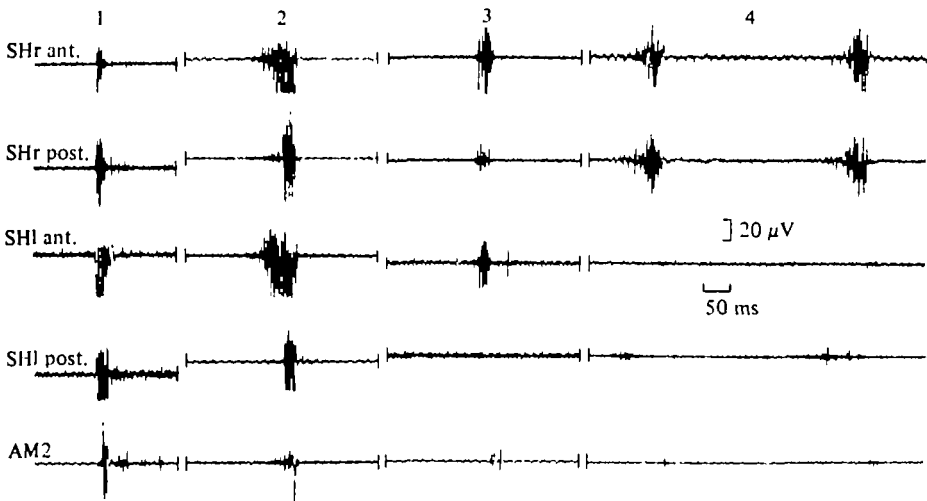


Fig. 5. Patterns of asymmetrical activity in the sternohyoideus muscle. Ant. and post. refer to the anterior and posterior portions of the sternohyoideus (see Fig. 2 for electrode locations). 1, the symmetrical pattern during the initial strike; 2-4, various different electromyographic patterns seen during manipulation. Number 4 represents a common pattern seen during Type II manipulations with complete asymmetry between the right and left sides. Abbreviations as in Fig. 1.

The possibility of anteroposterior asymmetry within each half of the sternohyoideus was investigated by the synchronous recording of two sites, anterior and posterior, within each half of the sternohyoideus (Fig. 1: EL; Fig. 5). A number of basic patterns occurring mostly during Type II manipulations could be defined. Both the anterior and posterior portions of the contralateral sternohyoideus often showed synchronous activity while the corresponding sections of the ipsilateral sternohyoideus were silent (Fig. 5: 4). This represents the 'typical' asymmetrical muscle activity pattern in which only one side is active.

Occasionally incomplete asymmetry occurred, both the anterior and posterior portions of the contralateral side being active with either the anterior or posterior fibres of the ipsilateral side (Fig. 5: 3). Such variability was not detected in other cranial muscles.

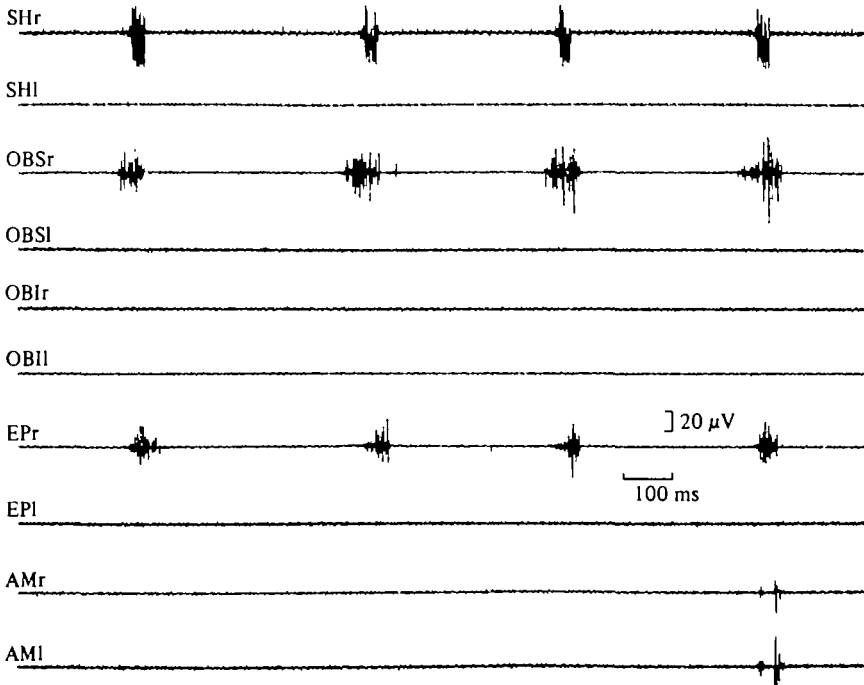


Fig. 6. The electromyographic pattern during Type IIa manipulations of the prey. Abbreviations as in Fig. 1.

In some cases the anterior divisions of both sides were active up to 40 ms before activity in the posterior divisions (Fig. 5: 2). This most often occurred during jaw movements associated with direct posterior movements of the prey toward the buccal cavity. These motions were vigorous and concomitant symmetrical activity occurred in the adductor mandibulae. During the initial strike at the prey all four sections of the sternohyoideus muscle are active synchronously (Fig. 5: 1).

The Type IIa pattern involves asymmetrical activity in the sternohyoideus, obliquus superioris, and epaxial muscles (Fig. 6; Table 1). The contralateral side of all three is active while the ipsilateral side is silent. No activity is detected in the obliquus inferioris muscles. The pattern of jaw movements is very different from the Type I sequence (Fig. 3). Slight depression of the hyoid occurs as the head moves to the contralateral side carrying the prey firmly between the jaws. The mouth then opens slightly (Fig. 3: Type II) and the prey continues to move. Peak gape is significantly less than in Type I movements and is just sufficient to allow free movement of the prey. After the prey has moved contralaterally for 10–15 ms the jaws start to swing back towards the midline while closing on the prey. The net result of one cycle such as this is to move the head of the prey several millimetres closer to the jaws. Return of the gar head to the midline seems to result primarily from elastic recoil in the ipsilateral head muscles since they are all electrically silent during the return swing (Fig. 6). The success of this pattern of manipulation is due entirely to the momentum imparted to the prey during the initial contralateral swing. Usually from 4 to 10 cycles of this pattern are repeated (e.g. Fig. 6), each moving the head of the prey closer to the jaws.

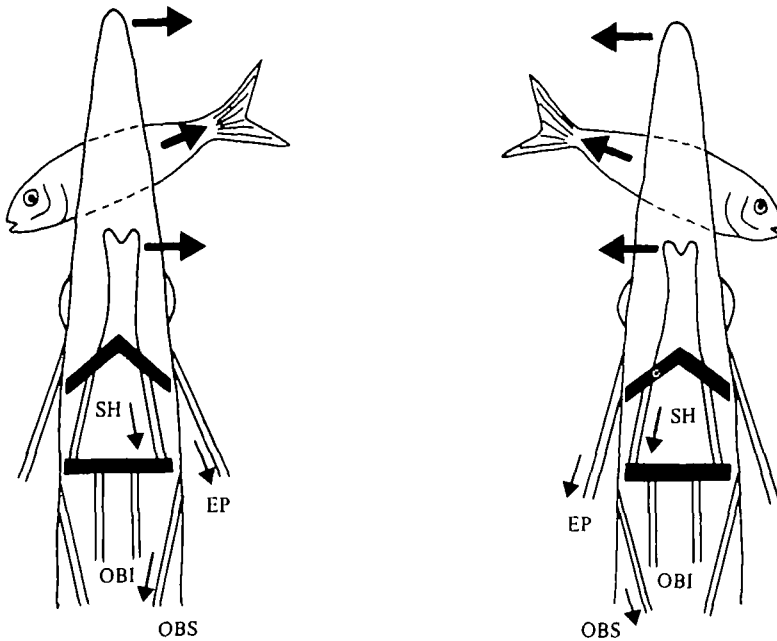


Fig. 7. Schematic diagram summarizing the movement and electromyographic pattern during Type II manipulations. Heavy arrows represent the direction of movement of the prey and head of the gar; light arrows represent contraction of the appropriate muscles as indicated by high-speed films synchronized with electromyographic recordings. The heavy black bar represents the pectoral girdle, the V-shaped bar indicates the position of the hyoid apparatus. Note that the contralateral muscles are active and that although the head of the gar moves in the same direction as the prey, the momentum of the prey actually results in the ipsilateral relative movement of the gar head (see text).

The second pattern of Type II activity, Type IIb, is remarkable in the presence of activity only in the contralateral sternohyoideus muscle: both sides of the obliquus superioris and epaxial muscles are silent. The movement pattern in Type IIb sequences is similar to Type IIa except that the lateral swing of the head is not as great. Electromyographic recordings of Type IIb muscle activities resemble those of Fig. 4, with all other muscles being inactive.

One notable feature of the Type II pattern is the general lack of activity in the adductor mandibulae. Unless the prey is actively struggling or 'crushing' of the prey is occurring, no activity in the jaw adductors is observable during Type II manipulations. Mouth closing seems to occur by elastic recoil in the adductor mandibulae and other jaw closing muscles such as the preorbitalis profundus and superficialis (Fig. 1: PP, PS). No differential activity within the adductor mandibulae was observed.

Both Type IIa and IIb manipulatory patterns also generate rotational movements of the prey which serve to align the prey with the axis of the jaws and orient the prey with the head pointing into the buccal cavity.

The prey is usually positioned at somewhat of an angle to the long axis of the jaws (Fig. 7) and as the contralateral muscles move the head of the gar laterally, the prey rotates about its centre of mass, the tail moving towards the tip of the jaws and the head towards the basihyal. When the jaws close on the prey before returning to the midline, the prey is held in the new position. By repeated Type II movements

which move the head of the prey into a position between the jaws and rotate the prey around its centre of mass, the preferred orientation of the prey for swallowing is achieved.

Swallowing

Swallowing begins when the head of the prey is positioned just anterior to the opening of the buccal cavity and the axis of the prey lies within 25° of the long axis of the jaws. Swallowing occurs very rapidly (30–50 ms) and the prey is usually sucked into the buccal cavity on the first attempt. The head of the gar is held straight and no activity is generally observed in the obliquus superioris, epaxial muscles, or the adductor mandibulae (Table 1; Fig. 2: swallow). Symmetrical activity occurs in the sternohyoideus and obliquus inferioris (Fig. 2) resulting in rapid mouth opening.

Occasionally lateral head movements occur after the prey has been sucked into the buccal cavity. These movements may aid in deglutition, positioning the prey just anterior to the oesophagus and facilitating passage of the prey into the digestive tract. During these lateral head movements asymmetrical activity is seen in the sternohyoideus on the same side as the direction of the head movements.

While the preferred orientation of the prey for swallowing is with the head pointing posteriorly, sometimes swallowing is attempted with the head in the anterior position. If the prey is relatively small, usually deglutition can proceed normally and the food is successfully swallowed. More often, swallowing prey in the reverse orientation is unsuccessful due to the posterior inclination of the scale rows. In these cases a protracted attempt to swallow the prey is followed by ejection of the prey from the buccal cavity. The prey is then rotated a full 180° by a series of Type I and II manipulatory movements before being swallowed head first. Attempts to extricate the prey from the buccal cavity may take up to 10 min.

DISCUSSION

Functional significance of asymmetrical muscle activity

The only published report of bilateral recordings of asymmetrical cranial muscle activity in fishes is that of Liem (1978). Slight asymmetries in timing were found between right and left pharyngeal muscle activity during mastication of prey. Sibbing (1976) recorded bilaterally from carp pharyngeal muscles and found no asymmetrical patterns.

Liem (1980*a, b*) has reported asymmetrical activity in the jaw muscles of algae scraping and invertebrate picking cichlid fishes during relatively slow bottom feeding. The asymmetrical patterns may function to increase the efficiency of prey capture on uneven substrates but a more precise definition of the functional significance of asymmetrical muscle activity patterns is not yet possible.

Slight or even major differences in timing between muscles on opposite sides of the head could be regarded as fabrication noise (Seilacher, 1973), a by-product of the design of an aquatic prey capture mechanism, and not relevant to an analysis of the functional anatomy of the feeding mechanism. However, the pronounced and well-defined pattern of asymmetrical muscle activity in the spotted gar suggests

that bilaterally asymmetrical patterns of muscle activity form an integral part of the prey capture mechanism. Asymmetrical activity patterns may have been overlooked in previous investigations because of a tendency to regard variations from the modal pattern as fleeting and because of 'EMG averaging' often conducted to give a single representative electromyographic profile from many experiments.

The functional significance of asymmetrical muscle activity in the gar is directly related to manipulation of the prey prior to deglutition. Unilateral muscle activity allows lateral movements of the head which in turn permit fine adjustments in prey orientation.

The Type IIb pattern of manipulation involving only one side of the sternohyoideus muscle reveals the complex movement pattern that may be evoked by a single muscle. Unilateral activity in the sternohyoideus results both in lateral bending of the head and slight mandibular depression. Lateral movements of the head are effected by the lateral component of the force exerted on the hyoid apparatus by activity in only one side of the sternohyoideus (Fig. 7). This lateral component results in an ipsilateral bending of the head through about 10° . Only slight mandibular depression is observed during unilateral sternohyoideus activity (Type IIb). This is due to protraction of the pectoral girdle, which accompanies sternohyoideus activity not opposed by concomitant activity in the obliquus inferioris.

These hypotheses of sternohyoideus and obliquus inferioris function were tested by back-stimulation of these muscles via the intramuscular bipolar electrodes with a muscle stimulator. Unilateral stimulation of the sternohyoideus evoked ipsilateral bending of the head and slight mandibular depression. Even bilateral stimulation of the sternohyoideus at tetanic frequencies failed to elicit complete mandibular depression unless the obliquus inferioris was simultaneously stimulated. These experiments demonstrate the key role of antagonistic muscle complexes in regulating the motion of bony elements of the jaw (also see Lauder & Liem, 1979), and confirm that the sternohyoideus may play an hitherto unrecognized role in the feeding mechanism of fishes: mediating lateral movements of the head during prey manipulation.

The pectoral girdle is highly mobile in gars and activity in either the sternohyoideus or obliquus inferioris will result in protraction or retraction of the pectoral girdle respectively. Synchronous activity in both muscles is necessary for complete mandibular depression to occur. This is exactly the pattern observed during feeding: large gapes are only achieved during the strike, Type I manipulatory patterns, and to some extent also during swallowing. Only during these events is the obliquus inferioris muscle active synchronously with the sternohyoideus.

Unilateral stimulation of the epaxial muscles and obliquus superioris also confirmed the role of these muscles in ipsilateral bending of the head.

The clear role of asymmetrical movements of the head during the manipulation of prey by gars and the seeming necessity of such manipulations in long-jawed fishes if prey are to be swallowed head-first suggests that teleost fishes with elongate upper and lower jaws may show similar patterns of asymmetrical activity to those seen in the gar. Several families of teleosts possess highly elongate jaws (e.g. Ctenoluciidae, Ichthyoboridae, Belonidae, Scomberesocidae) capable of wide gapes and having a relatively small opening into the buccal cavity. Such a morphology tends

to place constraints on the size of prey that may be ingested and dictates that prey usually be swallowed head first, necessitating manipulation of the prey once it has been captured between the jaws.

A preliminary analysis of prey capture in *Boulengerella* (Ctenoluciidae) (Lauder, unpublished data), a long-jawed characoid fish, has revealed that while the prey is invariably swallowed head-first after a series of manipulatory movements similar to those of the gar, the manipulations are always of the Type I movement pattern or involve only lateral head bending. Movement patterns never resemble the Type II pattern characteristic of asymmetrical activity in the sternohyoideus. In addition, the initial prey capture does not involve strong lateral movements of the jaws. Rather, the jaws may be opened as the prey is approached head-on and final prey capture is effected by a forward body lunge, not primarily by lateral head movements.

Thus, in *Boulengerella*, prey manipulation does not involve Type II movements. Although more data are needed before the lack of a Type II pattern can be convincingly correlated with obligatory sternohyoideus symmetry, it may be that the lack of a median sternohyoideus septum in teleosts prevents total differential activity between the right and left sides of the sternohyoideus. Asymmetrical sternohyoideus activity has also been noted in *Polypterus* and *Amia* (Lauder, 1980) which also have a median sternohyoideus septum.

Asymmetrical muscle activity in other vertebrates

In a recent review of mammalian mastication, Hiiemae (1977) has noted that despite the wide variety of mammalian dentitions and jaw movement patterns, the electromyographic pattern is remarkably similar within mammals. Only two studies to date have reported complete asymmetry (i.e. total absence of activity in one muscle of a pair) between right and left side muscles. Kallen & Gans (1972) reported complete asymmetry in the medial and lateral pterygoids of the little brown bat and DeVree & Gans (1975) found complete asymmetry between right and left anterior masseters (apple mastication only) and the zygomaticomandibularis (also only during apple mastication). Most other studies have reported asymmetry in the time of onset of activity or in the pattern of activity (e.g. Gorniak, 1977; Herring & Scapino, 1973). The analysis of asymmetrical patterns of activity is often explicitly neglected (Weijs & Dantuma, 1975).

Rosenberg & Gans (1977) reported asymmetrical muscle activity in the jaw muscles of *Sphenodon*. Zweers (1974) recorded unilateral jaw muscle electromyograms in the mallard.

In order to fully understand the patterns and significance of muscle asymmetry in vertebrate feeding mechanisms, variations between right and left side activity must not be ignored and synchronous bilateral recording of muscle pairs is essential. Bilateral asymmetry in vertebrate muscle activity patterns may be widespread.

Neural control of asymmetrical muscle activity

Because of the extremely rapid movements of the jaws during the initial strike by the gar (prey capture occurs in 25–30 ms) it is likely that the pattern of jaw movements is governed by central nervous system outflow that elicits a preprogrammed sequence of muscle activity. During the process of initial prey capture jaw movements are probably not subject to modification by peripheral feedback. A similar

situation occurs during the Type I and II manipulatory movement patterns: each shows a characteristic relatively invariant movement pattern which is presumably governed by a 'pattern generator' in the central nervous system generating the preprogrammed motor outflow.

The frequency with which the Type I and Type II patterns are recruited during manipulation varies greatly between feeding sequences and depends on the position of the prey between the jaws. In addition, as shown above, the specific Type I or II pattern elicited, i.e. right- or left-side asymmetry, depends on the direction of rotation needed to orient the prey so that the head faces posteriorly.

All muscles in the gar that exhibit asymmetrical activity during prey capture are innervated by occipital or spinal nerves. Cranial nerve-innervated muscles in *Lepisosteus* never show asymmetrical activity. This pattern does not occur, however, in cichlid fishes (Liem, 1980a, b) where trigeminal and facial musculature has been shown to exhibit occasional asymmetrical activity.

The choice of which pattern to generate and the frequency of generation must depend on tactile cues, stretch receptors within the jaw muscles, visual cues, or some combination of these. Prey are non-uniform along their antero-posterior axis, varying in squamation, thickness, and compressibility. Thus peripheral receptors (or visual cues; the gar may visually determine the orientation of the prey and thus the needed direction of rotation) may govern the choice of central-nervous-system program. Evidence for the interaction of these peripheral inputs with the motor output awaits electrophysiological and histological studies of proprioception in fishes.

G. Lauder was supported during this study by an NIH Predoctoral Fellowship in Musculoskeletal Biology (5T32 GM077117). We thank the Biology Department, Harvard University, for support as well as the Raney Fund Award of the American Society of Ichthyologists and Herpetologists (to G. Lauder) for partial funding of this research. Karel Liem and William Fink provided many helpful comments on this manuscript. We also acknowledge K. Hartel, A. Coleman, L. Nobrega, D. Kraus and Carolyn Pearson for assistance in the preparation of this paper.

REFERENCES

- ALEXANDER, R. MCN. (1966). The functions and mechanisms of the protrusible upper jaws of two species of cyprinid fishes. *J. Zool., Lond.* **149**, 288-296.
- ALEXANDER, R. MCN. (1967a). The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. *J. Zool., Lond.* **151**, 43-64.
- ALEXANDER, R. MCN. (1967b). Mechanisms of the jaws of some atheriniform fish. *J. Zool., Lond.* **151**, 233-255.
- BALLINTJIN, C. M., VAN DEN BURG, A. & EGBERINK, B. P. (1972). An electromyographic study of the adductor mandibulae complex of a free-swimming carp (*Cyprinus carpio* L.) during feeding. *J. exp. Biol.* **57**, 261-283.
- BASMAJIAN, J. V. & STECKO, G. (1962). A new bipolar electrode for electromyography. *J. appl. Physiol.* **17**, 849.
- DEVREE, F. & GANS, C. (1975). Mastication in pygmy goats, *Capra hircus*. *Annals Soc. r. zool. Belg.* **105**, 255-306.
- EDGEWORTH, F. H. (1935). *The Cranial Muscles of Vertebrates*. Cambridge University Press.
- ELSHOUD-OLDENHAVE, M. J. W. & OSSE, J. W. M. (1976). Functional morphology of the feeding system in the ruff - *Gymnocephalus cernua* (L. 1758) - (Teleostei, Percidae). *J. Morph.* **150**, 399-422.

- GORNIAK, G. (1977). Feeding in golden hamsters, *Mesocricetus auratus*. *J. Morph.* **154**, 427-458.
- HERRING, S. W. & SCAPINO, R. P. (1973). Physiology of feeding in miniature pigs. *J. Morph.* **141**, 427-460.
- HIEMAE, K. M. (1977). Mammalian mastication: a review of the activity of the jaw muscles and the movements they produce in chewing. Chapter 23 in *Studies on the Development and Function of Teeth* (ed. P. M. Butler and K. A. Joysey). London: Academic Press.
- KALLEN, F. C. & GANS, C. (1972). Mastication in the little brown bat, *Myotis lucifugus*. *J. Morph.* **136**, 385-420.
- LAUDER, G. V. (1979). Feeding mechanisms in primitive teleosts and in the halecomorph fish *Amia calva*. *J. Zool., Lond.* **187**, 543-578.
- LAUDER, G. V. (1980). Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morph.* (in the Press).
- LAUDER, G. V. & LIEM, K. F. (1979). The feeding mechanism and cephalic myology of *Salvelinus fontinalis*: form, function, and evolutionary significance. Chapter 10 in *Chars: Salmonid Fishes of the Genus Salvelinus* (ed. E. K. Balon). The Netherlands: Junk.
- LIEM, K. F. (1970). Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Fieldiana, Zool.* **56**, 1-166.
- LIEM, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morph.* **158**, 323-360.
- LIEM, K. F. (1980a). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. Invertebrate pickers of Lake Tanganyika. *J. Zool., Lond.* (in the Press).
- LIEM, K. F. (1980b). Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* (in the Press).
- LIEM, K. F. & OSSE, J. W. M. (1975). Biological versatility, evolution, and food resource exploitation in African cichlid fishes. *Am. Zool.* **15**, 427-454.
- LUTHER, A. (1913). Über die vom N. trigeminus versorgte muskulatur der ganoiden und dipneusten. *Acta Soc. Sci. fenn.* **41**, 1-72.
- MAYHEW, R. L. (1924). The skull of *Lepidosteus platostomus*. *J. Morph.* **38**, 315-341.
- 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.
- PATTERSON, C. (1973). Interrelationships of holosteans. In *Interrelationships of Fishes* (ed. P. H. Greenwood, R. S. Miles and C. Patterson). London: Academic Press.
- ROSENBERG, H. I. & GANS, C. (1977). Preliminary analysis of mastication in *Sphenodon punctatus*. *Am. Zool.* **17**, 871.
- SIBBING, F. A. (1976). Pharyngeal mastication in *Cyprinus carpio* (L.). *Revue Trav. Inst. Pêch. marit.* **40**, 744-745.
- SEILACHER, A. (1973). Fabricational noise in adaptive morphology. *Syst. Zool.* **22**, 451-465.
- WEIJS, W. A. & DANTUMA, R. (1975). Electromyography and mechanics of mastication in the albino rat. *J. Morph.* **146**, 1-34.
- WILEY, E. O. (1976). The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *Univ. Kansas Publ. Mus. nat. Hist. Misc.* **64**, 1-111.
- WINTERBOTTOM, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. natn. Sci. Philad.* **125**, 225-317.
- ZWEERS, G. A. (1974). Structure, movement, and myography of the feeding apparatus of the mallard (*Anas platyrhynchos* L.). A study in functional anatomy. *Neth. J. Zool.* **24**, 323-467.