

Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fishes

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Keywords

Functional morphology, Vertebral column, Suction feeding, Jaw protrusion, Feeding

Synopsis

Luciocephalus pulcher possesses one of the most protrusible jaws known among teleosts, the premaxillae extending anteriorly a distance of 33% of the head length during feeding. Jaw bone movement during feeding proceeds according to a stereotypical pattern and resembles that of other teleosts except for extreme cranial elevation and premaxillary protrusion. Anatomical specializations associated with cranial elevation include: a highly modified first vertebra with a separate neural spine, articular fossae on the posterior aspect, greatly enlarged zygapophyses on the second vertebra with complex articular condyles, and highly pinnate multi-layered epaxial musculature with multiple tendinous insertions on the skull.

Luciocephalus, despite the extreme jaw protrusion, does not use suction during prey capture: rather, the prey is captured by a rapid lunge (peak velocity of about 150 cm per sec) and is surrounded by the open mouth. Previous hypotheses of the function of upper jaw protrusion are reviewed in relation to jaw movements in *Luciocephalus*. Protrusion is not obligatorily linked with suction feeding; behavioral aspects of the feeding process limit the possible range of biological roles of a given morphological specialization, and make prediction of role from structure risky.

Introduction

Luciocephalus pulcher (Gray) is a predominantly piscivorous acanthopterygian fish which has received the attention of ichthyologists (e.g. Alfred 1966, Liem 1967, Sterba 1962, Tweedie 1952, Weber & de Beaufort 1922) because of its specialized ambush strategy during prey capture, its unusual reproductive pattern involving oral incubation, and its ability to breathe air. This primary freshwater

fish possesses a rather restricted geographical distribution inhabiting small, clear streams of the Malaysian peninsula, Borneo, Banka, and Biliton.

The precise phyletic relationship of *Luciocephalus pulcher* has been problematic as reflected in Berg's (1940) classification in which *L. pulcher* is depicted as a monotypic order Luciocephaliformes. Weber & de Beaufort (1922), Gosline (1968) and Nelson (1969) have suggested that *L. pulcher* may be more closely allied to the Anabantoidae than to any other perciform assemblage, although no clearly defined synapomorphies have been offered. Liem (1963, 1967) has shown that *L. pulcher* and the Anabantoidae share the foramen exoccipitale, which does

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not seem to occur in any other teleost. This synapomorphy may indicate that *Luciocephalus* and the Anabantoidei are members of a monophyletic lineage although the former possesses a suite of autapomorphic characters. The caudal extension of the swimbladder and the highly modified first epibranchial bone may represent additional synapomorphies reflecting the phyletic relationship of *Luciocephalus* to the Anabantoidei.

Luciocephalus also possesses one of the most specialized and spectacularly protrusible jaw mechanisms among teleosts (see below, Liem 1967), but, yet, no studies have been made on the feeding behavior, prey capture strategy and jaw movements in live, unrestrained specimens.

This paper is part of an ongoing study on the respiratory and trophic biology of *Luciocephalus*. Here we will focus on the unique prey capture apparatus. Upper jaw protrusion, which is extreme in *Luciocephalus*, has often been incorporated in models on adaptation and optimality in prey capture by acanthopterygian fishes (e.g. Alexander 1967b, Osse 1969, Schaeffer & Rosen 1961, Liem 1970). Because *Luciocephalus* exhibits one of the most protrusible upper jaws among teleosts, the study of its prey capture may furnish us with important data to test the validity of current hypotheses linking upper jaw protrusion with optimization of inertial suction.

Under laboratory conditions, *Luciocephalus* feeds exclusively on live fish. The prediction is that *Luciocephalus* occupies a narrow piscivorous feeding niche, since its behavioral and biomechanical repertoires are stereotypical. Its specialized jaw mechanism (Liem 1967) supports such a notion. This study focuses on the kinematic profile of prey capture and attempts to correlate the osteological and myological specializations with the unusual nature of the kinematics in order to gain a functional perspective on the morphological specializations. We will discuss our findings in the light of current hydrodynamic models and hypotheses of suction feeding in teleosts (Lauder 1980a, 1980c), and describe the behavioral approach and locomotor strategy of the predator.

Materials and methods

Prey capture was studied in two live unrestrained *Luciocephalus* by high-speed cinematography (200 frames per second). A Photosonics 16-1PL high-speed camera was used for cinematography as described previously (Liem 1978, Lauder 1980b). Each strike was analyzed frame by frame with a Kodak Analyst stop-frame projector and measurements made from the projected image with dial calipers.

The two live specimens were obtained from a local aquarium store which imports fishes from Singapore. Only one specimen was dissected for anatomical study (Museum of Comparative Zoology, Fish Department # 54136) because of the scarcity of preserved specimens. Both specimens studied experimentally have been deposited in the MCZ fish collection.

Results

Behavioral observations

When prey is introduced into the experimental aquarium, a slow stalking approach is initiated by *Luciocephalus*. The approach to the prey may be divided into three phases. During the early stages of the stalk, forward motion is accomplished by the pectoral, dorsal, and anal fins only. The body is held straight and the caudal fin is collapsed. Body velocities during this phase range from 1 to 5 cm per second. A second phase is often present and is initiated at a distance of about one body length from the prey. The caudal fin is expanded and undulatory body movements occur resulting in velocities of from 30 to 50 cm per second. At a distance of about 90% of the head length from the prey the final phase is initiated (see Fig. 1, 2) and rapid mouth opening and cranial elevation occur; average velocity during this phase is 130 cm per second.

All strikes are initiated between 87 and 103% of head length distance from the prey and if this strike distance is reached during the first (slow) phase of the stalk, then the second intermediate velocity phase is omitted. These three phases of the prestrike stalk are behaviorally distinct and were present

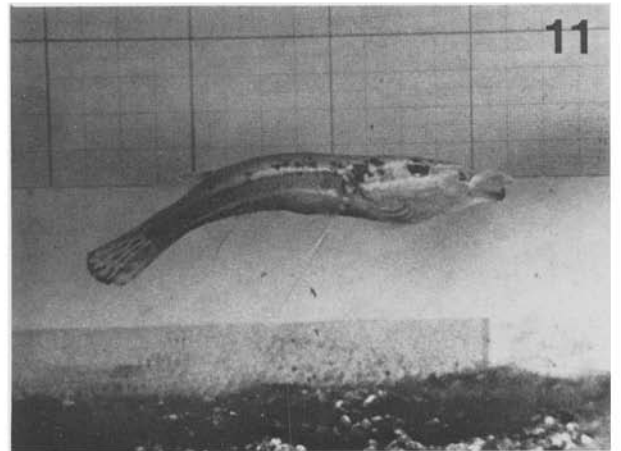
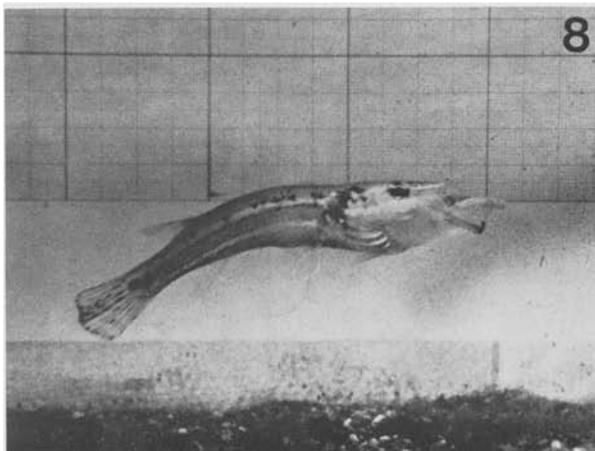
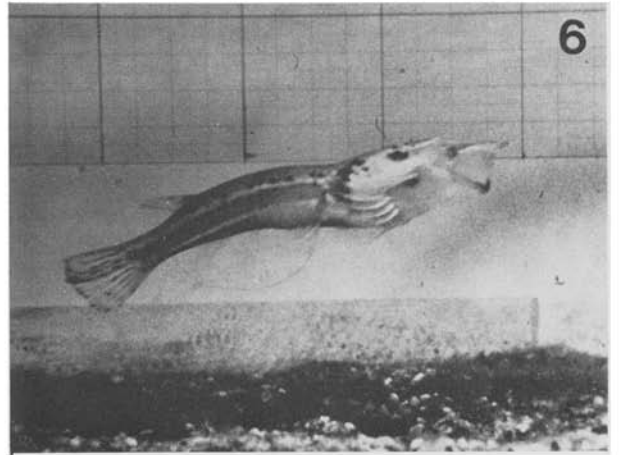
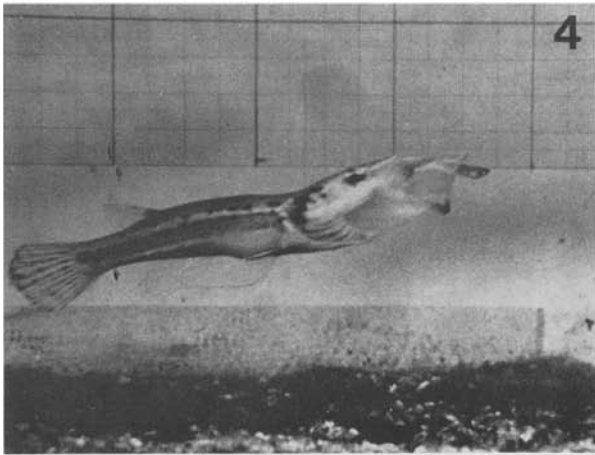
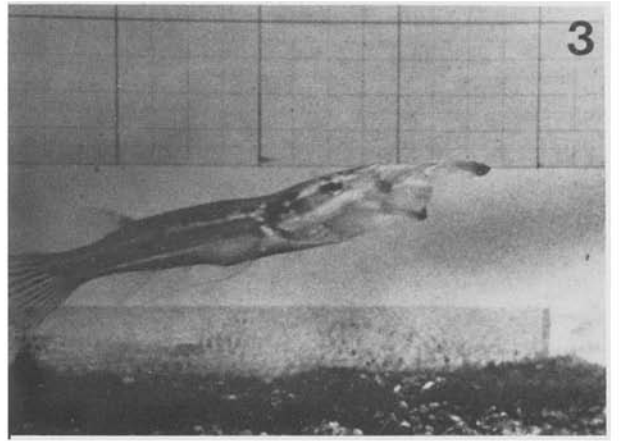
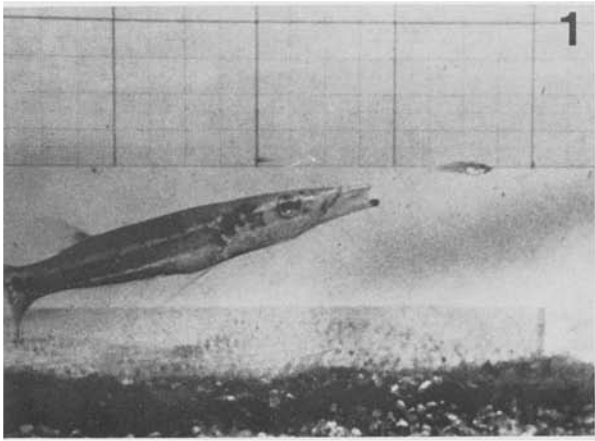


Fig. 1. Frames 1, 3, 4, 6, 8, and 11 printed from a high-speed film of *Luciocephalus* feeding on a guppy (*Poecilia*). Note the movement of the predator and prey relative to the background grid. Time between successive frames is 0.005 sec.

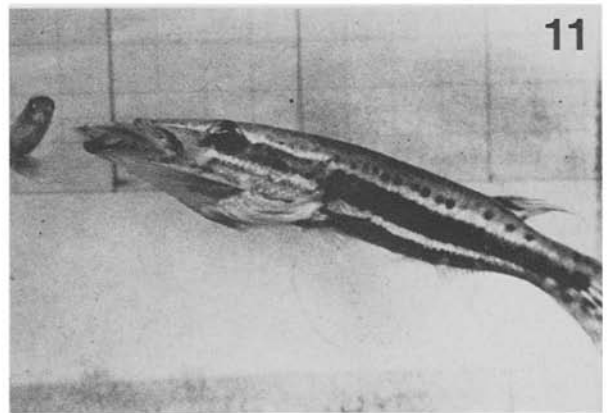
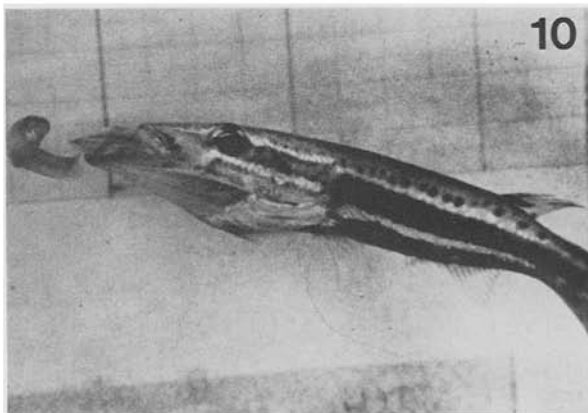
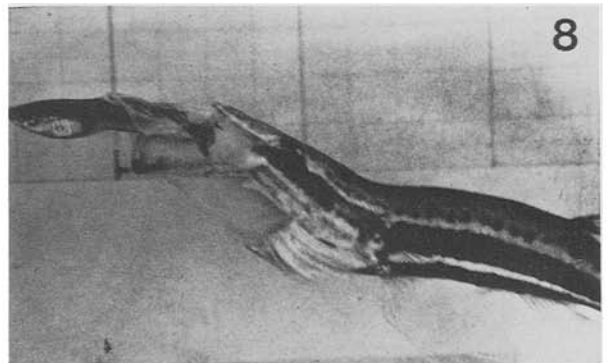
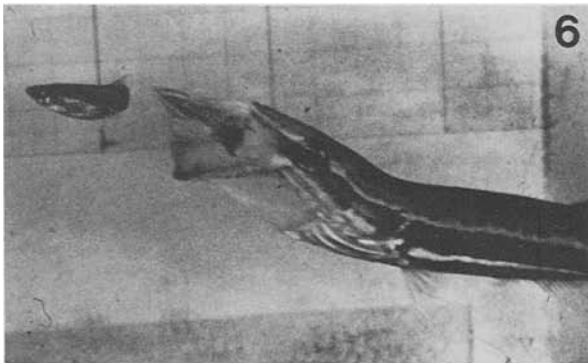
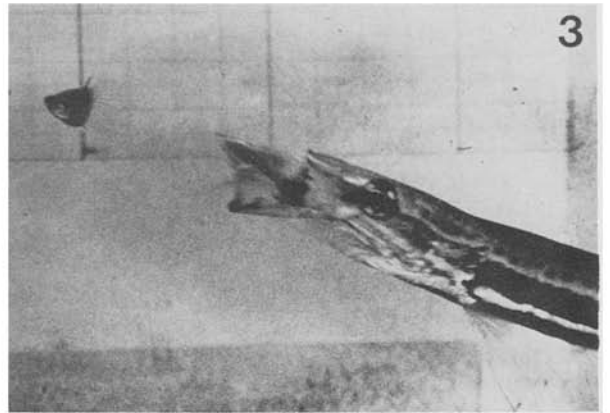
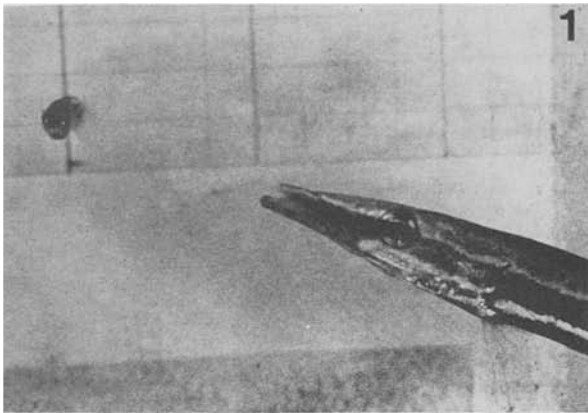


Fig. 2. Frames 1, 3, 6, 8, 10, and 11 printed from a high-speed film of *Luciocephalus* attempting to feed on a guppy. Time between successive frames is 0.005 sec. Note the extreme premaxillary protrusion and cranial elevation. The prey detects the first jaw movements between frames 1 and 3 and a Mauthner-initiated startle response is clearly evident.

both in successful and unsuccessful feedings.

As the mouth closes on the prey during the strike, one or more air bubbles are often seen escaping posterior to the operculum. This air appears to come from the suprabranchial chamber and air inhalation is often initiated shortly after feeding to replace the lost air.

Kinematics

The kinematic profile of jaw bone movement is similar to that of other teleosts with the exception of extreme cranial elevation and premaxillary protrusion during the expansive phase of prey capture. Mouth opening, cranial elevation, upper jaw pro-

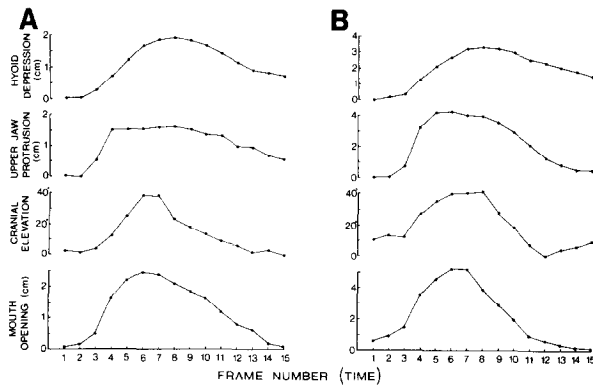


Fig. 3. Graphic representation of mouth opening, cranial elevation, upper jaw protrusion, and hyoid depression versus time during a successful feeding attempt (A) and unsuccessful attempt (B). Scales for all parameters except cranial elevation are relative.

trusion, and hyoid depression all begin within 0.01 sec intervals of each other as the mouth opens (Fig. 1, 3A). The entire strike, expansive plus compressive phases, lasts an average of 0.075 sec. Upper jaw protrusion peaks first (Fig. 3) followed by mouth opening and cranial elevation, and finally by hyoid depression. Cranial elevation peaks at nearly a 40° angle to the axis of the vertebral column (Fig. 3). Mouth opening usually reaches its maximum value before the prey crosses the plane of the mouth during the strike (Fig. 1).

The kinematic profile of unsuccessful feeding attempts is virtually identical to that of successful strikes both in the magnitude of movement and in relative timing (Fig. 2, 3B). The failure of most feeding attempts is due either to the escape response by the prey (Fig. 2) or to inaccurate aiming of the strike by the predator. The kinematic profiles are virtually identical for all feeding attempts.

All strikes were initiated from a distance of between 87 and 103% of head length from the center of mass of the prey, and the mean initiation distance for unsuccessful feedings (95%) was not significantly different from that for successful strikes (87%) as there was considerable variation. The strike initiated at the greatest distance from the prey, 103% of head length, was successful.

Suction feeding

The importance of suction in prey capture by *Luciocephalus* was quantified indirectly by measur-

ing the positions of the prey and predator during feeding relative to a fixed point located between them. In a fish feeding with no suction, the prey will remain stationary relative to a fixed line as the predator uses body velocity to overtake the prey (see Fig. 4A). The other extreme, exclusive use of suction, will result in a stationary predator and movement of the prey into the buccal cavity will occur (see Fig. 4B).

Luciocephalus uses suction only to a negligible degree and relies almost exclusively on body velocity to overtake and surround the prey with the buccal cavity (Fig. 4C). The same relationship holds for unsuccessful strikes although prey escape manoeuvres often result in movement away from the predator (Fig. 4D). The pattern of prey capture in *Luciocephalus* can be put in the 'ram feeding' category (Liem 1980b).

Figure 4E provides comparable data on *Salvelinus* which uses very little suction, and Figure 4F on *Lepomis* which uses suction as it closely approaches the prey.

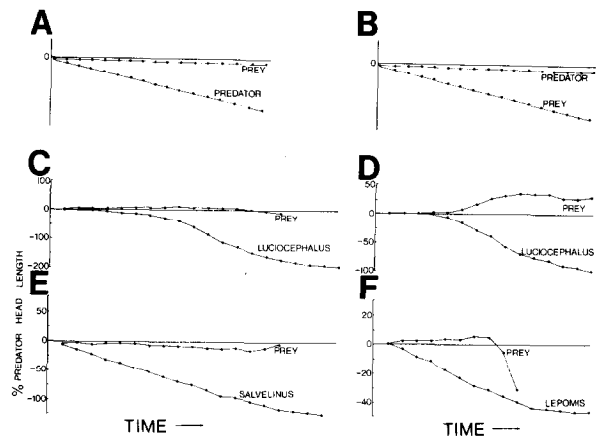


Fig. 4. A, B. Theoretical relationships for relative positions of predator and prey for feeding without suction (A) and with suction (B). Movement of the predator and prey is measured relative to a fixed line (see text). Ordinate scale is in percent predator head lengths. C. relative positions of predator and prey during a successful capture by *Luciocephalus*. D: an unsuccessful feeding attempt by *Luciocephalus*. E: relative positions of predator and prey during feeding by *Salvelinus*, and F, *Lepomis*. Note the similarity between the *Luciocephalus* profile, C, and the theoretical curve for no suction, A. In E, the prey was approached slowly and then rapid suction drew the prey into the buccal cavity of the predator.

Anatomy

Vertebral specializations

The anterior two vertebrae are the only two specialized osteological elements of the vertebral column. The third, fourth, and subsequent vertebrae conform to the generalized trunk vertebra of perch-like fishes.

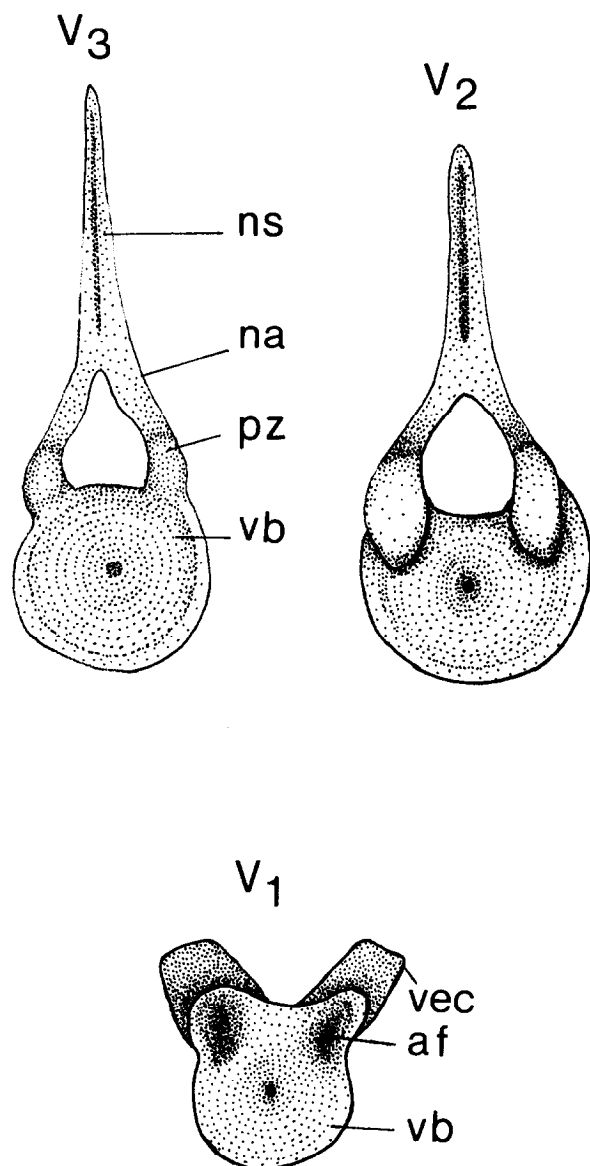


Fig. 5. V_1 , posterior aspect of the first vertebra; V_2 , anterior aspect of the second vertebra; V_3 , anterior aspect of the third vertebra. af, articular fossa; na, neural arch; ns, neural spine; pz, prezygapophysis; vb, vertebral body; vec, process contributing to the vertebral-exoccipital joint.

We describe the third vertebra (Fig. 5: V_3) as representative of the unspecialized configuration. The centrum is equally biconcave. Between successive centra is a compact intervertebral disc with a narrow axial strand that passes through the small channel in the center of the centrum. Strong intervertebral inelastic fibers run between the bony rims of the centra. As in all teleosts a flexible inner intervertebral ligament is present which keeps adjacent vertebrae from telescoping because it is capable of compression on the side of flexion of the vertebral column and subsequent recovery (Francois 1966, Laerm 1976, Symmons 1979). A large and distinct dorsal longitudinal ligament is present and runs posteriorly from the area dorsal to the foramen magnum. The ventral longitudinal ligament is lacking. It has been suggested that the joint between anterior vertebrae is a ring joint; i.e., it works by adjacent vertebral margins moving on a ring (Symmons 1979), allowing movements in both the horizontal (lateral bending) and vertical plane (head lifting). The neural arch and spine are slender structures, with weakly developed pre- and postzygapophyses (Fig. 5: V_3). A pleural rib is associated with the centrum, although no special supporting process for the rib is present.

The first vertebra is greatly modified. The neural spine and dorsal portion of the neural arch are separated from the rest of the vertebra as an independent element between the neurocranium and the second vertebra (Fig. 6: na_1 , ns_1). The elongate centrum is attached very closely to the basioccipital. Because of the strong connective tissue and close adherence between the margins of the basioccipital and first vertebra, movements at this joint are limited. Anterodorsally the first vertebra extends over the basioccipital to reach the exoccipital condyles, thus further anchoring the first vertebra to the skull. The posterior part of the first vertebra is differentiated into a modified joint, with an hypertrophied intervertebral ring. The postzygapophyses are expanded and contain posterodorsally-located concavities, accommodating the greatly enlarged convex articular condyles of the prezygapophyses of the second vertebra (Fig. 5: V_1).

Correspondingly the anterior aspect of the second vertebra is much modified in having large and

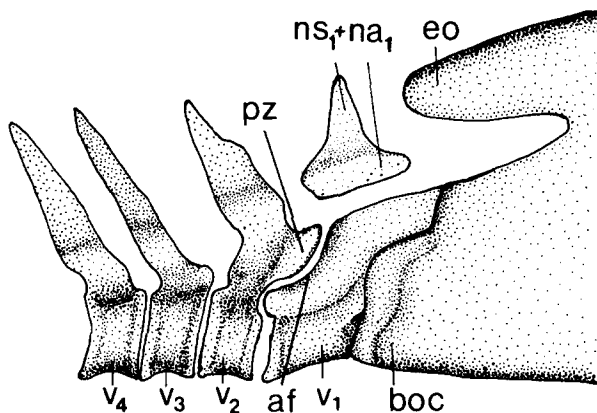


Fig. 6. Lateral view of the right side of the posterior part of the neurocranium and the four anterior vertebrae. af, articular fossa of the first vertebra; boc, basioccipital region; eo, epioccipital region; na₁ & ns₁, neural arch and neural spine of first vertebra; pz, modified prezygapophysis of second vertebra; V₁-V₄, first-fourth vertebrae.

elaborate prezygapophyses (Fig. 5, 6:V₂). The anterior concavity of the centrum is much shallower than the posterior one. Consequently, the distance between the first and second centra is twice as large as that between other adjacent vertebrae. The internal intervertebral ring is hypertrophied and allows considerable movement between the two elements in the sagittal plane. As discussed by Symmons (1979) the internal intervertebral ring, the notochord, and intervertebral discs occupying the cavities between amphicoelous vertebrae in teleosts provide mechanical strength, and resilience to the intervertebral joint. In *Luciocephalus* the internal intervertebral ring is narrow on the lateral sides and thickened on the dorsal and ventral sides. In contrast, the fibrous external intervertebral ring is especially well developed on the lateral sides and thin on the ventral and dorsal sides. Such a configuration of the internal and external intervertebral rings allows bending in the sagittal plane, and reduces lateral bending in the horizontal plane.

The greatly enlarged prezygapophyses of the second vertebra represent a specialized condition. They form distinctly convex articular condyles, with long slopes to move along the corresponding articular fossae on the posterior aspect of the first vertebra (Fig. 9). A well developed articular disc is found between the prezygapophyses of the second vertebra and the articular fossae of the first vertebra. The structural characteristics of this joint seem

to indicate that movement in the sagittal plane could take place while at the same time protecting the spinal cord from excessive bending and constriction. As in all advanced teleosts a ventral longitudinal ligament is absent. However, a dorsal longitudinal ligament is present, attaching anteriorly to the neurocranium in the area dorsal to the foramen magnum. As shown above, the attachment of the first vertebra to the skull is quite rigid, prohibiting movement in any plane. Symmons (1979) has hypothesized that the dorsal longitudinal ligament could provide potential elastic energy during bending of the column. We have not determined whether such a function is present in *Luciocephalus*.

Myological specializations

Anteriorly the epaxial muscle mass in *Luciocephalus* is differentiated into a complicated multiplicity of subdivisions, tendons and aponeuroses.

The most superficial layer is highly pinnate (Fig. 7). Lateral fibers join a superficial tripartite aponeurosis one part of which attaches on the epioccipital process of the skull. The other parts are associated with muscle fibers, which occupy the fossa between the epioccipital process and the posterior process of the supraoccipital bone, and the muscle fibers of the intermediate superficial bundle. The medial bundle of the superficial epaxial muscle possesses two longitudinal aponeuroses running as far back as the seventh vertebra (Fig. 7). Anteriorly the medial aponeurosis joins the middle branch of the tripartite aponeurosis.

The deep epaxial muscles associated with the neurocranium are divided into three subdivisions. The medial and lateral heads are simple, parallel-fibered muscles with fleshy insertions on, respectively, the supraoccipital and exoccipital. The intermediate head is distinctly delineated by peripheral aponeuroses. The posterior fibers of the intermediate head run from the peripheral aponeuroses toward a central tendon, which attaches on the lateral surface of the epiotic process. Joining this tendon are the muscle fibers occupying the post-temporal fossa (Fig. 7).

The complexity of the anterior epaxial muscles of *Luciocephalus* is unusual among teleosts (see

Winterbottom 1974 for the generalized condition) and may be correlated with movements over a wide angle. It is common for multiple aponeuroses, tendons and muscular subdivisions to occur in situations where force must be concentrated on restricted areas, and movements over a wide angle must be executed (see Dullemeijer 1974, pp. 55-60, 139-147). The configuration of the epaxial muscles in *Luciocephalus* seems to indicate that muscle pull

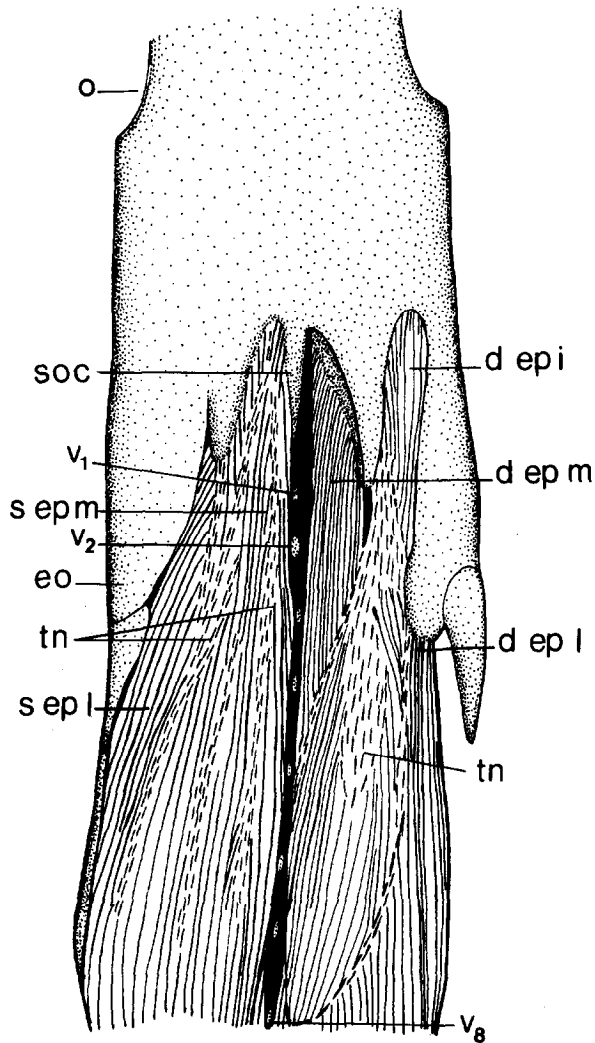


Fig. 7. Dorsal view of anterior epaxial muscles of *Luciocephalus pulcher*. Left half depicting superficial layer; right half depicting muscles after removal of the superficial layer. Tendons and aponeuroses depicted by broken lines. d ep i, intermediate head of deep epaxial muscles; d ep l, lateral head of deep epaxial muscles; d ep m, medial head of deep epaxial muscles; eo, epiotic region; o, orbit; s ep l, lateral head of superficial layer of epaxial muscles; s ep m, medial head of superficial epaxial muscles; tn, tendons and aponeuroses; v₁, v₂, v₈, first, second and eighth neural spines.

is concentrated on several key sites of the posterior neurocranium. The multiple insertion sites are positioned at different angles (Fig. 8) to accommodate the different angles between the neurocranium and the posterior vertebral column.

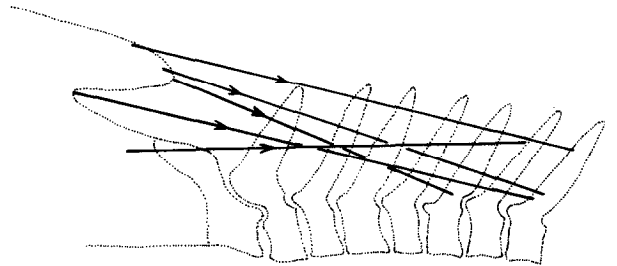


Fig. 8. Diagram depicting the principal directions of forces (heavy lines) of the different heads of the epaxial muscles superimposed on the first 8 vertebrae and posterior part of the neurocranium (dotted lines) as seen from the left lateral side.

Discussion

Prey capture: behavior and kinematics

The kinematics of jaw-bone movement have been studied in a number of actinopterygian fishes in the last fifteen years. Comparisons with previous work (Alexander 1966, 1967a, Lauder 1979, 1980b, 1980c, Lauder & Liem 1980, Liem 1967, 1970, 1978, Nyberg 1971, Osse 1969) reveal that the general biomechanical pattern recorded for *Luciocephalus* is common to many teleosts. Nearly simultaneous peak mouth opening and cranial elevation followed by peak hyoid depression seem to occur in all teleost fishes studied to date. However, in contrast to the variability noted in the kinematic profile of some species which alter the jaw movement pattern in response to the position and type of prey encountered (see Lauder 1981, Liem 1978, 1979, 1980a). *Luciocephalus* possesses an extremely consistent pattern of jaw kinematics that does not depend on the particular attack situation.

Three features of the movement pattern are especially noteworthy: the extreme degree of cranial elevation during the expansive phase (see Fig. 1, 2), the concomitant morphological specializations (Fig. 5, 6, 7, 8), and the pronounced protrusion of the premaxilla. The amount of protrusion in *Luciocephalus* (in proportion to head length) is equal to

the highest values recorded for teleosts (Table 1). A number of genera have been cited as having extremely protrusible jaws – e.g., *Epibulus*, *Leiognathus*, *Gerres*. In none of these cases has the amount of protrusion been quantified experimentally. We note that by manipulating freshly dead specimens, it is possible to cause a much greater degree of jaw protrusion than is ever observed in vivo. For example, experimental observations on *Monocirrhus* (Liem 1970) revealed that maximal protrusion is 33% of head length (Table 1), whereas protrusion of up to 55% of head length was produced by manipulating dead specimens. All values given in Table 1 were obtained from high-speed films of feeding behavior and are thus not comparable with 'in vitro' measurements.

Alexander (1966, 1967a) has noted that in certain acanthopterygians (*Pterophyllum* and *Gasterosteus*) and in some cyprinids (*Leuciscus idus* and *Gobio gobio*) the premaxillae remain protruded as the mouth closes. This does not occur in *Luciocephalus* (Fig. 3) where retraction of the premaxillae is coincident with mouth closure. Lauder (1980c) found in *Lepomis* that during slower feedings on worms, the premaxillae remained protruded as the mouth closed, but during rapid feeding on elusive prey, mouth closure and premaxillary retraction were coincident.

A large number of hypotheses have been adduced during the last twenty years to explain the function-

nal significance of the protrusible jaw, one of the most striking features of many advanced teleost fishes (Liem & Lauder 1981). We review these hypotheses now as a prelude to a consideration of their applicability to *Luciocephalus* with its extreme degree of protrusion.

The most commonly hypothesized function of upper jaw protrusion is that the predator gains an added velocity advantage as the prey is approached (Table 2). The additional velocity of the premaxilla as it rapidly moves toward the prey effectively moves the mouth opening anteriorly resulting in a greater velocity of flow into the buccal cavity at the position of the prey. Theoretical considerations suggest that the velocity of water drawn into the mouth drops off rapidly with increasing distance (Alexander 1967a) and thus the effect of moving the jaws toward the prey could be significant. Alexander (1967b) has questioned the significance of this effect in fishes which protrude their premaxillae less than 10% of their head length (see Table 1). However, in the largemouth bass, where protrusion is about 7% of head length (Table 1), Nyberg (1971) measured an 'additional velocity' due to protrusion of 27 cm per second or 87% of the average attack velocity. In *Luciocephalus* the comparable figures are 51 cm per second and 39%. The added velocity due to protrusion might seem to be an important factor in prey capture by *Luciocephalus* especially since protrusion averages 33% of head length. However, protrusion peaks early in the strike (Fig. 3) and predator body velocity is used to trap the prey in the mouth cavity (strategy one of Alexander 1967a), not suction (Fig. 4). Thus extreme protrusion appears not to be obligatorily correlated with suction feeding, but may be important in ambush predators such as *Luciocephalus* which rely on sudden accelerations from short distances to trap prey.

Most of the other major hypothesized functions of protrusion (Table 2) seem much less likely to apply to *Luciocephalus* and may be of limited generality. Increased hydrodynamic efficiency due to the creation of a circular mouth opening (Table 2: hypothesis 2; Osse 1969) is also common to primitive teleosts which lack protrusion (Lauder 1979). A more rapid closure of the mouth opening was found for *Pterophyllum* and *Gasterosteus* by

Table 1. Amount of premaxillary protrusion in various teleost genera, as determined by high-speed cinematography.

Species	Maximum upper jaw protrusion ¹	Reference
<i>Luciocephalus</i>	33%	this paper
<i>Monocirrhus</i>	33% ²	Liem (1970)
<i>Serranochromis</i>	32% ²	Liem (1978)
<i>Helostoma</i>	13% ²	Liem (1967b)
<i>Micropterus</i>	7% ²	Nyberg (1971)
<i>Zeus</i>	about 25%	Alexander (1967b)
<i>Xiphophorus</i>	15% ²	Alexander (1967c)
<i>Lepomis</i>	17%	Lauder (unpubl.)
<i>Myoxocephalus</i>	25%	Lauder (unpubl.)
<i>Hemitripterus</i>	12%	Lauder (unpubl.)
<i>Perca</i>	12%	Lauder (unpubl.)
<i>Pterophyllum</i>	23% ²	Alexander (1967a)

¹ Expressed as a percentage of head length.

² Values calculated from figures or data presented in the indicated reference.

Table 2. Hypothesized functions of jaw protrusion in teleosts.

Hypothesized function	Reference	Species studied
1) Jaws approach prey more rapidly than without protrusion	Nyberg (1971); also Gosline (1961), Schaeffer & Rosen (1961), Patterson (1964), Alexander (1967b)	<i>Micropterus</i>
2) Hydrodynamic efficiency of mouth opening is increased	Osse (1969)	<i>Perca</i>
3) Aids in gripping prey	Greenwood (1974); also Gosline (1971), Alexander (1967a)	Cichlidae
4) Allows increased suction efficiency	Nyberg (1971); also Alexander (1967a)	<i>Micropterus</i>
5) Allows jaw to close while buccal cavity expanded	Alexander (1966, 1967b)	<i>Leuciscus</i>
6) Allows jaws to close more rapidly	Alexander (1967a, b)	<i>Pterophyllum</i> , <i>Gasterosteus</i>
7) Allows predator's body to remain horizontal while feeding from the bottom	Alexander (1966, 1967a, b)	<i>Gobio</i>
8) Allows functional independence of upper and lower jaw movements	Alexander (1967c)	atheriniforms

Alexander (1967a, b) but Lauder (1980c) found in *Lepomis* that the mouth was closed with protruded premaxillae only in slower strikes. Protrusion may function as an aid in grasping prey (Table 2: hypothesis 3) for bottom feeding or algae-scraping fish because the mouth may be fitted to the substrate and the body may be maintained in a horizontal position during feeding (hypothesis 7).

Finally, an underlying assumption of most current research on advanced teleost feeding mechanics is that protrusion is correlated with increased suction efficiency (an appropriate definition of 'efficiency' might be difficult to agree upon, however) (see Table 2: hypothesis 4). The validity of this assumption depends on the timing and rapidity of buccal expansion relative to the position of the prey. In many fishes with protrusible jaws, prey can be clearly observed as they are carried into the mouth cavity of the predator as a result of buccal expansion (Lauder 1979, 1980c, Liem 1970, Osse 1969). In *Luciocephalus*, however, the prey remains nearly stationary throughout the feeding sequence (Fig. 1, 4; compare the relative positions of predator and prey against the background) despite the enormous jaw protrusion. Protrusion is thus not an obligatory correlate of suction feeding. In this case, the behavior of the predator (initial mouth opening followed later by a rapid forward lunge) limits the potential increase in suction 'efficiency' obtainable by protrusion.

This analysis of *Luciocephalus* emphasizes the difficulty of predicting function from morphology

and the crucial role that behavior plays in determining which potential functions of a structure are realized. Although the extent of jaw protrusion is generally predictable from morphology alone (Liem 1967), only inclusion of behavioral information about the prey capture process allows the conclusion that protrusion in *Luciocephalus* is not correlated with suction feeding. Behavioral features of the feeding process may thus severely limit the possible roles a given morphological specialization may play and make prediction of biological role from structure alone extremely risky.

Comparative anatomical considerations

The anatomical specializations in fishes employing neck bending have received a great deal of attention in recent years (Howes 1979, Lesiuk & Lindsey 1978, Lindsey 1978, Pietsch 1978, Tchernavin 1953).

In the predatory characoid *Rhaphiodon vulpinus*, upward rotation of the head occurs about a pivot between the four anterior fused vertebrae and the fifth vertebra (Lesiuk & Lindsey 1978). The anterior face of the fifth vertebra bears slight convexities on either side which fit into the concave face of the centrum ahead to form a hinge. Force to rotate the neurocranium is probably provided by the massive epaxial muscles pulling on strong cablelike tendons inserted on the pterotic. Lesiuk & Lindsey (1978 p. 997) suggest that *Rhaphiodon* attacks its prey from beneath by bending its head up and that it 'seems well adapted to pulling down prey which is pla-

ning above the surface.'

In the cyprinid *Macrochirichthys macrochirus*, rotation of the skull is accomplished by the action of the elaborate upper section of the epaxial muscle and its associated tendons, and the rotation of the pectoral girdle (Howes 1979). Howes ascribed an important function for the cranial intermuscular bones which appear to form a rigid frame-work.

The precise kinematic profiles of cranial elevation for both *Rhaphiodon* and *Macrochirichthys* are not available. Consequently the biological role of neck-bending in these taxa remains a matter of speculation. *Chela maassi*, an Asian cyprinid, can snap its head back so that the dorsal surface is almost at right angles to the contour of the back (Lindsey 1978, pp. 44–45). This action swings the large pectoral fins downward. According to Lindsey (1978) the pivot for this action is between the first vertebra and skull, and on either side between the upper end of the cleithrum and a large rounded expansion of the transverse processes of the first two vertebrae. Neck-bending in *Chela* is said to be employed as an escape mechanism (Lindsey 1978).

In *Luciocephalus*, neck-bending is an integral part of the prey capture strategy. The underlying structural specializations are found between the first and second vertebrae and the multilayered and multi-tendinous epaxial muscles. The pivot for the neck-bending action is provided by the greatly enlarged prezygapophyses of the second vertebra and deep articular fossae of the first vertebra (Fig. 9). Although neck-bending in *Rhaphiodon*, *Macrochir-*

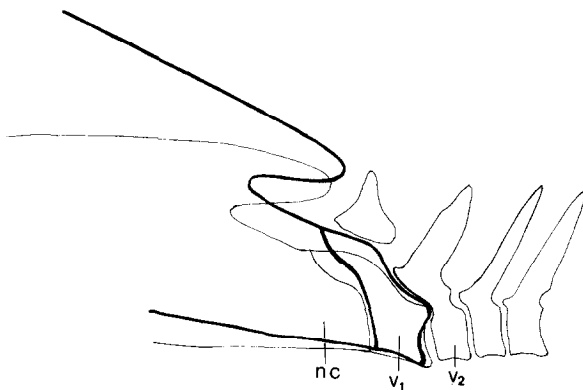


Fig. 9. Diagram of the left side of the anterior four vertebrae and posterior part of the neurocranium in two positions. Light lines express the resting position; heavy line represents position during neck-bending.

ichthys, *Chela* and *Luciocephalus* seems to represent a striking example of convergent evolution, the resemblance is only superficial. In all four genera the epaxial muscles become modified to provide the force causing neck-bending. There is now substantial experimental evidence that the epaxial muscles play a key role in opening the mouth by means of head lifting in primitive actinopterygians (Lauder & Liem 1980, pp. 376–377). In more advanced actinopterygians the epaxial muscles retain their original role of head lifting during the expansive phase of the prey capture cycle (e.g. Osse 1969, Liem 1978) and gain an important new role in providing one of the multiple kinematic pathways by which upper jaw protrusion is realized in some acanthopterygians (Liem 1979, 1980a).

The osteological specializations in the neck-bending apparatus are seemingly more drastic than the myological ones. In *Luciocephalus* the prezygapophysis of the second vertebra becomes enlarged to form the principal pivoting device during neck-bending (Fig. 6, 9). Judging from published literature such a morphological specialization is not duplicated in any other group of teleosts. The osteological modifications of the other neck-bending teleosts involve different vertebrae, the pectoral girdle, ribs and skull. There thus appear to be multiple morphological patterns which are related to the function of neck-bending in teleosts.

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