# Terrestrial feeding in the Mudskipper *Periophthalmus* (Pisces: Teleostei): A cineradiographic analysis

DEBRA L. SPONDER AND GEORGE V. LAUDER*

*The Museum of Comparative Zoology, Harvard University,
Cambridge, MA 02138, U.S.A.*

(With 2 plates and 4 figures in the text)

Mudskipping gobies (Periophthalminae) are among the most terrestrial of amphibious fishes. Specializations associated with terrestrial prey capture and deglutition have been studied in *Periophthalmus koelreuteri* by light and X-ray cinematography which permits direct visualization of pharyngeal jaw movement during deglutition. Anatomical specializations of the pharyngeal jaws are described and include depressible teeth, a large ventral process on ceratobranchial five, and muscular modifications.

Multiple terrestrial feedings occur by *Periophthalmus* without a return to the water, and cineradiography reveals that the buccal cavity is often filled with air during terrestrial excursions in contrast to some previous hypotheses. Transport of the prey into the oesophagus occurs primarily by anteroposterior movement of the upper pharyngeal jaw. The lower pharyngeal jaw plays a limited role in food transport and may serve primarily to hold and position prey. The bite between upper and lower pharyngeal jaws occurs between the anterior teeth, and both jaws are protracted together during raking of food into the oesophagus. Functional specializations correlated with terrestrial feeding include obligatory use of pharyngeal jaws for swallowing even small prey items and positioning of the prey in the pharynx by pharyngeal jaw and hyoid movements alone.

This analysis of terrestrial feeding allows hypotheses of design constraints imposed by the aquatic medium on fishes to be raised and tested.

## Contents

## Introduction

The mudskipping gobies of the subfamily Periophthalminae are among the most terrestrial of known amphibious fishes. They inhabit the areas in and around the mangrove swamps and intertidal regions of Africa, Asia and Australia. *Periophthalmus* migrates up and down across the intertidal zone with the tide and rarely penetrates the water to any

*Present address: Department of Anatomy, University of Chicago, 1025 East 57th St., Chicago, Illinois 60637, U.S.A.

depth. Some species spend over 90 % of their time on dry land although they make frequent brief sorties into the water (Gordon *et al.*, 1969, 1978).

Physiological modifications relating to the amphibious habit have been studied extensively over the last decade. Ammonia and urea metabolism have been examined (Gordon *et al.*, 1969, 1978; Gregory, 1977; Morii, 1979; Morii *et al.*, 1978, 1979), as has vision (Graham, 1971) and cutaneous and branchial respiration (Harms, 1929; Schottle, 1932; Willem & Boelaert, 1937; Teal & Carey, 1967; Singh & Munshi, 1968; Tamura *et al.*, 1976; Graham, 1976). Gill area is apparently inversely related to buccopharyngeal surface and the proportion of time spent on land (Schottle, 1932).

Feeding by mudskippers can occur either in water or on the land but *Periophthalmus* appears to primarily seek food out of the water (Kyle, 1926; Hora, 1935; Stebbins & Kalk, 1961; Macnae, 1968; Gibson, 1969; Gordon *et al.*, 1969; Polunin, 1972). Prey detection occurs chiefly if not entirely by sight (Stebbins & Kalk, 1961) and all mudskippers have excellent vision in air as a result of a strongly curved cornea and a flattened lens; underwater the lens cannot form a clear image on the retina and mudskippers are hyperopic (Graham, 1971).

Species of *Periophthalmus* appear to differ in their ability to remain out of water following prey capture. Some investigators have noted that once the water in the buccopharyngeal cavity is lost as a result of feeding, the fish must return immediately to the water (Stebbins & Kalk, 1961; Macnae, 1968; Polunin, 1972; Gordon *et al.*, 1978). Gordon *et al.* (1978) found that *P. cantonensis* ". . . definitely carries small volumes of water about with it in its buccal cavity, during excursions on dry land. The loss of this water . . . seems to be one of the main stimuli prompting the fish to make contact with liquid water . . .". Yet, in another species, *P. sobrinus*, there was very little water carried in the buccopharyngeal cavity on land and there appeared to be no correlation between the timing of visits to the water and feeding activities (Gordon *et al.*, 1969).

In this paper the terrestrial feeding behaviour of *Periophthalmus koelreuteri* in the laboratory with light and X-ray cinematography is examined. Studies on the mechanics of feeding in other amphibious fishes are in progress by D. Sponder. Our goals here are (1) to determine if water is held in the buccal cavity during terrestrial excursions and if water is necessary for either deglutition or initial prey capture, (2) to study the feeding mechanism of a fish not using the inertial suction feeding process common to nearly all teleosts (Lauder, 1979, 1980*a*; Liem, 1978), and (3) to compare the mechanics of pharyngeal jaw movement during deglutition with models formulated by Liem (1970), Karrer (1967), and Kayser (1962). X-ray cinematography allows direct observation and measurement of interior bone movements and permits a precise test of mechanical models. Finally (4), previous analyses of aquatic feeding behaviour in fishes have not assessed the constraints or limitations imposed by the aquatic medium on patterns of prey capture and manipulation. What role does a high density medium play both in determining the range of functional solutions to problems of prey capture, and as an element in the feeding process itself? These questions can be approached in the context of highly modified systems such as terrestrial feeding in which the constraints are greatly altered.

## Materials and methods

High-speed cinematography at 100 frames per second was used to examine the basic pattern of feeding behaviour on land (Plate II(a)). A Photosonics 16 mm 1PL camera was used in conjunction

with three 600 W Smith Victor filming lights and Kodak 4X Reversal film. A total of 30 sequences were analysed frame by frame on a Kodak Analyst projector. Sequences were recorded using shrimp (*Euphausia*), goldfish (*Carassius auratus*), squid (*Loligo*), and earthworms (*Lumbricus*) as food.

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 80–100 frames per second (Plate II(b)). Camera speed during each experiment was calibrated with an oscilloscope. Kodak Plus-X Reversal film was exposed at 120 mA and 38 kV. Two filming setups were used: (1) The fish were placed in a covered narrow plexiglass box and all water was removed, (2) a large rock for terrestrial excursions was placed in the centre of a 40 l plexiglass box containing 10 l of water. Both earthworms filled with a mixture of barium and milk of magnesia, and shrimp were used as food. Over 40 sequences of pharyngeal jaw movement have been analysed.

Two commercially purchased specimens of *Periophthalmus koelreuteri* were used for the experiments. Multiple experiments were conducted on healthy specimens kept under laboratory conditions over a period of 9–11 months. The fish were held in aerated, filtered 80 l aquaria (27°C, specific gravity of the water was 1·005) with dry areas above the water for terrestrial sojourning.

Scanning electron micrographs of the pharyngeal jaws of *Periophthalmus koelreuteri* (MCZ Fish Department number 54404) and one of the experimental fish (MCZ 54517) were taken to aid interpretation of jaw movements from the X-ray films (Plate I).

## Results

### Anatomy

The general anatomy of the pharyngeal jaw apparatus will be described as a basis for interpreting the subsequent movement analysis.

The principal bony elements that comprise the upper pharyngeal jaws (Fig. 1(b), UJ) are the second, third, and fourth pharyngobranchials, and these elements are firmly attached to each other by connective tissue. The right and left upper pharyngeal jaws are independent structural units and may function as separate mechanical systems. There are no articulations between the skull base and the upper pharyngeal jaws which are free to slide anteroposteriorly as a result of muscle action (Fig. 1(b), UJ).

The lower pharyngeal jaws consist of left and right fifth ceratobranchials which are closely tied to each other in the midline by strong connective tissue (Fig. 1(b), LJ). The lower jaw complex functions as one mechanical unit, and although the lower jaws are attached anteriorly to the basibranchial elements of the branchial basket, its movements are relatively independent. A prominent process extends ventrally from each lower jaw (Fig. 1(b), LJ; Plate I(e)) and serves as the insertion for the pharyngohyoideus and pharyngocleithralis internus muscles (Fig. 1, PH, PCI). These two muscles respectively mediate protraction and retraction of the lower pharyngeal jaws. The ventral process varies considerably in size and shape among individuals. The pharyngocleithralis externus extends posteroventrally from its insertion on the lateral edge of the fifth ceratobranchial to take origin from the pectoral girdle (Fig. 1, PCE). Another muscle originates from the ventral limb of the pectoral girdle near the cleithral symphysis to insert on ceratobranchial three. We consider this muscle possibly to represent a ventral subdivision of the pharyngocleithralis externus (Fig. 1, PCEV) although its homology is by no means well established.

The dorsal branchial muscles of interest here are the levatores externi, the levator posterior, and retractor dorsalis (Fig. 1, LE, LP, RD). The levatores externi extend postero-ventrally from the otic region of the skull to insert on the epibranchials (Fig. 1(b), UJ) while the retractor dorsalis governs upper jaw retraction. A small adductor arcus branchi-alum approximates the posterior aspects of the upper and lower jaws (Fig. 1, $AD_5$).
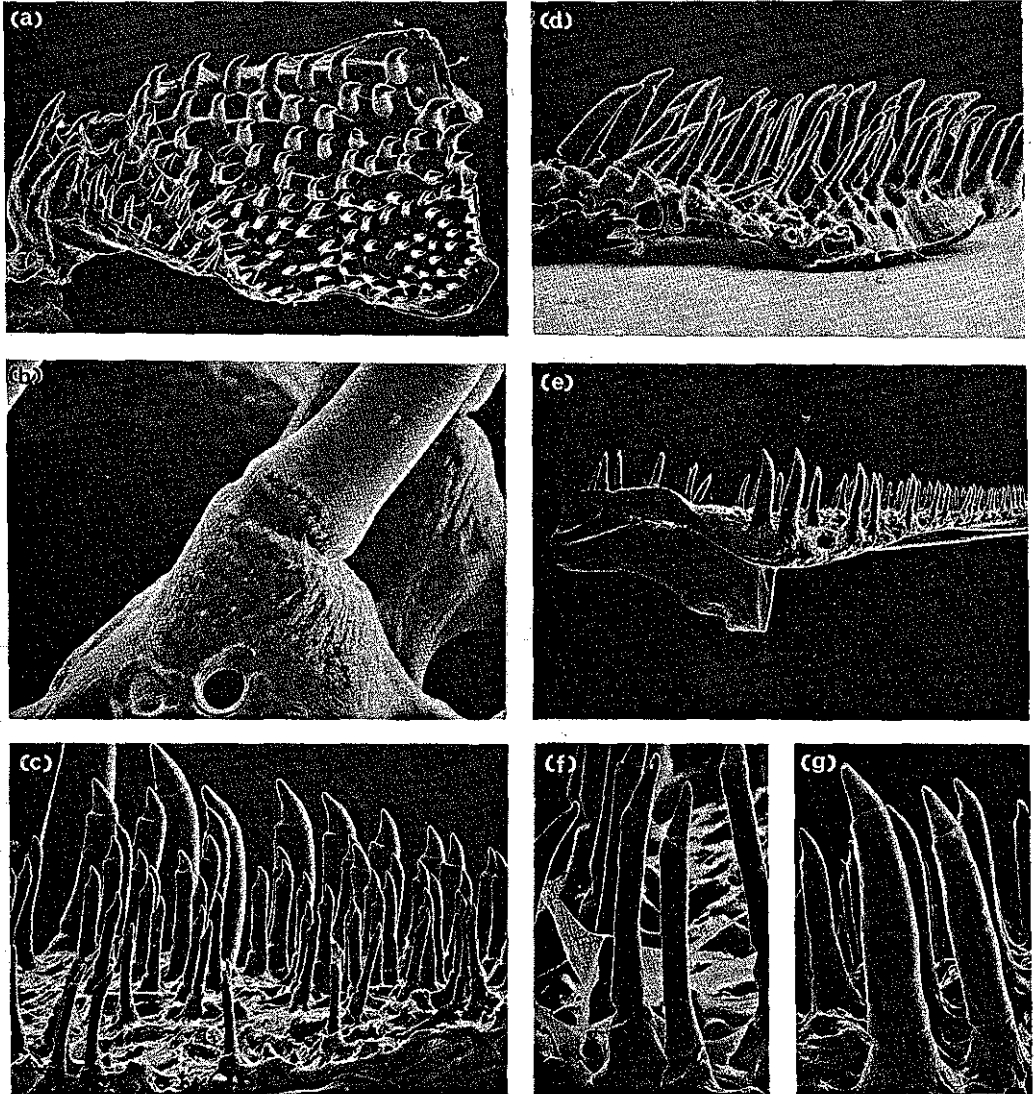


PLATE I. Scanning electron micrographs of the dentition of the pharyngeal jaws of *Periophthalmus koelreuteri*. (a) Right upper pharyngeal jaw; (b) base of depressible tooth from jaw in (a); (c) teeth from left lower pharyngeal jaw; (d) lateral view of upper right third pharyngobranchial; (e) right lower pharyngeal jaw showing the ventral muscular process. Posteromedial aspect of jaw is in the centre of the photo; (f) enlargement of teeth in right corner of (e); (g) enlargement of teeth on posteromedial area of jaw in (e). Note the opposite curvature of teeth on the upper and lower jaws. Anterior is to the left in all pictures.
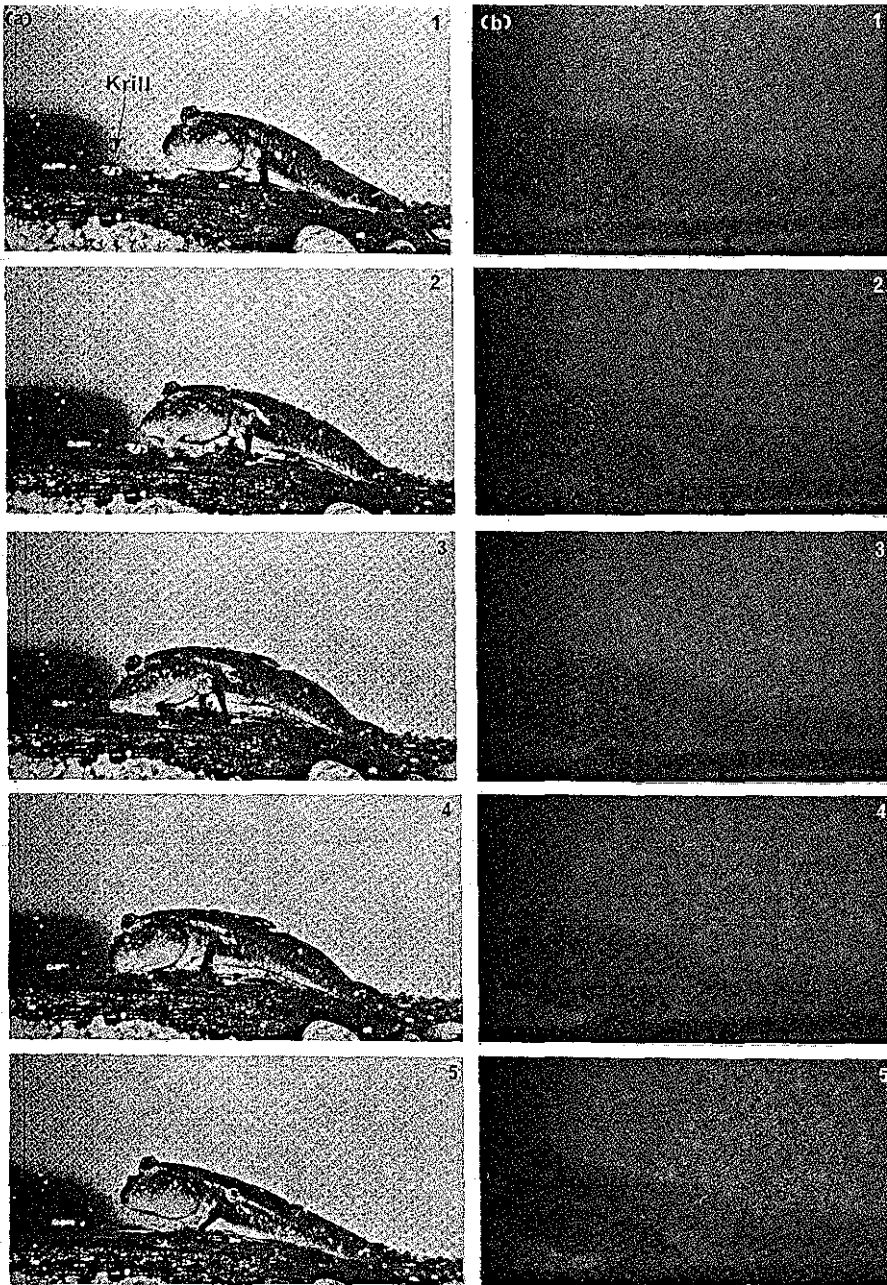
PLATE II. (a) Representative frames from 16 mm film showing initial prey capture by *Periophthalmus koelreuteri* out of water. 1–5 indicate frames 1, 5, 21, 27 and 45 of the original film. Time between sequential frames was 0·01 s. The bottom frame shows the characteristic posture during deglutition. (b) Representative film frames from an X-ray film taken at 85 frames per second to show the various stages of deglutition. 1, Prey (a barium injected earthworm) is completely in the mouth cavity (dark area below eye). Prey from earlier feeding sequences can be seen in the stomach. 2, Pharyngeal jaws have just made contact with the prey. 3, 4, Two stages in the raking phase of transport. Note movement of the large pocket of barium. 5, Prey is in the stomach.

The sternohyoideus muscle is divided into two distinct bundles, the smaller of which attaches to the pectoral girdle (Fig. 1, $SH_1$) while the larger portion (Fig. 1, $SH_2$) completely bypasses the pectoral girdle to merge with the ventral body musculature.

The tips of the upper and lower pharyngeal jaw teeth point in opposite directions and the teeth are depressible. The teeth of the upper jaw point posteriorly (Plate 1(a), (d)),
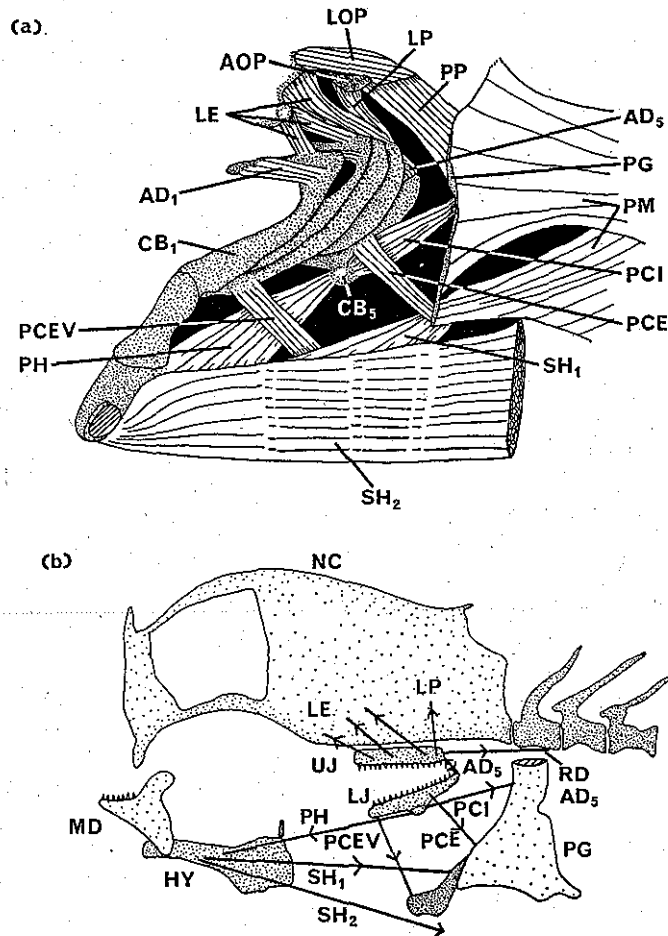


FIG. 1. (a) Lateral view of the branchial apparatus and muscles of *Periophthalmus koelreuteri* after removal of the operculum, suspensory apparatus, gills, and membranes. $AD_1$, first adductor arcus branchialum muscle; $AD_5$, fifth adductor; AOP, adductor operculi; $CB_1$, first ceratobranchial; $CB_5$, fifth ceratobranchial (lower pharyngeal jaw); LE, levatores externi; LOP, levator operculi; LP, levator posterior; PCE, pharyngocleithralis externus; PCEV, ventral division of the pharyngocleithralis externus; PCI, pharyngocleithralis internus; PG, pectoral girdle; PH, pharyngohyoideus; PM, pectoral fin musculature; PP, protractor pectoralis; $SH_1$, dorsal division of the sternohyoideus; $SH_2$, ventral division of the sternohyoideus. (b) Schematic diagram of the position and line of action of major branchial muscles influencing pharyngeal jaw movement in *Periophthalmus*. The ventral division of the pharyngohyoideus externus muscle actually inserts on ceratobranchial three but its effect on ceratobranchial five is ventral depression as indicated here. HY, hyoid apparatus, LJ, lower pharyngeal jaw; MD, mandible; NC, neurocranium; UJ, upper pharyngeal jaw.

while those of the lower jaw curve anteriorly (Plate 1(c), (e)). The upper jaw teeth vary in size with the larger ones situated on the medial and central areas (third pharyngobranchial) and the smaller teeth on the lateral and anterior jaw margins. Upper jaw teeth are posteriorly depressible as the result of an anteroventrally inclined tooth base (Plate I(b)) with a collagenous attachment to the tooth shaft.

Lower pharyngeal teeth are also larger on the medial jaw surface (Plate 1(e)) but they are depressible anteriorly. The tooth base is inclined posterodorsally (Plate 1(f)) and the teeth thus swing *anteriorly*. This arrangement may allow stabilization of the tooth during anterodorsal puncturing movements but would result in tooth depression during jaw retraction.

### Initial prey capture

Following detection of the prey on land, *Periophthalmus* rapidly propels itself out of the water using the caudal and pectoral fins. Rapid locomotion towards the prey then occurs by alternate use of the pectoral and pelvic fins (see Harris, 1960). At the time of emergence from the water, the buccal and opercular cavities are usually expanded and the mouth and opercular membrane are tightly closed (Plate II(a), frame 1). X-ray cinematography reveals that when *Periophthalmus koelreuteri* leaves the water to feed, there is little or no water in the buccopharyngeal cavity: the mouth and gill cavities are expanded with air. All or most of the water remaining in the buccal cavity is lost when the fish first opens its mouth to take in food, and water can then be seen draining out of the open mouth onto the ground.

During terrestrial excursions, many prey items were often captured and swallowed in succession without any return to the water. When water was inaccessible, the fish ate as many as three large earthworms extending over a period of half an hour. The limits to this activity were not tested.

When *P. koelreuteri* is only a few centimeters in front of the prey, it pivots forward on the pelvic fins bringing the jaws closer to the prey. The premaxilla slides anteroventrally and the mandible is depressed as the mouth is pressed against the substrate (Plate II(a), frames 2, 3). The jaws then close on the prey while still pressed against the ground and the head is elevated to the rest position (Plate II(a), frames 4, 5). During this stage slight movements of the hyoid and opercular membrane are visible. The opercular valve stays closed throughout the prey capture sequence and the lateral expansion of the buccal and opercular cavities is maintained during mouth opening and closing (see Plate II(a)). X-ray cinematography reveals that during this time deglutition is occurring by complex movements of the pharyngeal jaws (Plate II(b); see below).

### Pharyngeal jaw movements: deglutition

Swallowing of the prey begins after the initial capture has been completed and while the body and head are held in the characteristic "swallowing posture" shown in Plate II(a) (frame 5).

The first movements of the pharyngeal jaws comprise the initial contact phase of swallowing. These movements are depicted in Fig. 2 which shows two complete grabbing cycles by the jaws as they first make contact with the prey, in this case, an earthworm filled with barium. As the prey is moved toward the pharyngeal jaws as a result of hyoid compression and cranial elevation, the pharyngeal jaws separate to a wedge condition

which is open anteriorly (Fig. 2, frames 0–6). The jaws then are adducted and become
nearly parallel before the "bite" occurs between the anterior portions of the jaws (frames
8–16) during retraction. In this first cycle, the jaws failed to make contact with the prey
and a similar movement cycle is repeated: a wedge shaped opening phase accompanied by
protraction, followed by a pharyngeal jaw "bite" with concomitant jaw retraction (Fig. 2,
frames 30–44). As the jaws close on the prey, an obvious compression of the barium filled
space occurs (frames 40–44). One frame of this initial contact phase is shown as Plate
II(b), frame 2.

After initial contact has been made, the transport phase begins. While numerous small
variations and irregular movements of the jaws occur, the dominant transport movement
is a raking motion (Fig. 3). The upper jaw rotates dorsally and a wedge configuration is
again achieved with the lower jaw remaining essentially horizontal. The upper jaw may
actually reach almost an 80° angle with the horizontal during this stage. Protraction of
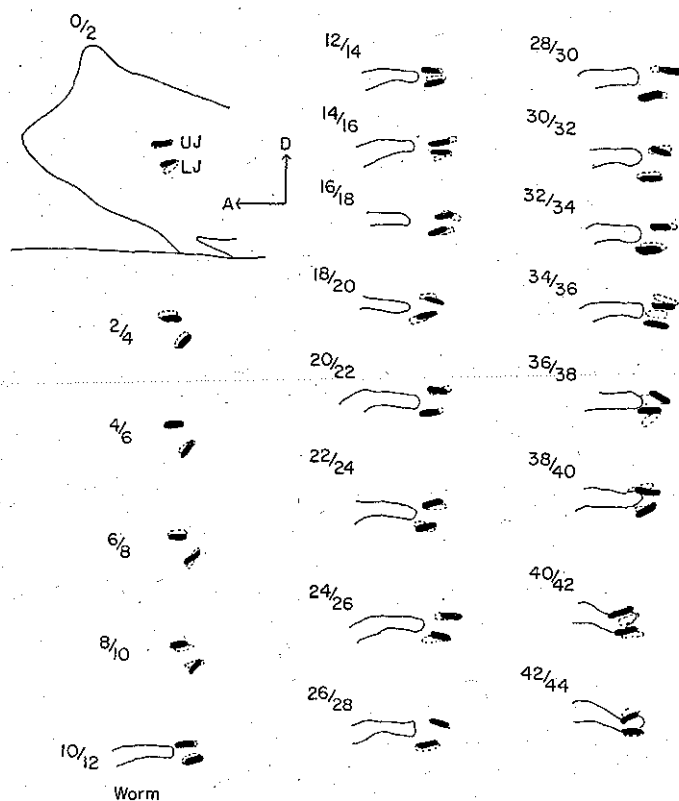


FIG. 2. Movements of the pharyngeal jaws during initial prey contact as revealed by X-ray cinematography. An
outline of the fish is shown at the upper left along with the positions of the pharyngeal jaws. Numbers next to the
diagrams indicate the frame number of the cine film. The first number is associated with the black jaw outline, while
the dashed outline represents the position of the pharyngeal jaws at the time of the second frame number. The
dashed outline in any given frame is the same as the solid outline in the following frame. A, anterior; D, dorsal.
The position of the posterior end of the barium injected worm is also indicated.

both jaws then occurs as the upper jaw pivots anteriorly engaging the prey with the post-eriorly recurved teeth (Fig. 3, frames 3–5). The jaws then close anteriorly in a "bite" and retract, raking the prey towards the oesophagus (frames 5–6). Changes in the lateral profile of the jaws during these stages may be due to rotation of the jaws about a vertical axis, an effect that could not be measured because dorsoventral cineradiography does not reveal the pharyngeal jaws. The raking stage is shown in Plate II(b), frames 2–4. These raking movements may be frequently interrupted with pauses of from several seconds to up to 10 min in duration. The prey thus does not advance towards the oesophagus at a uniform velocity and in one continuous motion.
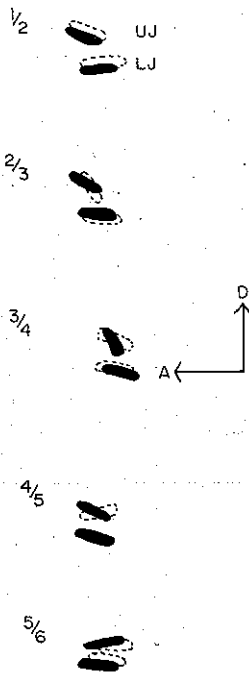


FIG. 3. Diagram depicting the pattern of pharyngeal jaw movement during the raking phase of food transport. Abbreviations as in the previous figures.

The movement trajectory of the anterior tip of the upper and lower pharyngeal jaws during raking is depicted in Fig. 4. The upper jaw moves over a much greater horizontal distance and during the final retraction stroke (Fig. 4, stage 3) the lower jaw remains nearly stationary while the upper is strongly retracted. Maximum anteroposterior excursion of the upper pharyngeal jaws does not exceed the length of the jaw while the lower jaw moves less than half its length. The anterior tip of the lower jaw also exhibits a nearly circular trajectory in contrast to the flattened oval path of the upper jaw.

After the prey has passed the pharyngeal jaws, it enters the esophagus where it may be seen passing to the stomach (Plate II(b), frames 4, 5).
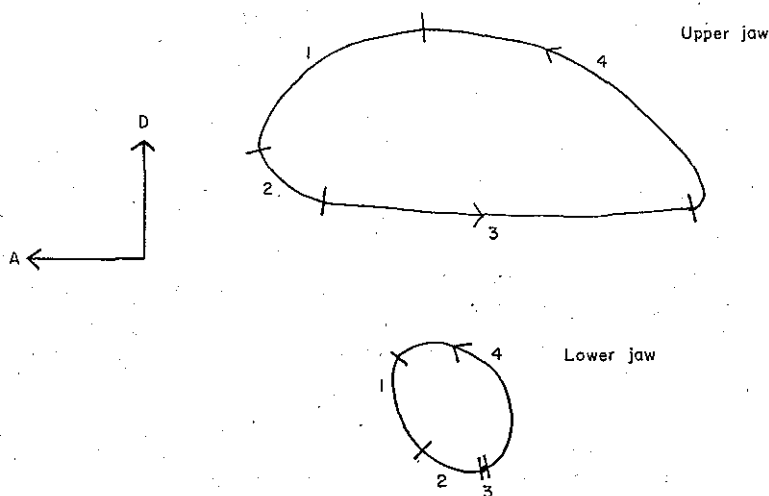
FIG. 4. Upper and lower pharyngeal jaw movement trajectories during raking of food into the oesophagus. Four arbitrarily defined phases are indicated (1–4) and the movement of the anterior tip of each jaw is plotted relative to a fixed reference point. During phase 3, the lower jaw does not move. Note the much greater excursion of the upper jaw relative to the lower. A, anterior; D, dorsal. The arrow indicates the direction of movement.

## Discussion

The feeding apparatus of teleost fishes has been characterized as a "non-rigid fluid filled two-chambered system with an inherent oscillatory capacity" (Liem, 1978). Evidence of this hypothesis is derived from fishes employing the gape-and-suck feeding strategy (see Alexander, 1967, 1969; Osse, 1969; Nyberg, 1971; Liem, 1978; Lauder, 1979, 1980b), in which the capture, and presumably, swallowing of prey, is dependent on the creation of water flow into the mouth. The process of prey capture and swallowing has not been investigated in any fishes feeding on land where limitations due to the lack of a supporting medium are most evident.

Indeed, only a few investigators have considered pharyngeal jaw movements in fishes. Van den Berghe (1928) studied *Cottus bublas* and *Blennius pholis* by removing the buccal floor of living specimens and stimulating the mucus of the palate. He observed protraction of the upper pharyngeal jaws and that the right and left upper jaws could move independently. Liem (1970) inferred pharyngeal jaw movements in nandid fishes from tooth-marks in the skin of prey removed from the stomach. More recently, Liem (1973, 1978) has experimentally studied the specialized pharyngeal jaw apparatus of cichlid fishes. Karrer (1967) and Kayser (1962) reconstructed movements of the upper and lower pharyngeals during deglutition in several other teleosts and hypothesized that the lower pharyngeal jaws move forward and backward in a regular, repeated sequence. Karrer (1967) proposed an "alternating hypothesis" in which the upper jaws are protracted while the lower jaws are retracted. This movement pattern is not seen in *Periophthalmus* where both jaws are protracted and retracted together (Figs 3, 4). In fact, the anteroposterior excursion of the lower jaw is less than that of the upper. Also of interest in this regard is the opposite orientation of tooth depression: the upper teeth depress posteriorly while the lower teeth depress anteriorly. The rigidity of the upper teeth to anterior forces correlates well with the

pronounced retraction stroke observed during raking (Fig. 4) while the anterior depressibility of the lower jaw teeth may reflect a primarily puncturing and cutting function during elevation (Fig. 4: stage 4, lower jaw). The lower pharyngeal jaw appears to play a relatively small role in food transport and primarily serves to support the prey during raking and biting by the upper jaw.

At the present time it is impossible to assess the generality of the above conclusions regarding pharyngeal jaw movement and the swallowing process, as so few other studies have been conducted. The pharyngeal apparatus of *Periophthalmus* is relatively generalized in structure and clearly functions primarily as a food transport system. Prey may be subdued to some extent by crushing and puncturing actions of the pharyngeal jaws but little or no food preparation occurs. Transport of the prey into the esophagus is accomplished by a regular repeated sequence of upper and lower pharyngeal jaw protraction, a bite, as both jaws pivot towards each other, and jaw retraction while maintaining the bite. The prey is thus moved posteriorly while being held firmly between the anterior teeth of the pharyngeal jaws. During the recovery stroke, separation of the jaws occurs and they are protracted to the initial biting position. The upper jaw is primarily responsible for prey transport. This pattern closely fits the inferred movements in nandid fishes (Liem, 1970).

The mechanics of pharyngeal jaw movement in cichlid fishes, the only other group studied to date, are very different. The upper jaw is of limited anteroposterior mobility, articulating with the pharyngeal apophysis of the skull, and transport of the prey is effected by the lower jaw. In addition, the bite occurs between the posterior jaw margins (Liem, 1978). The pharyngeal jaws of cichlids are specialized for the mastication of prey, an additional function not present in nandids and *Periophthalmus*, as well as for prey transport. If future work shows the pattern of pharyngeal jaw movement in *Periophthalmus* to be primitive for percoid fishes, then pharyngeal jaw function in cichlid fishes is even more specialized than previously recognized.

During aquatic feeding in more generalized teleosts, deglutition is accompanied by small movements of the opercular bones which serve to position the prey in the pharynx (Lauder, unpublished data on sunfishes). Small prey items pass directly into the oesophagus and stomach with the flow of water entering the mouth at the initial strike, and the pharyngeal jaws may only function to transport larger prey.

In *Periophthalmus*, however, the operculum moves very little during deglutition and the pharyngeal jaws are active even during the swallowing of small prey items. The lack of a high density medium such as water to maneouver the prey in terrestrial feeding situations renders the use of the pharyngeal jaws and hyoid obligatory for prey positioning. Throughout the feeding sequence, the laterally expanded condition of the opercular cavity is maintained and the opercular and branchiostegal membranes seal off the gills from the exterior environment. The opercular cavity is filled with air throughout most of these feeding cycles.

Two other feeding behaviours in addition to terrestrial feeding have been observed. During capture of prey on the water surface or prey in flight (insects) the fish rapidly overtakes the prey with an open mouth. During aquatic feeding, suction is used to a limited extent as the prey is very closely approached and then drawn into the buccal cavity by suction. Large prey are often trapped in crevices of the substrate and then positioned for swallowing without suction. Prey captured underwater are usually carried out of the water to be positioned for swallowing. Aquatic captures appear to be

significantly less successful than terrestrial feeding attempts, perhaps due to poor visual acuity underwater (Graham, 1971).

There are a number of reported observations of terrestrial feeding by other amphibious fishes: Graham (1970), *Mnierpes macrocephalus*; Chave & Randall (1971), *Gymnothorax pictus*; Stevens & Parsons (1980), *Dialommus fuscus*; Greenwood (1966), *Clarias*; Tesch (1977), *Anguilla*. Further work is necessary to determine if these fishes are actually capturing and swallowing prey on land.

However, not all amphibious fishes feed on land. *Monopterus* (Liem, 1981) is highly amphibious and yet appears not to feed terrestrially. The ability to capture prey on land may be related to the versatility in the feeding repertoire. Fishes able to feed terrestrially may be derived from forms with a broad feeding repertoire (*sensu* Lauder, In press), which are not limited to one feeding mode. *Monopterus* has an extremely narrow feeding repertoire consisting of only high-speed inertial suction (Liem, 1981), a system that is dependent on the movement of surrounding medium to draw prey into the mouth—ineffective in a terrestrial situation. *Periophthalmus*, on the other hand, has a diverse feeding repertoire that encompasses suction as well as biting patterns and a wide range of jaw opening speeds. This range of behavioural and mechanical alternatives is an important component of terrestrial feeding in fishes.

## Summary

The process of prey capture and deglutition in the amphibious fish *Periophthalmus koelreuteri* was studied by X-ray cinematography. This technique revealed that (1) The buccopharyngeal cavity is often filled with air during terrestrial excursions, in contrast to some previous hypotheses. (2) The pharyngeal jaw transport of food from the buccal cavity to the oesophagus is accomplished by at least two movement patterns: an initial grasping and "biting" process, and a raking movement. (3) During raking, the lower jaw moves in a small circular path while the upper jaw undergoes much larger anteroposterior excursions. (4) The lower jaw plays a relatively small role in food transport and serves to support and puncture prey during swallowing. (5) Both the lower and upper jaws are protracted and retracted together.

Specializations for terrestrial feeding primarily involve obligatory use of the pharyngeal jaws and hyoid to position the prey during swallowing, and a versatile feeding repertoire not limited to inertial suction.

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