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**PHARYNGEAL JAW MOVEMENTS IN
OREOCHROMIS NILOTICUS (TELEOSTEI : CICHLIDAE) :
PRELIMINARY RESULTS
OF A CINERADIOGRAPHIC ANALYSIS**

by

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ABSTRACT

Feeding in *Oreochromis niloticus* (implanted with metallic markers in the bones) was studied by cineradiography (50 fr/s) along lateral and dorso-ventral axes to visualize the movement patterns of the pharyngeal jaws during the different phases of food uptake. The images were digitized and plotted, indicating that the food particles are macerated in a single power stroke. During this cyclic movement the caudally pointing teeth of the upper pharyngeal jaw and the rostrally pointing teeth of the lower pharyngeal jaw move in opposite directions. The stereotyped movement pattern is not affected, either by varying size or varying hardness of the food items.

INTRODUCTION

Cichlids and other Labroidei are characterized among pharyngognath teleosts by a highly specialised pharyngeal mill (*e.g.* LIEM and GREENWOOD, 1981; LAUDER and LIEM, 1983; KAUFMAN and LIEM, 1982). The paired upper pharyngeal jaws (UPJ's), composed of the infrapharyngeal elements and some dermal tooth plates of the second, third and fourth branchial arches (ISMAIL *et al.*, 1982), articulate with the neurocranial base. The lower pharyngeal jaw (LPJ) consists of the « fused » fifth ceratobranchials and the associated dermal tooth plates, and is suspended in a muscular sling (*e.g.* LIEM, 1978; LIEM and GREENWOOD, 1981; LAUDER and LIEM, 1983).

Trophic specialisation, as found in cichlids, is reflected in the myology, osteology and dentition of the pharyngeal mill (*e.g.* GREENWOOD, 1981; TREWAVAS, 1983; WITTE and BAREL, 1976). In order to gain insight into the functioning of this complex apparatus, we plan movement analysis, with simultaneous EMG recordings on a variety of trophic types.

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This note reports on an initial analysis of the cineradiography of the « herbivorous » (cf. TREWAVAS, 1983) tilapiine *Oreochromis niloticus* Linnaeus, 1758, feeding on particles of varying size and hardness.

MATERIAL AND METHODS

Two specimens of *Oreochromis niloticus* (length 20-28 cm), obtained from a Belgian nursery in Tihange, were observed while housed in an experimental tank ($50 \times 40 \times 40$ cm; temp = 25°C) that has one corner extended into a narrow « feeding » corridor ($50 \times 6 \times 20$ cm). The lateral and ventral walls of the corridor were provided with thin perspex windows (2 mm).

The animals were filmed along lateral, as well as dorso-ventral axes, with a Siemens Tridoros-Optimatic 800 (35 kV for lateral view, 40 kV for dorso-ventral view; pulse duration : 2 ms) and a 17 cm Sirecon-2 image intensifier. Feeding sequences were recorded on Gevapan 30 negative film at 50 frames/s, with an integral Arriflex 16 mm camera.

Under superficial anaesthesia (MS 222), two metallic markers were inserted in each of the pharyngeal jaws, and into selected bony elements of the head (Pl. 1). The fishes were filmed while they were ingesting radiopaque pellets (35 % barium sulphate). The films were projected with an Analector projector (Old Delft), and movement analysis, as well as data conversion and model-like representation of the pharyngeal jaw positions and displacements, were carried out by means of a HP 9826 computer system.

RESULTS

When the fishes suck sinking particles, the films show that these travel directly through the bucco-pharyngeal cavity suspended by the induced water flow. During this transport (in about 0.1 s) the UPJ and LPJ retract simultaneously, while their posterior borders move slightly upwards (Fig. 1A, 1B; compare with rest position in Fig. 1D). The particles impact on the « closed » pharyngeal jaws, by the time that the mouth is almost completely closed against the protruded praemaxillaries. The food items become clamped between the UPJ and LPJ by a rotation of both, opposite to each other (= « opening »), coupled to a simultaneous protraction. The LPJ is pulled ventrally to the food particle (Fig. 1A, 42-78). At the same time, hyoid elevation and further mandibular adduction compress the bucco-pharyngeal cavity. Thus, the contained fluid is forced caudally and further caudal transport by this flow helps to position the food particle between the jaws.

In dorso-ventral view films, one sometimes observes particles start to shift laterally towards the opercular cavity. In such cases a series of small and fast buccal and opercular abducting and adducting movements return the particle to a midline position between the UPJ and LPJ.

Soft food items are squeezed by small backward translations and rotations of the UPJ around the neurocranial articulation, relative to an almost immobile LPJ (Fig. 1B). The UPJ moves mainly anteriorly to its rest position (= position of the pharyngeal mill in a quietly respiring specimen; see Fig. 1D). This movement occurs about 2.3 times a second. Protraction is two to three times faster than retraction : apparently the latter is the power stroke of the cycle.

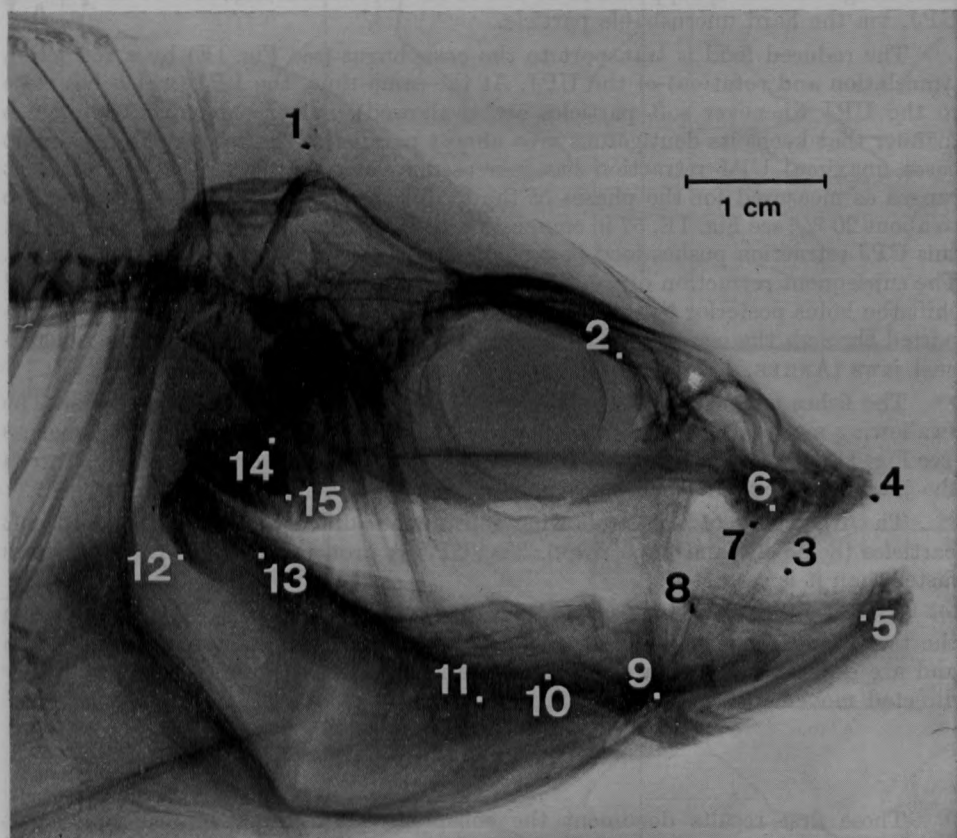


PLATE I

Radiograph in lateral view of a specimen of *Oreochromis niloticus* with implanted pellets marking the location of bones. 1, 2, neurocranium; 3, 4, praemaxillary; 5, mandibula; 6, 7, 8, maxillary; 9, 10, 11, hyoid arch; 12, 13, lower pharyngeal jaw; 14, 15, upper pharyngeal jaw.

Further mastication involves similar movements of the UPJ, but of increased amplitude (mainly by increase of the rotational component of the UPJ-movement). The rest position is situated approximately midway extreme protraction and retraction. Throughout pharyngeal mastication, the site of extreme UPJ protraction is very consistent. During retraction of the UPJ, the LPJ rotates to shift its caudal part upwards and forwards. Thus, this phase of the cycle is characterized by a close approach, and an opposite movement of the caudally pointing teeth of the UPJ and the rostrally pointing teeth on the rear end of the LPJ (scraping) : the food is then crushed (Fig. 1C, 50-62; power stroke). During reversal, the UPJ and LPJ are decoupled (Fig. 1C, 70-74), allowing a faster return to the starting position of the crushing phase (± 2 times). The movements occur 1.25 times per second.

Whenever very hard particles are to be crushed one sees comparable movements of the UPJ and LPJ, although the path of the markers of the lower jaw may be

more irregular. This is supposed to be due to the mechanical influence of the pushing UPJ, via the hard uncrushable particle.

The reduced food is transport to the oesophagus (see Fig. 1E) by a retraction (translation and rotation) of the UPJ. At the same time, the LPJ (which lies close to the UPJ whenever soft particles are swallowed), moves antero-ventrally, in a manner that keeps its dentigerous area almost parallel to that of the UPJ. In most cases, maximal UPJ retraction has increased in comparison to the displacement ranges as measured for the phases of the feeding sequence prior to swallowing (up to about 20 %; see Fig. 1E, 57 in comparison to for instance Fig. 1C, 70). Apparently, this UPJ retraction pushes food beyond the anteriorly moving rear end of the LPJ. The subsequent retraction of the LPJ and the simultaneous protraction of the UPJ shift the bolus posterior to the caudal margin of the UPJ. Thus, food can be transported through the oesophagus sphincter, as the latter is connected to the pharyngeal jaws (ANKER, 1978; GOEDEL, 1974; VANDEWALLE, 1972).

The fishes attempted to swallow whole those particles too hard to crush. The swallowing mechanism as postulated above is clearly illustrated by these sequences (see Fig. 1E, 45-69). If food items are too large, they are returned to a position between the jaws (reserved peristaltic movements), and may be spit out.

The frequency of the swallowing movements differs between hard and soft particles (being 2/s and 1.5/s resp.). The UPJ is protracted about 1.5 to 2 times faster than it is retracted.

After a soft particle has been swallowed, small fragments of food remain between the teeth, and the fish performs cleaning movements. These start from occlusion and are characterized by a sudden protraction of the UPJ and a rostro-ventrally directed movement of the LPJ.

DISCUSSION

These first results document the conspicuous uniformity of the movement pattern. Except for food uptake and cleaning, the UPJ and LPJ move in opposed directions. This differs from the situation for piscivorous cichlids (LIEM, 1978), which shift both jaws in the same direction for a great part of the maceration cycle. However, in the present species, the postero-dorsal rotation of the UPJ, simultaneously with the antero-ventral movement of the LPJ, is a continually repeating pattern. Moreover, the UPJ seems to have a fixed degree of protraction, and the rest position generally lies in the middle of the cycle. Only the amplitude of the respective movements changes. In this respect, it seems very reasonable to hypothesize that the reduced displacement of the jaws observed during initial squeezing, results from mechanical obstruction by the food particle. Indeed, once the particle has been reduced, the pattern shifts to the regular, total movement pattern.

Fig. 1. — Computer generated illustrations of pharyngeal jaw positions. Seeming overlap of the upper pharyngeal jaw with the neurocranial base results from the schematic way of presentation. The profile contours of the jaws and the neurocranium were digitized for only one position (*i.e.* rest position). Thus, for this figure only the prominent antero-posterior movements can be considered (corrections for abductions and adductions of the jaws or rolling of the entire fish are impossible). Food particles are shown stippled. Numbers are those of frame numbers in the actual sequence. A, food uptake (soft particle); B, squeezing of a soft particle (extreme jaw positions superimposed); C, crushing of a soft particle; D, rest position (UPJ = upper pharyngeal jaw, LPJ = lower pharyngeal jaw, NCR = neurocranium, OB = orbital border); E, swallowing of a hard particle.

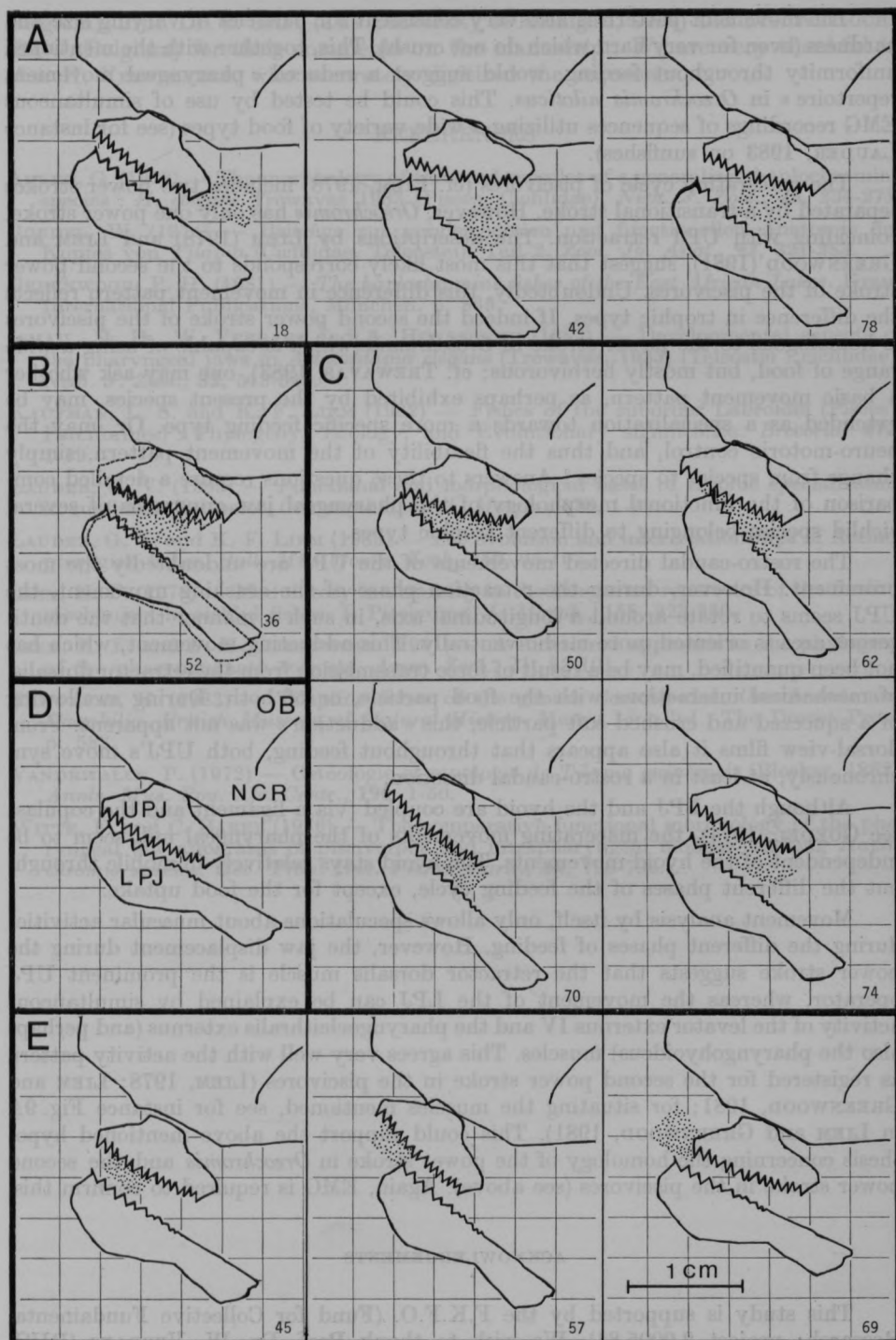


Fig. 1.

The movement pattern is also very consistent for particles of varying size and hardness (even for very hard which do not crush). This, together with the mentioned uniformity throughout feeding, would suggest a reduced «pharyngeal movement repertoire» in *Oreochromis niloticus*. This could be tested by use of simultaneous EMG recordings of sequences utilizing a wide variety of food types (see for instance LAUDER, 1983 on sunfishes).

The macerating cycle of piscivores (cf. LIEM, 1978) includes two power strokes separated by a transitional stroke. However, *Oreochromis* has only one power stroke, coinciding with UPJ retraction. The descriptions by LIEM (1978) and LIEM and GREENWOOD (1981), suggest that this most likely corresponds to the second power stroke of the piscivores. Undoubtedly, this difference in movement pattern reflects the difference in trophic types. If indeed the second power stroke of the piscivores is homologous to the power stroke of *Oreochromis* (which is capable of using a wide range of food, but mostly herbivorous; cf. TREWAVAS, 1983), one may ask whether a basic movement pattern, as perhaps exhibited by the present species, may be extended as a specialization towards a more specific feeding type. Or, may the neuro-motoric control, and thus the flexibility of the movement pattern, simply change from species to species? Answers to these questions require a detailed comparison of the functional morphology of the pharyngeal jaw apparatus of several cichlid species belonging to different trophic types.

The rostro-caudal directed movements of the UPJ are undoubtedly the most prominent. However, during the retraction phase of the crushing movement, the UPJ seems to rotate around a longitudinal axis, in such a manner that the dentigerous area is oriented more medio-ventrally. This adducting movement, which has not been quantified, may be a result of force transmission from the retractor dorsalis, of mechanical interactions with the food particle, or of both. During swallowing of a squeezed and crushed soft particle, this «adduction» was not apparent. From dorsal-view films it also appears that throughout feeding, both UPJ's move synchronously, at least in a rostro-caudal direction.

Although the LPJ and the hyoid are coupled (via a ligament and the copulas; see GOEDEL, 1974), the macerating movements of the pharyngeal mill seem to be independent of the hyoid movements. The hyoid stays relatively immobile throughout the different phases of the feeding cycle, except for the food uptake.

Movement analysis by itself, only allows speculations about muscular activities during the different phases of feeding. However, the jaw displacement during the power stroke suggests that the retractor dorsalis muscle is the prominent UPJ operator, whereas the movement of the LPJ can be explained by simultaneous activity of the levator externus IV and the pharyngocleithralis externus (and perhaps also the pharyngohyoideus) muscles. This agrees very well with the activity pattern as registered for the second power stroke in the piscivores (LIEM, 1978; LIEM and GREENWOOD, 1981; for situating the muscles mentioned, see for instance Fig. 9A in LIEM and GREENWOOD, 1981). This could support the above mentioned hypothesis concerning the homology of the power stroke in *Oreochromis* and the second power stroke in the piscivores (see above). Again, EMG is required to confirm this.

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