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CINERADIOGRAPHIC ANALYSIS OF THE PHARYNGEAL JAW MOVEMENTS DURING FEEDING IN *HAPLOCHROMIS BURTONI* (GÜNTHER, 1893) (PISCES, CICHLIDAE)

by

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SUMMARY

Analysis of lateral radiographic films reveals that the upper and lower pharyngeal jaws in *Haplochromis burtoni* (GÜNTHER, 1893) show opposite anteroposterior displacements during food reduction. Force is generated during upper jaw retraction by elevation and slight protraction of the lower pharyngeal jaw (compression phase) and subsequently by depression and strong protraction of the lower jaw (shearing phase). These results contradict previous findings in which the upper and lower pharyngeal jaws show synchronous protraction and retraction.

Keywords : Cichlids, feeding, pharyngeal jaws.

INTRODUCTION

The pharyngeal jaw apparatus of cichlids is (amongst that of some other teleostean families) characterized by two upper pharyngeal jaws, which articulate with the neurocranial base, and a single lower pharyngeal jaw (LIEM and GREENWOOD, 1981). Although it is suggested that a powerful upper-lower pharyngeal jaw bite exists (LIEM and GREENWOOD, 1981), experimental studies of the mechanisms of pharyngeal mastication are very scarce.

The first experimental study on pharyngeal mastication in cichlids (LIEM, 1973) emphasized muscle activities in *Haplochromis burtoni* (GÜNTHER, 1893) (an insectivorous-omnivorous cichlid, see JANSSENS DE BISTHOVEN *et al.*, 1990) during feeding on *Gammarus* species ; positions of the pharyngeal jaws during mastication were inferred from successive X-ray pictures. LIEM (1973) described a triphasic movement cycle in which the upper and lower pharyngeal jaws are protracted and retracted simultaneously. This pattern was confirmed by electromyographical and cineradiographical study on piscivorous cichlid species (LIEM, 1978), and subsequently generalized for all cichlid species (LIEM and GREENWOOD, 1981).

Recent cineradiographic studies (Aerts *et al.,* 1986 ; Claes and De Vree, 1989, 1991) revealed that pharyngeal food processing in *Oreochromis niloticus* (Linn, 1758) involves opposite anteroposterior movements of the upper and lower pharyngeal jaws. Preliminary results on *Cichlasoma friedrichsthali* (Heckel, 1840) (a Central-American carnivorous cichlid) and *Astatoreochromis alluaudi* (Pellegrin, 1903) (a haplochromine durophagous species) confirm this « opposite movement » pattern. Since *Oreochromis, Astatoreochromis* and *Cichlasoma* represent different lineages of the family (Greenwood, 1978), these results suggest that the alternating pattern is probably the most common in cichlids.

However, a comparison between these quantitative results and the movement profiles described by Liem (1973, 1978) is difficult, since Liem offers only a qualitative impression of the pharyngeal jaw movements in *Haplochromis burtoni* (Liem, 1973) and piscivorous cichlids (Liem, 1978). Therefore, a detailed quantitative re-examination of the kinematic pattern in these species is needed. In the present study, we report the results of a cineradiographical analysis of the pharyngeal jaw movements in *Haplochromis burtoni.*

MATERIAL AND METHODS

Two individuals of *Haplochromis burtoni* (Günther, 1893), purchased from a commercial supplier, were trained to feed on live crickets and earthworms in a

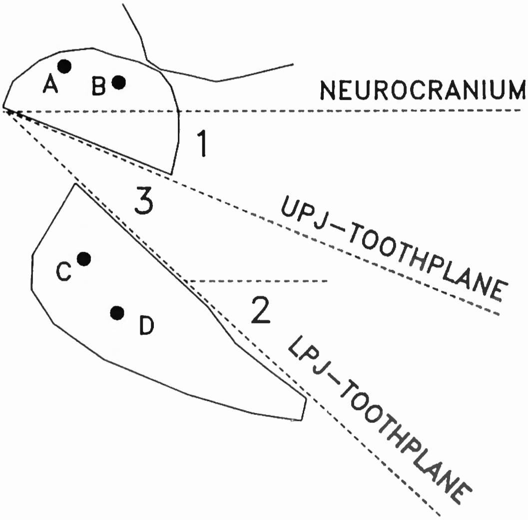

Fig. 1. — Position of the upper (A,B) and lower (C,D) pharyngeal jaw markers. Calculated angles are also indicated : between the upper pharyngeal jaws and the neurocranium (1), the lower pharyngeal jaw and the neurocranium (2) and between the upper and lower pharyngeal jaws (3).

narrow (6 cm) experimental aquarium tank, provided with thin (2 mm) plexiglass on the lateral walls. Lateral X-ray films (Gevapan 30 negative film, 80 ASA) were taken at 50 frames per second with an Arriflex 16 mm camera, attached to a Sirecon 2 image amplifier; X-rays were generated by a Siemens Tridoros 800 Optimatic at 1 meter distance from the image amplifier. All food items were impregnated with a solution of barium sulphate in order to make their position visible on the X-ray films. Small lead markers were implanted under anesthesia (MS 222) in the pharyngeal jaws and the neurocranium. The marker coordinates

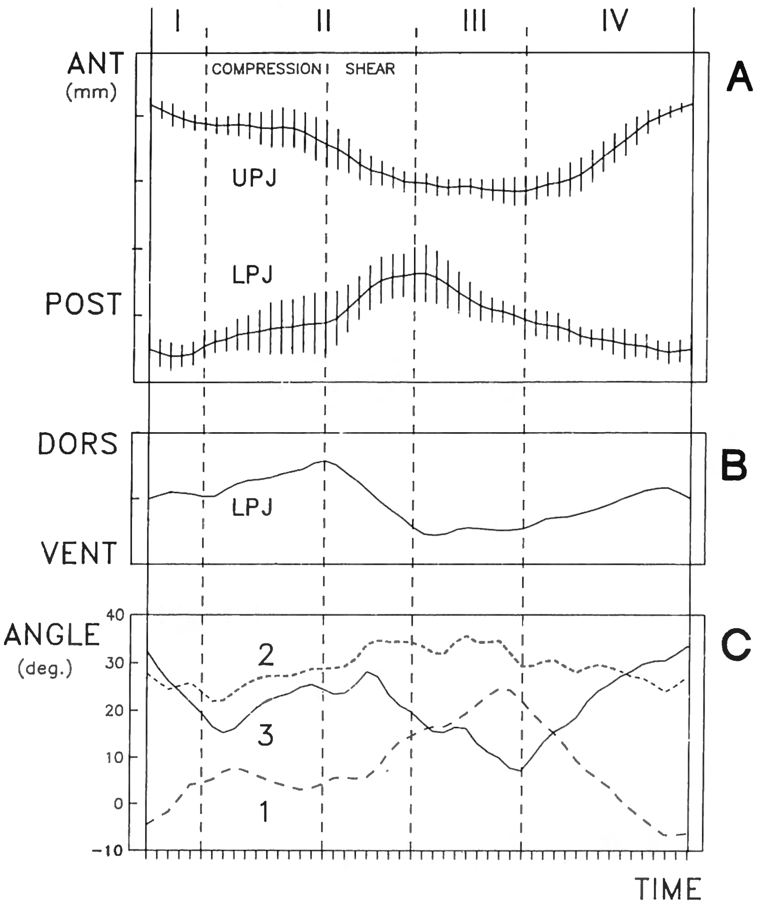

Fig. 2. — Time-displacement graph for a mean movement cycle during pharyngeal processing of an earthworm (N = 11). Upper and lower jaw movements are indicated by the displacements of marker A and C resp. (see Fig. 1). ANT, anterior; POST, posterior; DORS, dorsal; VENT, ventral; UPJ, upper pharyngeal jaw; LPJ, lower pharyngeal jaw. Angles are indicated in Fig. 1. I = preparatory, II = power, III = swallowing, IV = recovery. The vertical bars in A represent the standard deviation in each interval.

of selected film sequences were measured frame by frame, and recalculated to a reference grid defined by two markers on the neurocranium. Movement analysis involved (1) the construction of time-displacement graphs, which allows precise determination of the direction, amplitude and frequency of the pharyngeal jaw movements, (2) calculation of the angles between the toothplanes and the neurocranium (Fig. 1), which allows detection of pharyngeal jaw rotations around a transversal axis, and (3) calculation of mean movement cycles (Figs 2, 3). To facilitate the interpretation of the time-displacement graphs, a computer program was made to design successive pharyngeal jaw contours relative to the stationary neurocranium outline (Fig. 3). The methods of movement analysis are described in detail in CLAES and DE VREE (1991).

RESULTS

The pharyngeal jaw apparatus of *Haplochromis burtoni* closely resembles that of the related species *H. elegans*. Detailed descriptions of the pharyngeal jaw apparatus in *H. elegans* are given by BAREL *et al.* (1976) and ANKER (1978, 1989).

Pharyngeal food processing is effected by cyclic movements of the pharyngeal jaws. The protracted upper jaw position is chosen arbitrarily as the starting point of each cycle and practically corresponds with the most retracted position of the lower pharyngeal jaw (Figs 2 and 3). Subdivision of each cycle is based on the different movements of the upper and lower pharyngeal jaws. In this way, three major phases are distinguished during upper jaw retraction (preparatory, power and swallowing), while the period of upper jaw protraction is regarded as a separate phase (recovery).

The lower pharyngeal jaw is kept almost immobile during the preparatory phase, while the upper pharyngeal jaws are slightly retracted (Figs 2 and 3). The angle between the toothplanes of the upper pharyngeal jaws and the neurocranium (Angle 1 in Figs 1 and 2) increases, indicating a clockwise upper jaw rotation (head tip to the right in Figs 1 and 3), and resulting in tooth-food contact in preparation for the power phase.

During the power phase, the lower pharyngeal jaw moves anterodorsally and subsequently anteroventrally (Fig. 2) ; distinction between these movements allows further subdivision into compression and shearing phases. Upper jaw retraction and rotation decreases during the compression phase, while the lower pharyngeal jaw is lifted and simultaneously rotated clockwise (increase of angle 2 in Fig. 2) ; lower jaw protraction is limited during this phase (Figs 2 and 3 : compression). The shearing phase is characterized by strong lower jaw depression and protraction, while the upper pharyngeal jaws are further retracted and rotated clockwise (Figs 2 and 3 : shear). At the end of the power phase, the lower pharyngeal jaw is fully protracted and reaches its ventralmost position.

The lower pharyngeal jaw is retracted during the swallowing phase while kept in its ventralmost position. Although the upper pharyngeal jaws are only slightly retracted during the swallowing phase, they are further rotated caudodorsally,

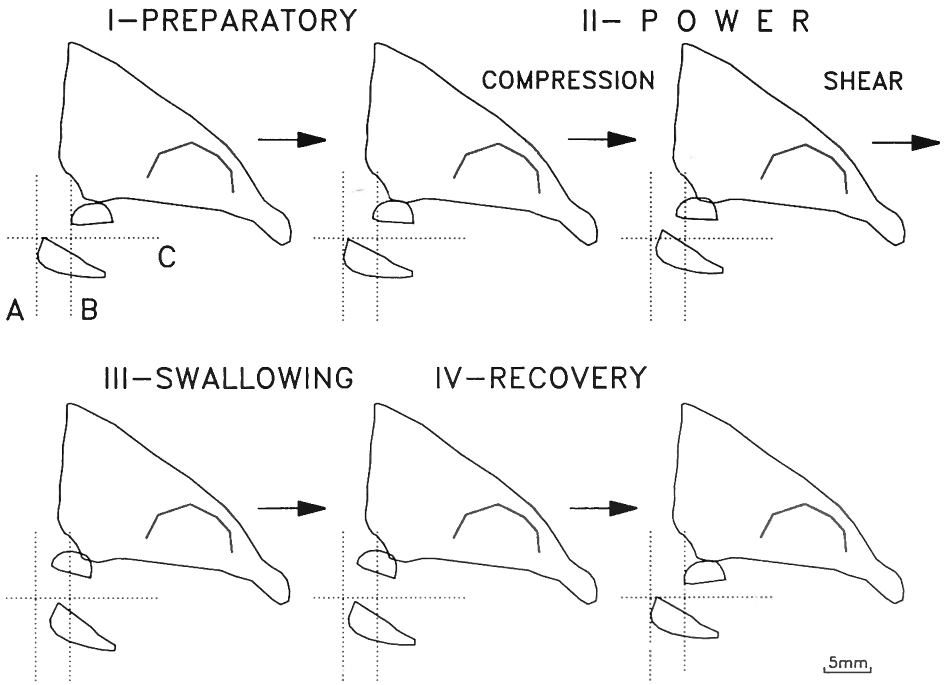

Fig. 3. — Outlines of the pharyngeal jaws and the neurocranium for the different phases, based on the same mean cycle as depicted in Fig. 2. Reference lines A,B and C indicate the position of the jaws at the start of the cycle. A = most posterior lower jaw position, B = most anterior upper jaw position, C = reference for dorsoventral lower jaw displacements.

enabling deglutition of the posteriormost food particles. The angle between the toothplanes of the upper and lower pharyngeal jaws (angle 3 in Figs 1 and 2) decreases to its minimal value as a result of the caudodorsal (clockwise) upper jaw rotation and a slight anticlockwise lower jaw rotation. Consequently, the toothplanes of the upper and lower pharyngeal jaws lie almost parallel to each other (Fig. 3).

Finally, the pharyngeal jaws move to their initial positions during the recovery phase : the upper pharyngeal jaws are protracted and rotated anticlockwise, the lower pharyngeal jaw is further retracted and moves sligtly upward (Figs 2 and 3).

Although the amplitudes of the displacements and the durations of the different phases may vary within a masticatory sequence, this kinematic pattern is basically stereotyped. The cycle duration ranges between 440 and 580 ms (N = 11, mean = 497 ms).

DISCUSSION

The first description of the pharyngeal biting mechanism in cichlids was based on experiments with *Haplochromis burtoni* (LIEM, 1973), feeding on *Gammarus* species. This experimental study emphasized muscle activities (electromyography) during pharyngeal food processing, whereas the movements of the pharyngeal jaws were deduced from successive X-ray pictures. LIEM (1973) described a triphasic movement cycle, in which the upper and lower pharyngeal jaws show synchronous anteroposterior displacements. During the first phase (phase « 1a », LIEM, 1973), the pharyngeal jaws are closed during protraction, resulting in the application of force on the food. During the second phase (phase « 1b », LIEM, 1973) the pharyngeal jaws are strongly retracted. The pharyngeal jaws are protracted and abducted during the third phase (phase « 2 », LIEM, 1973). The transition between the end of « phase 2 » and the onset of « phase 1a » (depicted in LIEM, 1973, Fig. 8) is not considered in the description of the movement cycle, although it should be regarded as a fourth phase.

A different triphasic movement pattern was described by LIEM (1978) for piscivourous cichlid fishes, and, in a later paper (LIEM, 1986, p. 321) also for *Haplochromis burtoni*. The movement cycle described in these papers consists of two power strokes separated by a transitional stroke. During the first power stroke (also called « shearing » in LIEM, 1986) the upper and lower pharyngeal jaws are protracted while approaching each other. The transitional stroke is sligthly retrusive. During the second power stroke (« crushing » in LIEM, 1986), the pharyngeal jaws close a second time during their retraction. Thus, according to LIEM (1978, 1986), cichlids masticate food during two « power strokes », separated by a « transitional stroke », while the upper and lower pharyngeal jaws show simultaneous protraction and retraction.

The results in the present paper clearly demonstrate that *Haplochromis burtoni* does not show either one of these triphasic movement patterns when feeding on crickets and earthworms. Based on quantitative cineradiography (i.e. measurement of bone displacements in a standardized reference grid), each movement cycle is subdivided into four main phases : a preparatory phase (upper jaw retraction, nearly stationary lower jaw), a power phase (upper jaw retraction, lower jaw lifting and protraction), a swallowing phase (upper and lower jaw retraction) and a recovery phase (upper jaw protraction, lower jaw retraction). Throughout most of the movement cycle (power phase, recovery phase), the upper and lower pharyngeal jaws thus move in opposite anteroposterior directions ; the moment of maximal upper jaw protraction corresponds with that of the most retracted lower jaw location. The morphology and orientation of the pharyngeal teeth suggest that this movement pattern produces an effective and continuous shear stress during the power phase. This movement pattern agrees with that of *Oreochromis niloticus* (CLAES and DE VREE, 1989, 1991).

It is unlikely that the differences between our results and the kinematic patterns described by LIEM (1973, 1978, 1986) are due to differences of food-types, since the movement pattern in *Haplochromis burtoni* is consistent when using earthworms and crickets. A detailed study of *Oreochromis niloticus* (CLAES and DE VREE, 1991) revealed a significant influence of food type on the durations of the different phases, but not on the basic movement pattern (relative directions of the upper and lower pharyngeal jaw displacements). It is more likely that deduction of movements from muscle activities does not allow a detailed description of the kinematics, increasing the chances of misinterpretations of valuable experimental results. Anyway, our results show that the movement pattern described by LIEM and GREENWOOD (1981) should not be generalized for the whole family. In expectation of further verifying research, the triphasic pattern in piscivorous cichlids (LIEM, 1978) should be regarded as exceptional within the cichlid family.

ACKNOWLEDGEMENTS

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REFERENCES

AERTS, P., F. DE VREE and P. VANDEWALLE (1986) — Pharyngeal jaw movements in *Oreochromis niloticus* (Teleostei, Cichlidae) : preliminary results of a cineradiographic analysis. *Annls. Soc. r. zool. Belg.*, **116** : 75-82.

ANKER, G. CH. (1978) — The morphology of the head-muscles of a generalized *Haplochromis* species : *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Morph.*, **28** : 234-271.

ANKER, G. CH. (1989) — The morphology of joints and ligaments in the head of a generalized *Haplochromis* species : *H. elegans* Trewavas 1933 (Teleostei, Cichlidae). III- The hyoid and the branchiostegal apparatus, the branchial apparatus and the shoulder girdle apparatus. *Neth. J. Zool.*, **39** : 1-40

BAREL, C. D. N., F. WITTE, and M. J. P. VAN OIJEN (1976) — The shape of the skeletal elements of the head of a generalised *Haplochromis* species : *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). *Neth. J. Zool.*, **26** : 163-265.

CLAES, G., and F. DE VREE (1989) — Asymmetrical pharyngeal mastication in *Oreochromis niloticus. Annls. Mus. Roy. Afr. Centr., Sc. Zool.*, **257** : 69-72.

CLAES, G., and F. DE VREE (1991) — Kinematics of the pharyngeal jaws during feeding in *Oreochromis niloticus* (Pisces, Perciformes). *J. Morphol.*, **108** : 227-245.

GREENWOOD, P. H. (1978) — A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. *Bull. Br. Mus. nat. Hist. (Zool.)*, **33** (5) : 297-323.

JANSSENS DE BISTHOVEN, L., J. SNOEKS, F. OLLEVIER and D. THYS VAN DEN AUDENAERDE (1990) — The food of *Haplochromis burtoni* (Pisces : Cichlidae) of Lake Mugesera (Rwanda). *Belg. J. Zool.*, **120** : 37-49.

LIEM. K. F. (1973) — Evolutionary strategies and morphological innovations : Cichlid pharyngeal jaws. *Syst. Zool.*, **22** : 425-441.

LIEM, K. F. (1978) — Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I- Piscivores. *J. Morphol.*, **158** : 323-360.

LIEM, K. F. (1986) — The pharyngeal jaw apparatus of the Embiotocidae (Teleostei) : A functional and evolutionary perspective. *Copeia* **1986**(2) : 311-323.

LIEM, K. F., and P. H. GREENWOOD (1981) — A functional approach to the phylogeny of the pharyngognath teleosts. *Am. Zool.,* **21** : 83-101.