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Modulatory Multiplicity in the Functional Repertoire of the Feeding Mechanism in Cichlid Fishes

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ABSTRACT Among piscivorous cichlids consistent differences have been recorded between ambush and pursuit hunters with respect to electromyographic, kinematic, pressure and behavioral profiles during prey capture by high speed inertial suction. Piscivorous cichlids possess a repertoire of at least two patterns of prey capture, each of which is characterized by an extreme regularity of the kinematic, pressure, electromyographic and behavioral profiles. The nature and locomotory behavior of the prey, visually analyzed by the predator during the prestrike stalk, determine which of the two preprogrammed patterns is recruited. Agile and elusive prey invariably will elicit a preprogrammed motor output (stereotyped motor pattern) that produces the greatest suction velocities in both ambush and pursuit hunters. The greater the kinematic and suction velocities, the greater the overlap of the firing sequences of antagonistic muscle complexes. The opercular and branchiostegal apparati function as an exceedingly effective anti-backwash device, damping potential fluid oscillations within the oropharynx. Mastication occurs by triphasic movements and actions of muscles of the upper and lower pharyngeal jaws in both ambush and pursuit hunters. The lower pharyngeal jaw is acted upon by a force couple of which the fourth levator externus on one hand and the pharyngocleithralis externus and pharyngohyoideus on the other hand are the antagonistic components. Furthermore, the lower pharyngeal jaw is suspended by a muscular sling, the tension of which can be modified continuously. It is postulated that the switch from insectivorous to piscivorous feeding regimes (and perhaps vice versa) is accomplished by very minor structural and functional modifications, because the modulatory multiplicity and total range of repertories of the feeding machinery of the two trophic groups overlap significantly. Piscivorous cichlids may not have arisen by orthoselection in gradually-changing lineages, but represent the differential success of subsets from a random pool of speciation events. Adaptive features identified as characteristic for piscivory could have evolved in multiple and independent lineages at a punctuational mode and tempo.

Recent experimental investigations on the eding mechanisms of selected species of leosts have yielded a wealth of specifics on he bone-muscle systems of the teleostean eding machinery. Although a coherent fabric outlining the causal factors that govern he functional organization of teleostean feeding systems has not been advanced, a general odel is emerging from the existing body of data. On the basis of the present available evidence, the model may be formulated as follows: The teleostean feeding apparatus is a nonrigid, fluid filled two-chambered system with an inherent oscillatory capacity. Muscles acting on the mobile walls of the two chambers control fluid movement mostly in a posterior direction (Elshoud-Oldenhave and Osse, '76). Initially, the *modus operandi* of this

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model is thought to be guided by a preprogrammed oscillator. Such preprogrammed (stereotyped) motor activity may not respond to peripheral sensory feedback mechanisms. Evidence for this hypothesis is derived from fishes employing the Inertial-Suction or Gape-and-Suck (Saugschnappen) feeding strategy (e.g., Osse, '69; Liem, '70; Nyberg, '71; Lauder et al., '79). The alleged adaptive significance of the non-modulating preprogrammed oscillator is to eliminate the delay that might otherwise occur if a peripheral sensory feedback mechanism were interposed. Thus, the model has put an existing body of data into a coherent entity for fishes utilizing high-speed inertial suction prey-capture tactics.

However, in subsequent studies on fishes with different feeding strategies (Ballintijn et al., '72; Liem and Osse, '75; Elshoud-Oldenhave and Osse, '76) convincing experimental evidence has been presented indicating that the sequence of neuromuscular events may be subject to modulation by peripheral sensory feedback responding to a given feeding situation.

This is the first of a series of papers, in which I will attempt to analyze experimentally the presence or absence of modulatory mechanisms in the feeding machinery of selected cichlids with varying trophic specializations. Unfortunately, the considerable complexity of modern experimental techniques (high speed cine and cineradiography synchronized with electromyography, pressure transducers, analysis of electromyograms, etc.) imposes constraints on the number of species and individuals that any one investigator can study. Therefore, it is not surprising that functional morphologists tend to formulate a pervasive functional design or body plan characterizing the entire higher taxon to which a studied species belongs. However, the search for characteristic functional designs is accompanied by a potential pitfall: Because the primary focus is on basic functional themes, modulatory expressions and variations are regarded as fleeting phenomena. The potential problem is analogous to that of the former typologists who regard variations as illusions because they represent only shadows of the type or "eidos." Therefore, it seems necessary and valid to explore the nature and biological meaning of modulatory mechanisms in the feeding machinery of the most diverse teleost family known, the Cichlidae (Poll, '56; Greenwood, '64, '74; Fryer and Iles, '72).

Adaptationists have regarded the num specializations in the trophic structur cichlids not only as relatively narrow, op adaptations, but also as evidence of evol by natural selection (e.g., Fryer and Iles Greenwood, '74; Liem and Osse, '75). Y most cases the analysis of trophic adapt in cichlids has not gone beyond the descri of a particular trait, which is assumed to solution to a postulated problem. However problem often is reconstructed from the tion! For example, in *Genyochromis ment* outer margin of the lower jaw is lined "row of teeth which, while actually bicus are functionally unicuspid" (Fryer and '72; p. 87). According to the adaptatio methodological program such a specializa demands an adaptive explanation. Altho "the act of taking a scale has never been served," Fryer and Iles ('72) proposed that functionally unicuspid, sharp tooth is optimal solution to the problem of scale sc ing and fin clipping. Furthermore, Fryer Iles postulate that the smaller cusp of tooth "serves to strengthen the larger." T explanation implies that fin clipping and sc scraping are problems that can be solved sharp and reenforced teeth. Thus, the speci ized dental trait is provided with an adapt explanation by finding the problem to whic is a solution.

In this series of papers, I will use experim tal methods and principles of functional sign to predict how the anatomical, physiol ical and behavioral versatility (plastici may play a major role in determining the sponse of a species to environmental alter tion. This phenotypic versatility and genet plasticity in cichlids is limited in rate a kind of response, so that the environment m change in a way and at a rate that could ou distance the species' adaptive response. By t application of experimental techniques a simple mechanical principles to differenti fitness, it should be possible to remove the a parent tautology in the theory of natural s lection, because a priori fitness determinati is made possible, and therefore the judgme of relative adaptation of two or more for can be made without prior knowledge of the reproductive performances. In this series papers I will focus on the degree that cichli species can track the trophic resources in seasonally changing environment. Once th relative versatility of the feeding apparatus known, I hope to be able to predict whic cichlids could exploit a greater share of the r tionists have regarded the numerous tions in the trophic structures of ɔt only as relatively narrow, optimal ns, but also as evidence of evolution l selection (e.g., Fryer and Iles, '72; d, '74; Liem and Osse, '75). Yet in s the analysis of trophic adaptation has not gone beyond the description ular trait, which is assumed to be a a postulated problem. However, the ten is reconstructed from the solu- xample, in *Genyochromis mento* the gin of the lower jaw is lined by a eth which, while actually bicuspid, onally unicuspid" (Fryer and Iles,). According to the adaptationist gical program such a specialization n adaptive explanation. Although taking a scale has never been ob- yer and Iles ('72) proposed that the y unicuspid, sharp tooth is the ution to the problem of scale scrap- clipping. Furthermore, Fryer and ate that the smaller cusp of the es to strengthen the larger." This n implies that fin clipping and scale e problems that can be solved by eenforced teeth. Thus, the special- trai rovided with an adaptive n by fi ing the problem to which it n.

ries of papers, I will use experimen- s and principles of functional de- ict how the anatomical, physiolog- ehavioral versatility (plasticity) major role in determining the re- species to environmental altera- henotypic versatility and genetic n cichlids is limited in rate and onse, so that the environment may way and at a rate that could out- species' adaptive response. By the of experimental techniques and hanical principles to differential ould be possible to remove the ap- ology in the theory of natural se- use a priori fitness determination sible, and therefore the judgment adaptation of two or more forms without prior knowledge of their performances. In this series of l focus on the degree that cichlid track the trophic resources in a hanging environment. Once the atility of the feeding apparatus is ope to be able to predict which d exploit a greater share of the re- ou s in short supply or who could survive nd eproduce on a lower resource level, or ould appropriate a resource that is inaccessible to their competitors.

MATERIALS AND TECHNIQUES

Fishes representing several piscivorous species were anesthetised in Tricainemethanesulfonate (Crescent Research Chemicals, Scot sdale, Arizona 85251) 200-300 mg/liter uri 30 to 45 minutes, water temperature 0-2 C. Bipolar wire electrodes (Evenohm S) were implanted through the skin into the various muscles using the method of Basmajian and Stecko ('62). Five pairs of electrodes per fish were implanted simultaneously. Electrode placement routinely was verified by X-ray photographs or occasionally by autopsy immediately after recording was completed. The electrodes were color coded and glued together (Testor's Plastic Cement) into cal that was fastened by means of a plastic lip either the second or third spine of the dorsal fin. The ends of the electrode wires were connected to a freely rotating slip-ring connector (Airflyte Electronics) that was connected to Gould-Brush differential preamplifiers and amplifiers. The electromyographic signals, together with a time base, and the signals of a pulse generator synchronizing the electric events with cine films taken with either a Photosonics IP or Eclair high speed noti picture camera, were stored on magnetic ape by means of a Honeywell 5600 tape recorder. Signals from the tape then were played back at reduced speeds (reduction by a factor up to 15) on a Gould Brush 260 Oscillograph for visual display.

Prey capture sequences were recorded by high speed cinematography at 200 frames sec^{-1}. An Eclair GV-16 mm camera was used in conjunction with three 600 W Smith-Victor filming lights and Kodak 4 × reversal film. For e h species a total of 33 opening and closing s uences were analyzed frame-by-frame on a anguard Motion Analyzer. Films of free-swimming fish compared with those of the same individuals wearing a clamp, electrodes and plastic tubes for pressure recordings. No significant differences in the kinematic profiles of the controls and the experimental fish have been found.

X-ray cinematography allowed direct observations of bone movements. Siemens radiograp equipment with a Sirecon image intensi r and an Eclair GV-16 camera yielded cineradiographic film at 200 frames sec^{-1}. Kodak Plus-X reversal film was exposed at 120 mA and 40 kv. Short pieces of surgical stainless steel wire (0.4 mm in diameter) were placed against the lower and upper pharyngeal jaws to facilitate the recording of bone displacement. Over 40 swallowing sequences have been analyzed for *Serranochromis robustus*, *Haplochromis livingstoni* and *Bathybates fasciatus*. Only five swallowing sequences have been recorded for *Cichla ocellaris*, *Rhamphochromis longiceps*, *Hemibates stenosoma* and *Haplochromis compressiceps*.

Intraoral pressure profiles of *Serranochromis robustus* and *Haplochromis compressiceps* were obtained by means of chronically implanted plastic tubes. The plastic tube (2.0-mm diameter) was implanted by forcing a hypodermic needle (17-gauge) through the ethmoid bone. The plastic tube was passed through the bore of the needle, which subsequently was withdrawn leaving the plastic tube in place. The plastic tube was secured to the roof of the buccal cavity by flaring the end, and to a clamp fixed to the dorsal spine. The plastic tube can be connected to a Statham P 23 Pressure Transducer. Pressure changes are monitored by a Gould Brush Transducer preamplifier. Signals from the transducer were stored on magnetic tape by means of a Honeywell 5600 tape recorder for further analysis. A total of 31 prey capture sequences were recorded for each of the two species. Pressure profiles were analyzed and interpreted in conjunction with the separately obtained electromyographic and kinematic profiles.

All piscivorous cichlid species studied here are wild caught. Multiple experiments were performed on healthy specimens kept under laboratory conditions over a period of 3 to 26 months. All specimens are deposited in the Fish Department of the Museum of Comparative Zoology (MCZ).

The following species have been studied experimentally:

Cichla ocellaris, total length 21 cm, Brazil, MCZ 52659.

Haplochromis compressiceps, total length 17.5, 15.0 and 14.5 cm, Lake Malawi, MCZ 52660.

Serranochromis robustus, total length 18.0 cm, Zambia, Africa, MCZ 52661.

Haplochromis livingstoni, total length 15.5 cm, Lake Malawi, MCZ 52662.

Haplochromis polystigma, total length 15.5, 16.0 cm, Lake Malawi, MCZ 52663.

Rhamphochromis longiceps, total length 22.0 cm, Lake Malawi, Field Museum 76063.

Boulengerochromis microlepis, total length 16.0 cm, Lake Tanganyika, MCZ 49303.

Hemibates stenosoma, total length 17.0 cm, Tanganyika, MCZ 50829.

In addition, anatomical observations were made on *Lamprologus compressiceps* (Lake Tanganyika, MCZ 48014), *Bathybates minor* (Lake Tanganyika, British Museum 1960.9.30-6146-6155), *Bathybates ferox* (Lake Tanganyika British Museum 1950.4.1 5456-5479), *Hemibates stenosoma* (Lake Tanganyika, British Museum 1961.11.22.976-989); *Rhamphochromis woodi,* Lake Malawi, Field Museum, 76073; *Rhamphochromis macrophthalmus,* Lake Malawi, Field Museum, 76084, *Crenicichla saxatilis,* Brazil, MCZ 46086.

RESULTS

Anatomy of prey capture apparatus

The general morphology of the head of some representative cichlids has been described thoroughly by Goedel ('74a,b), Vandewalle ('72) and Barel et al. ('76). Recently, the morphological adaptations of various aspects of the feeding apparatus of cichlids representing a wide range of trophic specializations have been analyzed (Greenwood, '74; Liem, '74; Liem and Osse, '75; Chardon and Vandewalle, '71). Here I will summarize such anatomical aspects as will make the motion and electromyographical analysis more easily understood, emphasizing features that are of critical importance in prey capture. I will focus on those structural characteristics common to all Cichlidae that use the advanced high-speed inertial suction (HSIS) feeding mechanism.

1. Neurocranium

Basically, the neurocranium forms the dorsal mechanical unit that moves dorsoventrally and laterally by bending motions of the anterior vertebral column involving the first four or five vertebrae. Anteriorly the ethmovomerine region underlies part of the upper jaw, and articulations anterior and posterior to the orbit connect the suspensory apparatus to the neurocranium (fig. 3). Posteriorly, the pectoral girdle is attached by means of the forked posttemporal to the epiotic and intercalary (fig. 1: eo, ic).

The morphology of the neurocranium in piscivorous cichlids employing high speed inertial suction feeding can be characterized by a specific set of specializations. As noted by Greenwood ('74) in piscivorous cichlids of Lake Victoria, there is a relatively lengthening of the entire preotic skull region (from the anterior tip of the vomer to the anterior margin of the prootic, fig. 1). Furthermore, there is a marked decrease in the angle at which the preorbital face of the skull slopes downwards (fig. 1). The relatively gentle ethmo-vomerine slope over which the ascending processes of the premaxillae slide (fig. 2: appm) will result in both a larger and a horizontally forward directed gape (fig. 7). During high-speed inertial suction (HSIS) feeding, a horizontally directed gape will be advantageous, because the fish can rely solely on a non-modulated oscillator. It is obvious that when the prey can be captured by the predator at the same level of its forward progress, time delays caused by modulatory and alignment mechanisms can be abolished altogether. All piscivorous cichlids that capture prey by a HSIS mechanism share the elongated preotic skull region with the gentle ethmo-vomerine slope (fig. 1). The specialized features are found in unrelated piscivorous cichlids from such diverse geographical regions as South America *(Cichla ocellaris, Crenicichla saxatilis),* Lake Tanganyika *(Hemibates stenosoma, Boulengerochromis microlepis, Bathybates minor, Lamprologus compressiceps, Haplochromis pfefferi),* Lake Malawi *(Rhamphochromis longiceps, Haplochromis compressiceps, H. polystigma, H. livingstoni),* the African rivers *(Serranochromis robustus),* and Lake Victoria (virtually all piscivorous species discussed by Greenwood, '74).

2. The suspensory apparatus

The suspensory apparatus is a roughly V-shaped complex (fig. 3) of which the tip of the anterior leg (represented by the palatine) articulates with the lateral ethmoid of the neurocranium. This articulation allows mediolateral movements of the suspensory apparatus in relation to the neurocranium. Similar movements occur at the joint between the posterior leg of the V-shaped complex and the neurocranium. Here the principal components of the joint are the hyomandibular (fig. 3: hm), the sphenotic (fig. 1: sph) and pterotic (fig. 1: st).

All piscivores employing the HSIS mode of feeding share a characteristic complex of mor-

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Abbreviations

boc, basioccipital
bs, basisphenoid
e, ethmoid
eo, epiotic
eoc, exoccipital
f, frontal

ic, intercalary
pa, parietal
pf, lateral ethmoid (prefrontal)
po, prootic
pp, prootic process
ps, parasphenoid

pts, pterosphenoid
pv, prevomer (vomer)
soc, supraoccipital
sph, sphenotic
st, pterotic
tf, trigeminofacial chamber

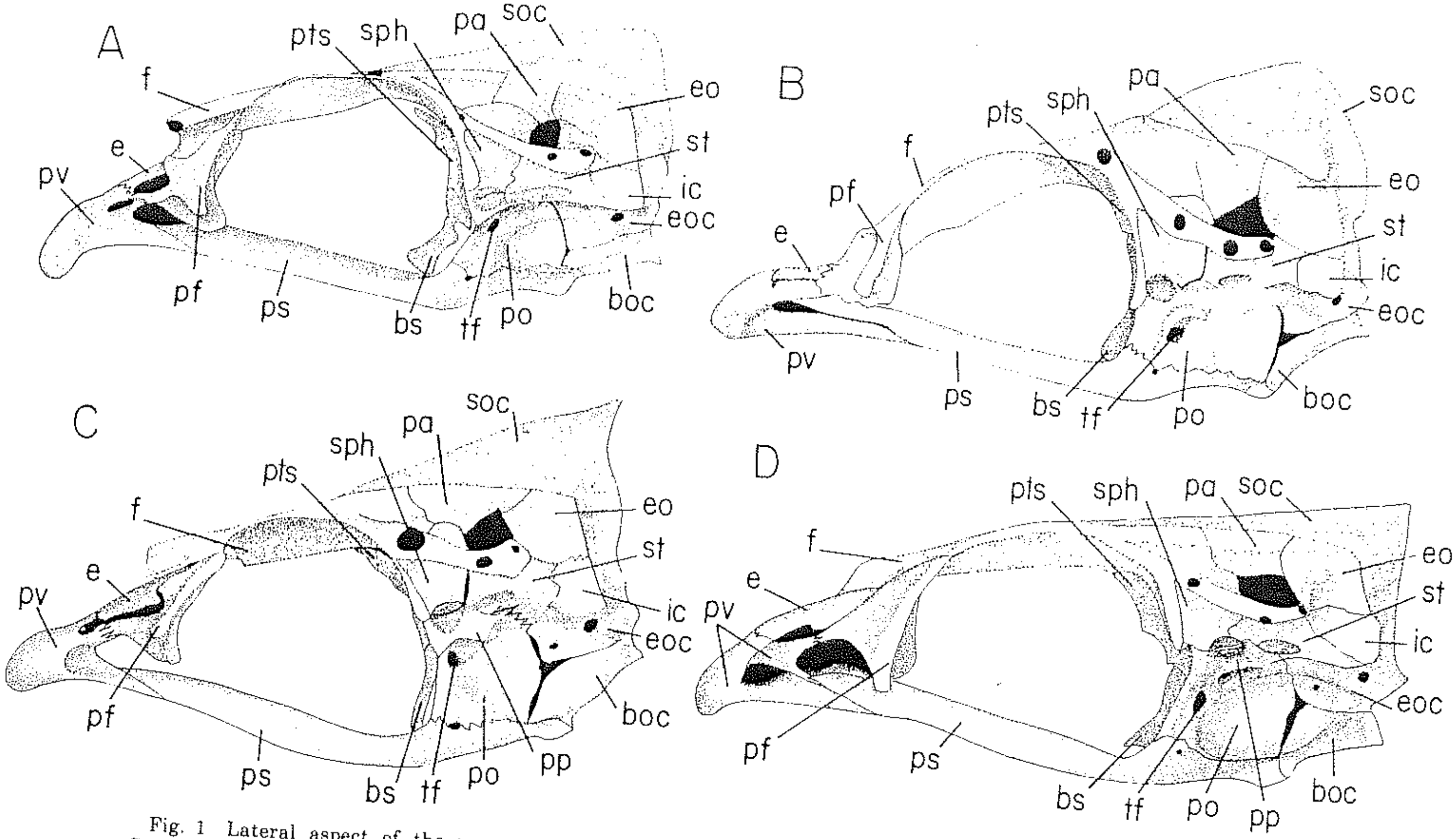

Fig. 1 Lateral aspect of the neurocranium. A. *Boulengerochromis microlepis;* B. *Lamprologus compressiceps;* C. *Hemibates stenosoma;* D. *Bathybates ferox.*

Abbreviations

a, articular
apa, ascending process of articular
apd, ascending process of dentary
appm, ascending process of premaxilla
con, cranial condyle
d, dentary
ect, ectopterygoid
ent, entopterygoid
hm, hyomandibula
mpt, metapterygoid
mx, maxilla
p, palatine
pm, premaxilla
pop, preopercular
ppm, premaxillary condyle of maxilla
q, quadrate
ra, retroarticular
sy, symplectic

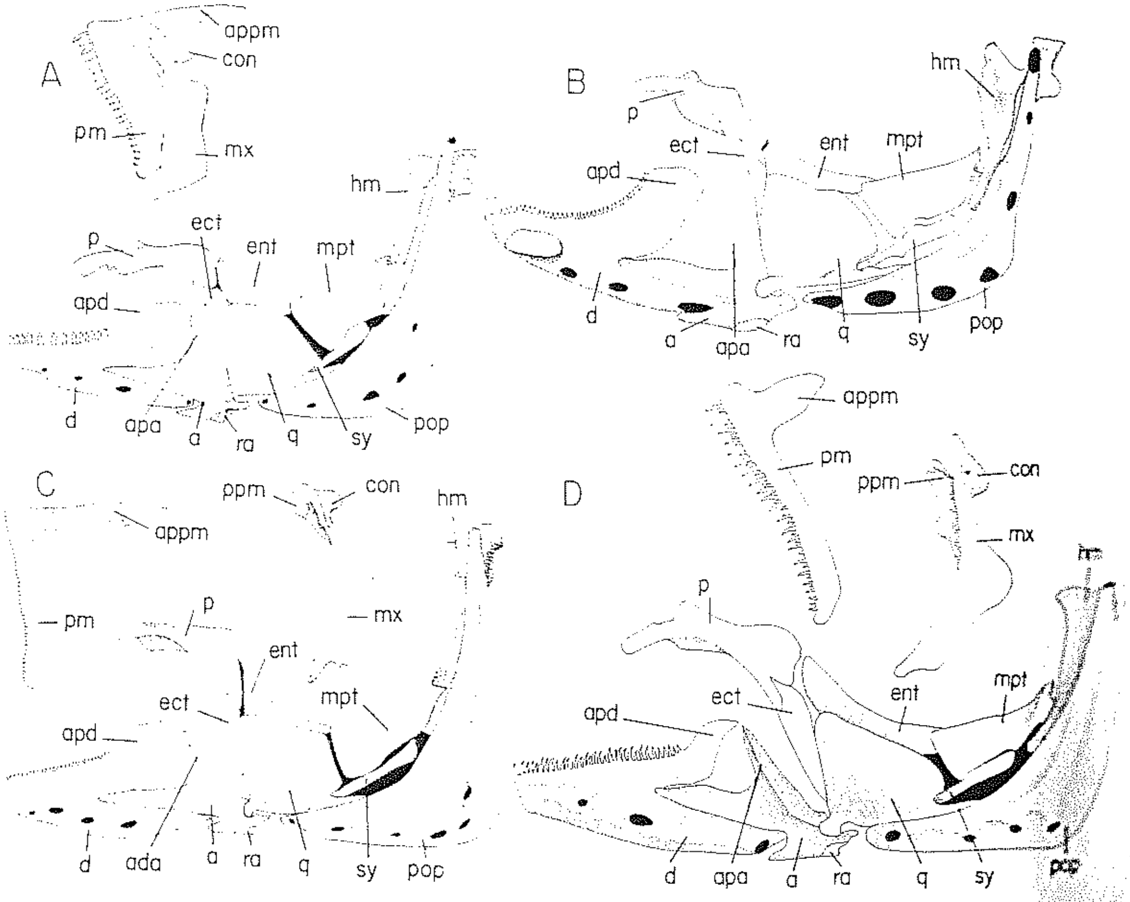

Fig. 2 Lateral aspect of suspensory apparatus and jaws. A. *Boulengerochromis microlepis;* B. *Lamprologus compressiceps;* C. *Hemibates stenosoma;* D. *Bathybates ferox.* Upper jaw in *L. compressiceps* is omitted.

phological specializations, although no single unique feature in the suspensory apparatus distinguishes this trophic group from others. Specializations mainly have affected the palatine and hyomandibular. Invariably, the hyomandibular possesses an elongate symplectic process, which is at least 2.5 times longer than its body (fig. 2: hm). In lateral view, the hyomandibular is slender, the depth being at least twice the width, restricting the area for muscle attachments, but increasing the moment arm of the levator arcus palatini muscle around the craniohyomandibular joint. Furthermore, the connection between the symplectic process of the hyomandibular and the posterior margin of the metapterygoid is loose, allowing considerable movement between the two.

The palatine (fig. 2: p) is not sutured to the entopterygoid. Its length, measured between the maxillary process and prefrontal process is quite long in proportion to the depth of the

Abbreviations

aap, adductor arcus palatini
am, adductor mandibulae
bpc, buccopharyngeal cavity
do, dilator operculi
ep, epaxial muscles
g, gills
gh, geniohyoideus
hy, hypaxial muscles
ihl, interoperculohyoid ligament
lap, levator arcus palatini
lim, interoperculomandibular ligament
lo, levator operculi
oc, opercular cavity
sh, sternohyoideus

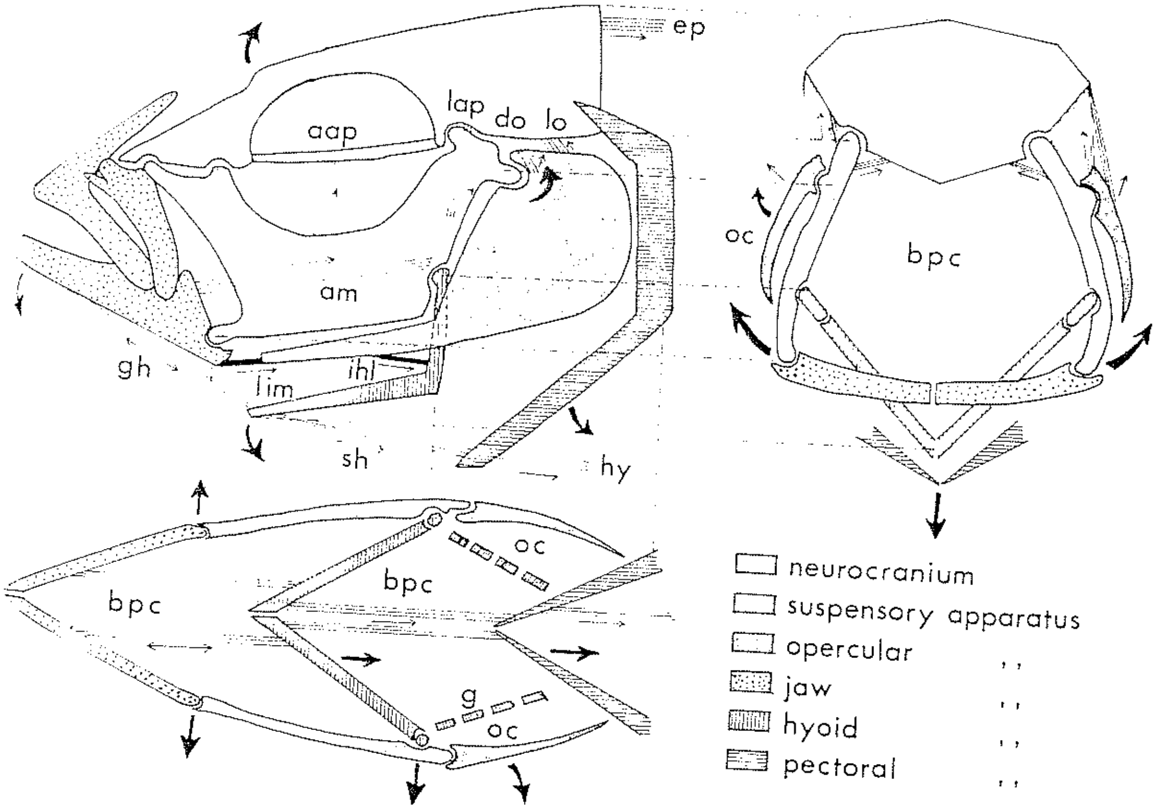

Fig. 3 Diagram of the major mechanical units, couplings and ligaments of the head of a piscivorous cichlid. Muscles and the principal direction of their forces are indicated respectively by light lines and light arrows. Heavy arrows depict major movements during the expansive phase of the feeding cycle.

…e, i.e., the greatest distance between the prefrontal process and the palatal flange. The …o between length and depth of the palatine lies between 2.3 and 4.5 in this trophic group.

Jaw apparatus

The mandible, invariably elongate (fig. 2), articulates by means of a synovial joint with the prominent condyle of the quadrate allowing movements around a transverse axis. All cichlids with a HSIS feeding mechanism possess a characteristic mandible. The ascending proce[illegible] of both the dentary and articular (fig. 2: a[illegible] apa) are attenuated and widely separated from each other. Furthermore, the distance between the quadratomandibular joint and the insertion site of the interoperculomandibular ligament is shortened considerably. The distance between the quadratomandibular joint and the anterior tip of the mandible is 8 (in *Boulengerochromis)* to 11 (in *Bathybates)* times the distance between the quadratomandibular joint and the insertion site of the interoperculomandibular ligament. In all piscivorous cichlids, the distance between the quadratomandibular joint and the ventral margin of the mandible immediately below it is minimized (fig. 2). An exceptionally elongated postarticular process immediately behind the quadratomandibular joint characterizes the mandible of all piscivorous cichlids (fig. 2).

Similarly, the upper jaw of all cichlids with HSIS feeding tactics is specialized. The dentigerous ramus of the premaxilla is elongate, to match the elongate mandible. In general, the ascending processes of the premaxillae exhibit a correlative elongation (fig. 2: appm). A spine-shaped articular process usually is present near the distal end of the ascending process of the premaxilla. The maxilla (fig. 2: mx) has undergone a correlative elongation in all piscivorous cichlids. As a result the maxilla is slender with a very constricted necklike region just below the well developed premaxillary and cranial condyles. Otherwise the maxilla resembles that of the generalized insectivorous *Haplochromis burtoni* (Liem and Osse, '75).

4. The opercular apparatus

No distinct specializations are found in the opercular apparatus of cichlids employing HSIS feeding strategies (fig. 4). A ball-and-socket joint connects the opercular apparatus to the posterodorsal knoblike corner of the suspensory apparatus. At this joint, the opercular can rotate in the parasagittal plane allowing the opercular apparatus to exert a pull on the posteroventral corner of the mandible (fig. 3) and can make abducting and adducting motions to create respectively low and high pressures in the gill cavity. Anterodorsally, the opercular exhibits a distinct dilatator process, serving as an insertion site of the dilatator-operculi muscle. As in all cichlids, the interopercular (fig. 4) is elongate with the anterior edge deeply notched to accommodate the interoperculomandibular ligament (fig. 3: lim; fig. 5: LIM). Dorsally, a distinctly reenforced flange is sometimes present to serve as the site of attachment for the interoperculohyoid ligament (fig. 3: ihl).

5. The hyoid and pectoral girdle apparatus

These two units are mentioned here only briefly because they conform in general configuration with those of other cichlids already described (Goedel, '74a). Neither of the two units exhibit any salient specialization that can be correlated with the high speed inertial suction feeding mechanism. Yet, both units play most important roles in jaw opening and the generation of suction (e.g., Liem, '70). The two hyoid rami are suspended from the posteromedial side of the suspensory apparatus by means of the interhyal that articulates with the posterodorsal edge of the epihyal. A well differentiated interoperculohyoid ligament links the epihyal with the interopercular (fig. 3: ihl). In this way movements of the hyoid are translated to the interopercular and the mandible (fig. 3, Osse, '69; Liem, '70). The pectoral girdle, of which the cleithrum represents the largest single bony element in teleosts, serves as the site of extensive attachments for such massive muscle masses as the sternohyoideus, hypaxial (fig. 3: sh, hy) and protractor pectoralis. Therefore, it is rather surprising that no unique feature has been found in this mechanical unit separating this trophic group from others.

6. Myology

a. Jaw muscles. The adductor mandibulae complex is subdivided into four parts: A_1, A_2, A_3 and A_w (intramandibular head). The most dorsal and superficial part is the parallel-fibered A_1, the fibers of which originate from the preopercular. In large-eyed forms (e.g., *Hemibates,* fig. 5: AM_1) the origin is confined to the lower half of the preopercular, whereas in small-eyed forms (e.g., *Serranochromis,* fig. 7: AM_1) the origin extends over almost the entire length of the vertical limb of the preopercular. Posteriorly the muscle covers the distal portion of the levator arcus palatini. While anteriorly it inserts by means of an elongate tendon on the medial aspect of the maxilla (figs. 5-7: AM, tam_1) just below the

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Abbreviations

a, articular
apa, ascending process of articular
apm, ascending process of premaxilla
bs, basisphenoid
d, dentary
e, ethmoid
ect, ectopterygoid
ent, entopterygoid
eo, epiotic
f, frontal
hm, hyomandibular
ic, intercalary
iop, interopercular
la, lacrimal
mpt, metapterygoid
mx, maxilla
n, nasal
op, opercular
pa, parietal
pf, lateral ethmoid
pls, pterosphenoid
pm, premaxilla
pop, preopercular
ps, parasphenoid
q, quadrate
r, retroarticular
sb, sesamoid bone
so, circumorbitals
soc, supraoccipital
sop, subopercular
sph, sphenotic
st, pterotic
sy, symplectic

Fig. 4 Lateral aspect of the skull, after the removal of the pectoral girdle and hyoid apparatus. A. *Boulengerochromis microlepis.* B. *Lamprologus compressiceps.*

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. lateral
ethmoid
s, pterosphenoid
n, premaxilla
p, preopercular
, parasphenoid
quadrate
retroarticular
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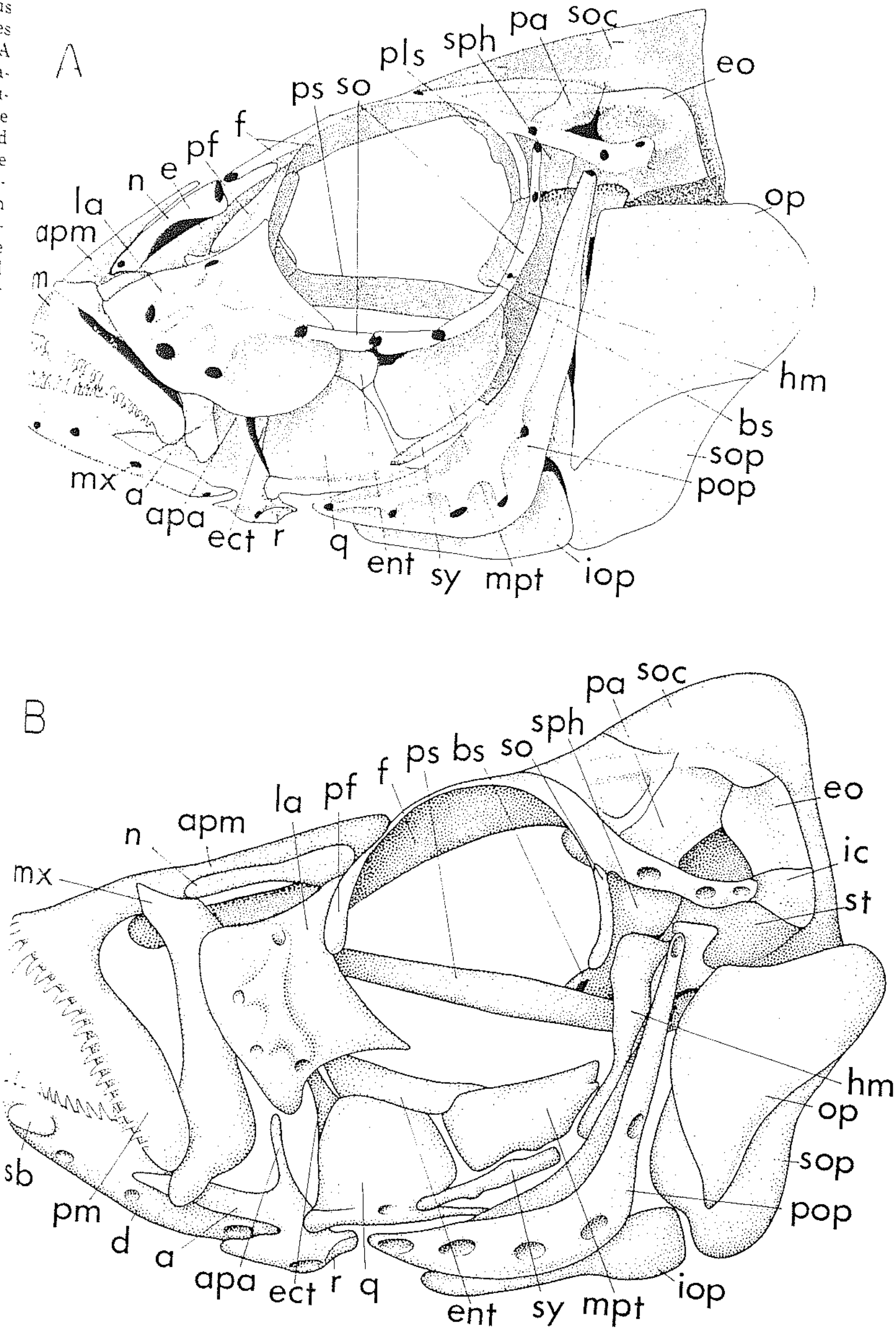

Figure 4

Abbreviations

AAP, adductor arcus palatini	LIM, interoperculomandibular ligament
AM_1, A_1 portion of adductor mandibulae	LO, levator operculi
AM_2, A_2 portion of adductor mandibulae	M, mandible
APPM, ascending process of premaxilla	MX, maxilla
CAR, rostral cartilage	OP, opercular
DO, dilator operculi	P, palatine
E, ethmoid	PM, premaxilla
EM, epaxial muscles	POP, preopercular
IOP, interopercular	Q, quadrate
LAP, levator arcus palatini	SOP, subopercular
LI, palatopalatine ligament	

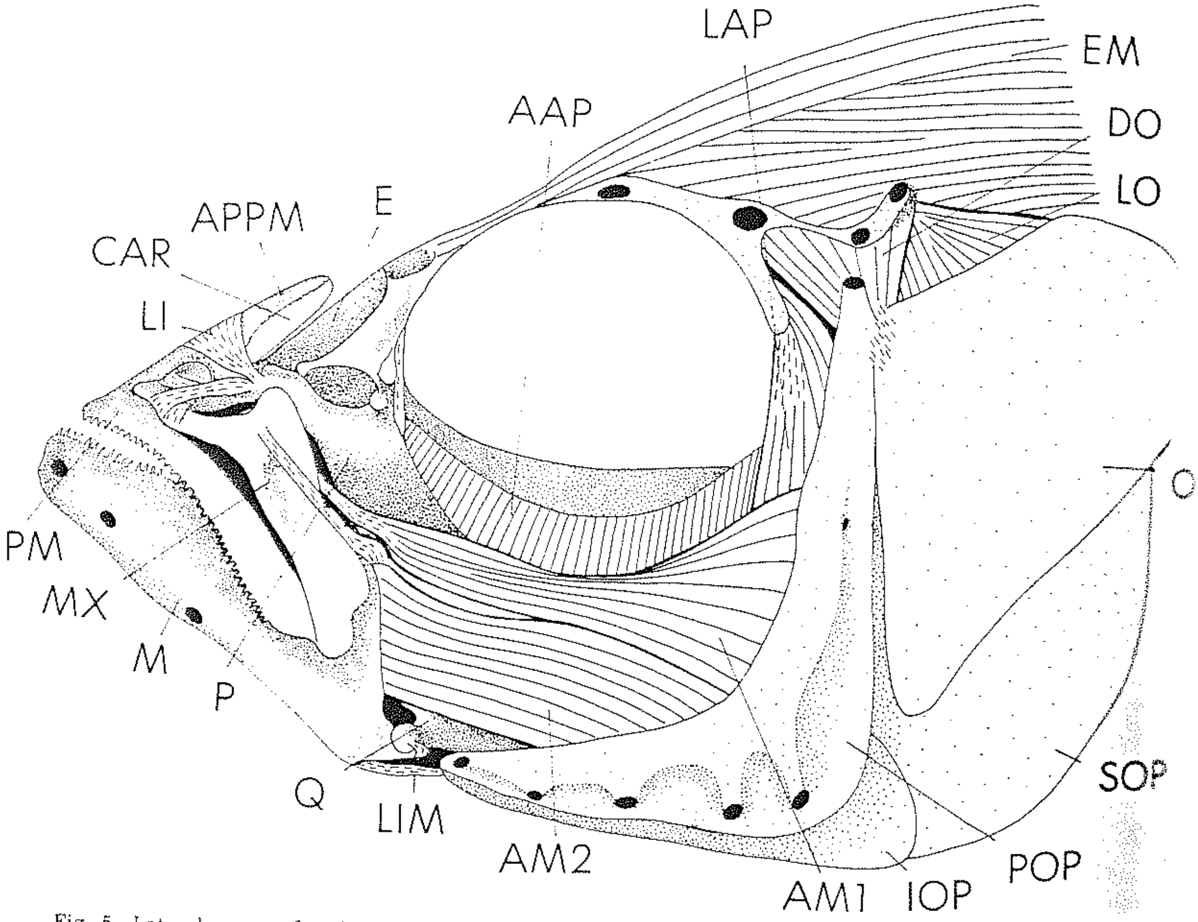

Fig. 5 Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball of *Hemibates stenosoma.*

premaxillary condyle. The tendon itself is part of an aponeurosis that is ventrally attached to the medial aspect of the articular just above the jaw joint. A_2 originates from the suspensory apparatus and inserts by means of one head on the mandible. The insertion is on the ascending process (fig. 5: AM_2) of the articular. A_3 represents the deepest head of the complex. It originates from the metapterygoid, symplectic and symplectic process of the hyomandibular; anteriorly A_3 becomes tendinous to insert on a sesamoid bone in Meckel's cartilage on the medial aspect of the mandible (fig. 6: tam_3), the coronomeckelian.

The *intermandibularis* (fig. 6: **im**) is an unpaired, parallel-fibered muscle connecting the two halves of the lower jaw. It lies dorsal to both the intramandibularis (A_w) and the geniohyoideus muscles.

b. Muscles of the suspensory apparatus. The

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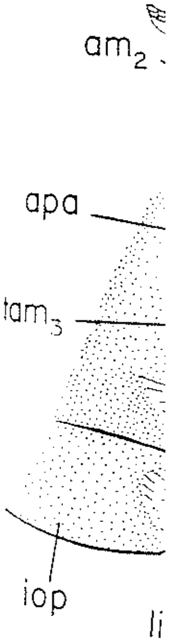

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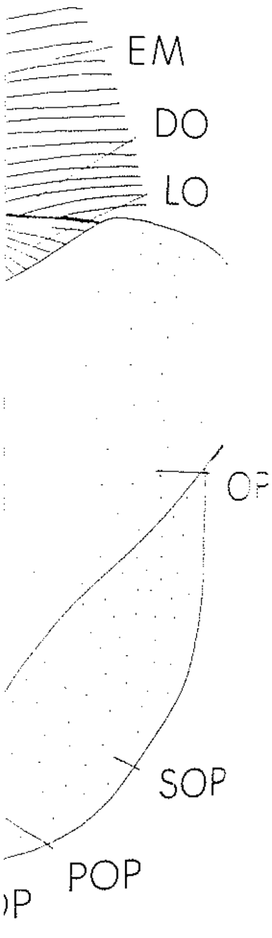

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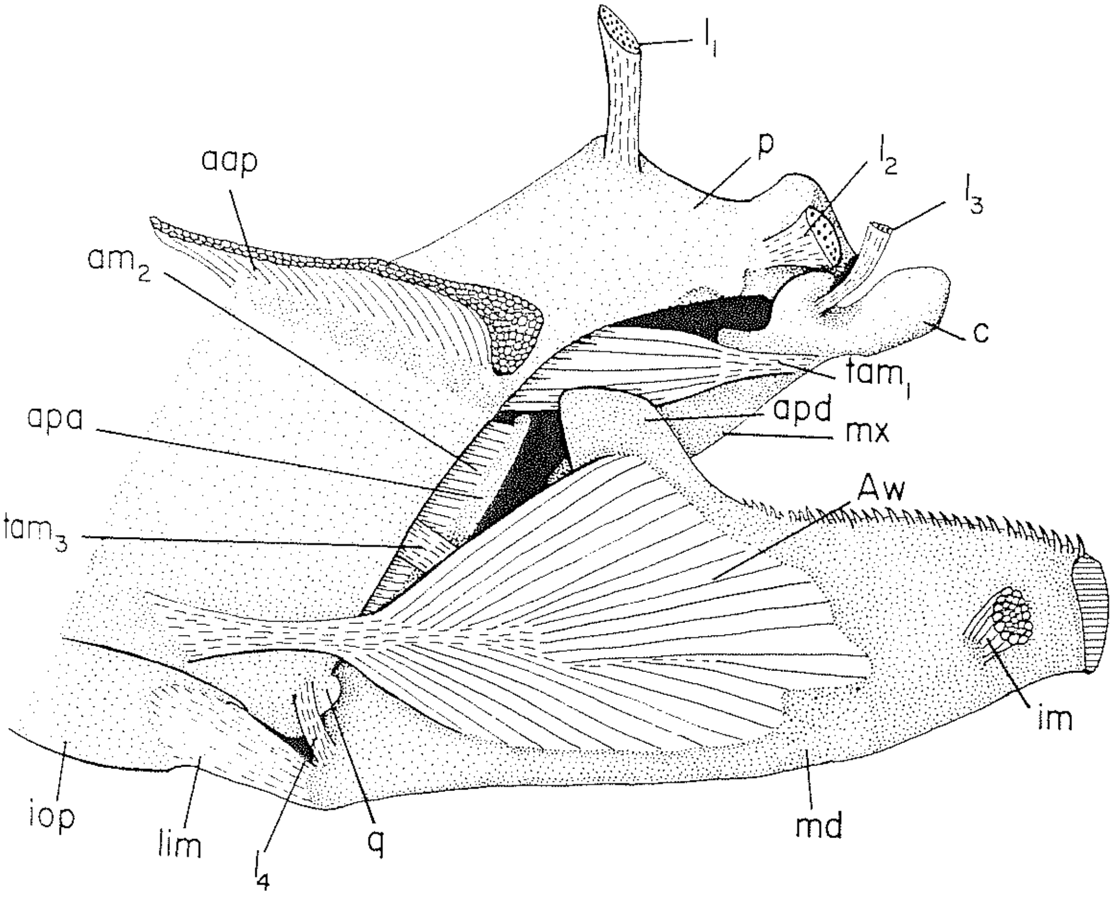
Abbreviations

aap, adductor arcus palatini
am₂, A₂ portion of adductor mandibulae
Aw, (intramandibularis) portion of adductor mandibulae
apa, ascending process of articular
apd, ascending process of dentary
c, cranial condyle of maxilla
im, intermandibularis
iop, interopercular
l₁, palatoethmoid ligament
l₂, palatovomerine ligament
l₃, ligament associated with premaxillary condyle of maxilla
l₄, medial collateral ligament of quadratomandibular joint
lim, interoperculomandibular ligament
md, mandible
mx, maxilla
p, palatine
q, quadrate
tam₁, tendon of A₁ portion of adductor mandibulae
tam₃, tendon of A₃ portion of adductor mandibulae



g. 6 Medial aspect of the left mandible, maxilla and interior portion of the suspensory apparatus with associated muscles and ligaments of *Hemibates stenosoma.*

ator arcus palatini muscle occupies the relatively narrow postorbital portion of the suspensory apparatus anterior to the preopercular. It originates from the postorbital process of the sphenotic and inserts on the anterior aspect of the dorsal portion of the vertical limb of the preopercular, the symplectic process of the hyomandibular and the muscular process of the metapterygoid (figs. 5, 7: LAP).

The *adductor arcus palatini* is parallel-fibered and forms the roof of the buccal cavity, connecting the dorsal rim of the suspensory apparatus to the basis of the neurocranium (figs. 5, 7: AAP). Its origin includes the ventrolateral edge of the parasphenoid, and part of the prootic: the insertion involves the dorsomedial edge of the palatine, entopterygoid and metapterygoid.

Further posteriorly, a short half-cylindrical muscle, the *adductor hyomandibulae,* bridges the gap between the medial aspect of the hyomandibular and prootic.

c. Muscles of the opercular. Immediately posterior to the adductor hyomandibulae is another half cylindrical muscle, the *adductor operculi*, originating from the exoccipital and inserting on the medial side of the opercular adjacent to the operculohyomandibular joint.

More laterally, the triangular *dilatator operculi* muscle originates from the pterotic and inserts on the lateral aspect of the anterodorsal corner of the opercular (figs. 5, 7: DO).

Just medial and posterior to the origin of the dilatator operculi, is the origin of the *levator operculi* muscle that runs to the medial aspect of the opercular (figs. 5, 7: LO). The insertion site is on a nearly horizontal ledge and the flat inner surface above this ledge.

d. Ventral muscles of the head. The cone-shaped *sternohyoideus* connects the urohyal of the hyoid arch with the cleithrum of the pectoral girdle and is a rather prominent muscle (figs. 3, 7,: SH, sh). In piscivorous cichlids, this muscle tends to be more elongate, exhibiting two myosepts.

Posteriorly, the *hypaxial musculature* attaches to almost the entire posterior surface of the cleithrum (figs. 3, 7: hy, HY). Its configuration is rather uniform in all cichlids studied.

The *geniohyoideus muscle* (also known as the protractor hyoideus) connects the hyoid rami with the mandible. Essentially, it is a parallel-fibered muscle forming part of the buccal floor. In all piscivorous cichlids studied, the geniohyoideus is extremely elongate and slender (figs. 3, 7: gh, GHA, GHP). The posterior attachment is confined to the lateral aspect of the ceratohyal, none of the fibers is associated with any branchiostegal ray. In cichlids belonging to most other trophic groups, associations between the geniohyoideus and one or more branchiostegal rays are common.

In general, this trophic group of cichlids possesses a weakly developed *hyohyoideus inferior* muscle. As in most teleosts, the medial parts of the left and right sides of the hyohyoideus inferior cross each other in the median, the left bundle traversing dorsally to the right one. The thin aponeurosis covering the ventral aspects of the hypohyal and ceratohyal serves as an origin. The hyohyoideus inferior inserts on the anterodorsal edges of the first, and occasionally, the second branchiostegal ray.

The *hyohyoideus superior muscle* is a ver thin, short-fibered muscle, that runs betwee adjacent branchiostegal rays and between th dorsomedial edge of the last branchiostega ray and the medial aspect of opercular and subopercular.

The *hyohyoideus transversus* subdivision interconnecting the most anterior branchiostegals of opposite sides, so prominently differentiated in other trophic forms (e.g., *Tropheus*, Liem and Osse, '75: fig. 13c), is virtually absent in the piscivorous cichlids studied. In its place one finds a fibrous transverse aponeurosis.

e. Epaxial muscles. As in all cichlids, the dorsal body musculature extends forward to insert on the dorsal and posterior aspects of the neurocranium (figs. 3, 5, 7: ep, EM).

Behavioral strategies of prey capture by piscivorous cichlids

Observations in the laboratory over extended periods indicate that piscivorous cichlids can be classified into two categories (Sohn, personal communication). (1) *Ambush hunters* wait stealthily for the prey; once the prey is in range, the predator lunges towards it. Among the ambush hunters are *Haplochromis livingstoni, H. compressiceps, H. polystigma* and *Lamprologus compressiceps.* (2) *Pursuit hunters* are strong, rapidly swimming fishes that swim towards their prey, pursuing it until it is lost or captured. Among pursuit hunters are the adults of *Bathybates ferox, Hemibates stenosoma, Boulengerochromis microlepis, Serranochromis robustus, Rhamphochromis macrophthalmus* and *Cichla ocellaris.*

Published accounts (e.g., Fryer, '59; Greenwood, '62; Matthes, '62; Buruga, '67; Fryer and Iles, '72) and my laboratory studies seem to indicate that piscivorous cichlids are not simultaneously effective as pursuit and ambush hunters. It is axiomatic that natural selection favors those anatomical, functional and behavioral features that increase the probability of capture of prey. If detection of the predator by the prey and pursuit ability are directly correlated, it follows that only species that possess either good pursuit ability or the appropriate cryptic apparatus, which is a prerequisite for a successful ambush strategy, have a high expectation of capturing prey.

Because the velocity of a swimming fish increases with size (Bainbridge, '63), it is not surprising that most hunting cichlids (e.g.,

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Boulengerochromis microlepis, the world's largest cichlid; *Rhamphochromis, Diplotaxodon, Bathybates, Hemibates* and *Cichla)* are the larger members of the family. Pursuit hunters maximize velocity, but as a trade-off, detectability by the prey is also augmented.

In contrast, ambush hunters often are well camouflaged (e.g., *Haplochromis livingstoni)* and depend upon an unseen approach maximizing the elements of surprise at close range. Stillness is also extraordinarily important to an ambush hunter (e.g., *Lamprologus compressiceps* and *Haplochromis compressiceps)* to avoid evoking the escape response of a prey. Among cichlids, ambush hunters do not reach the extraordinarily large sizes encountered among pursuit hunters.

Because any increase in the pursuit ability of the predator increases the probability that the predator will be detected, the highest expectation of a successful prey capture should result in a predator that is either a pure pursuit hunter or a cryptic ambush hunter, but not one of intermediate abilities. Therefore, it is not surprising that strictly piscivorous cichlids have certain narrow limits of morphology (e.g., Greenwood, '74), behavior, and as we will see, function.

It is important to note that in piscivorous cichlids the young of ambush hunters are often piscivores themselves as small size does not change their camouflage abilities (e.g., *Haplochromis compressiceps, H. livingstoni* and *Lamprologus compressiceps).* In sharp contrast, the juveniles of pursuit hunters are either invertebrate eaters (e.g., *Serranochromis robustus,* Toots and Bowmaker, '76; *Boulengerochromis microlepis)* or cryptic ambush hunters (e.g., *Hemibates stenosoma).*

Cinematographic records show clearly that ambush hunters employ varying approach velocities, especially when capturing an agile and elusive prey, which bases its escape response on an initial predator approach velocity that is lower than the final velocity. Pursuit hunters, on the other hand, do not vary their approach velocities. Instead, pursuit hunters rely solely on an accentuated acceleration, and maximize the kinetic energy gained in the form of momentum prior to the sudden opening of the mouth.

Functional analysis of prey capture

Representatives of both ambush and pursuit hunters have been analyzed under three conditions: capturing sluggish prey (goldfish, *Carassius auratus)* of varying sizes in midwater; capturing agile and elusive prey *(Fundulus heteroclitus,* chubs) of varying sizes from midwater; and feeding on brine shrimp *(Gammarus* sp.) by some of the predaceous species. Because the nature of the escape response of the prey and the behavioral strategy of the cichlid predator exert a pronounced influence on the total functional profiles, the data are presented under five categories.

Capture of sluggish prey by pursuit hunters

Pursuit hunters ranging in total length from 16-22 cm, were presented with live goldfish ranging in total length from 4-9 cm. Within this size range, prey size does not influence appreciably the electromyographic and motion patterns.

All pursuit hunters show consistently three distinct phases:

Preparatory phase. During this phase the initial volumes of both the orobranchial and opercular cavities are decreased. Volume reduction is accomplished by actions of the adductor mandibulae parts A$_2$, A$_3$, and A$_w$, the adductor arcus palatini and geniohyoideus anterior and posterior muscles (figs. 5-7: AM$_2$, AM$_3$, AAP, GHA), which, respectively, close the jaws tightly (fig. 7: stage 1), adduct the suspensory apparatus, and raise the buccal floor. As a result, the pressure in the oral cavity increases (fig. 9). The preparatory phase during the capture of sluggish prey, lasts consistently around 50 msec, with fluctuations of not more than 5 msec. Slight overlap between the activities of the adductor and levator arcus palatini does occur occasionally (fig. 7: AAP, LAP).

Expansive phase. This phase starts the moment the suspensory apparatus is abducted (fig. 8) and ends when jaw adduction commences. During this phase, there is an explosive unfolding of the orobranchial and opercular cavities, and the branchiostegal apparatus, effected by strong activity of the epaxial (figs. 3, 5, 7: EM), levator arcus palatini (LAP), dilatator operculi (DO), hyohyoideus inferior, and sternohyoideus (SH) muscles, which, respectively, lift the neurocranium (fig. 7: stage 3), move the sidewalls of the orobranchial chamber sideways, enlarge the opercular cavity, fan out the branchiostegal membrane, and depress the floor of the mouth (fig. 7: stage 4). At the same times, the mouth is opened and protruded rapidly by the action of the levator operculi (figs. 3, 7: LO and stages 2-4), sternohyoideus and epaxial muscles (see Liem, '70, for details of the couplings involved). The rapid increase in volume and the sudden opening and protrusion of the jaws are clearly reflected in the pressure curve (fig. 9) as an instant decrease in pressure. In all pursuit hunters capturing sluggish prey, the expansive phase lasts from 100-125 msec (fig. 7). Overlap of firings of antagonistic muscles is quite limited. For example, the levator arcus palatini and adductor arcus palatini muscle firings overlap for about 65 msec during a burst of 175 msec of the latter muscle (fig. 7: AAP, LAP). Otherwise, firings of antagonistic muscle pairs are well segregated. The electromyographic, kinematic and pressure profiles (figs. 7, 9) integrated with the anatomical features (fig. 3) support the hypotheses on the couplings of the head of perchlike fishes as proposed by Liem ('70) on the basis of surgical manipulations and Osse ('69) on the basis of electromyography of the perch.

Compressive phase. This phase is determined on the basis of the start of jaw adduction (fig. 8). During this phase, the pressure curve reverses abruptly (fig. 9), the jaws are adducted rapidly, but retraction of the jaws lags slightly behind mouth closure (fig. 7: stage 5), supporting Alexander's observations ('67). As in nandids (Liem, '70), adduction of the suspensory apparatus lags behind that of the jaws (fig. 8). Only after full closure of the mouth can we observe a rapid decrease in the volume of the orobranchial cavity (fig. 8), adduction of both the suspensory and opercular apparatus, folding of the branchiostegal membrane, and raising of the buccal floor. Closure of the mouth correlates with distinct bursts of all components of the adductor mandibulae muscle complex, whereas suspensory adduction correlates with activity in both the adductor arcus palatini (fig. 8: AAP) and adductor hyomandibulae muscles. Raising of the buccal floor occurs when activity of the geniohyoideus muscle is unopposed by the sternohyoideus (fig. 7: GHA, SH), and folding of the branchiostegal membrane coincides with the firing of the hyohyoideus superior. The duration of the Compressive Phase during the capture of sluggish prey by pursuit hunters is consistently shorter (100 msec in *Serranochromis*) than the Expansive Phase (fig. 7).

Capture of elusive prey by pursuit hunters

Both kinematic and electromyographic profiles differ in several salient characteristics from those recorded during the capture of sluggish prey. Differences involve the duration of the three phases, abbreviation of the capturing act, and considerable synchrony in the activity of all cephalic muscles.

Perhaps the most far-reaching change is the sharp reduction in duration of all three phases. Both the preparatory and compressive phases are reduced by half; the Expansive Phase is reduced by at least 25% (figs. 8, 9). In the last half of the Expansive Phase all muscles show simultaneous activity, resulting in a marked decrease in velocity and eventual levelling off of suspensorial abduction. Thus, co-contraction of counteracting muscles seems to decelerate the expanding movements during the last half of the expansive phase for a duration of 40 msec.

In the first half of the abbreviated Compressive Phase co-contraction of the adductor arcus palatini and its principal antagonist, the levator arcus palatini continues. Once activity of the latter ceases in the second half of the Expansive Phase, unopposed action of the adductor arcus palatini and adductor hyomandibulae adducts the suspensory apparatus within 25 msec. Of course, the onset of the Compressive Phase coincides with the rapid adduction of the jaws within a timespan of 40 msec (fig. 8). The pressure curve (fig. 9) reflects faithfully suspensorial adduction. During the first half, the pressure within the oral cavity rises slowly and slightly, but in the last half of the Compressive Phase the pressure curve rises steeply, reflecting the effects of an accelerated suspensorial adduction (fig. 8).

Fig. 7 On left, lateral and ventral aspects of the cephalic musculature of *Serranochromis robustus* is depicted. In the center, representative myograms taken during the capture of a slow moving goldfish. Surrounding the myograms are tracings of frames of a high speed motion picture. Frame numbers (1-6) accompanying the tracings correspond with the numbers indicated at the top of the myograms. The three phases are the preparatory (p), expansive (e), and compressive (c). Major movements of the cephalic components between successive frames are indicated by arrows. During the preparatory phase jaws are tightly closed, and the oropharynx compressed, while the expansive phase is characterized by an explosive unfolding and jaw opening, initiated by the levator operculi (LO) muscle and immediately followed by the epaxial (EM), sternohyoideus (SH), hypaxial (HY) and levator arcus palatini (LAP) and dilatator operculi (DO) muscles. During the compressive phase, the jaws are closed at high velocity by the adductor mandibulae complex (AM1-3) and the oropharynx compressed by the adductor arcus palatini (AAP) and geniohyoideus anterior (GHA) and posterior (GHP) muscles. At frame 6, the elements have returned to their resting condition.

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Abbreviations

AAP, adductor arcus palatini
AM_1, A_1 portion of adductor mandibulae
AM_3, A_3 portion of adductor mandibulae
c, compressive phase
DO, dilatator operculi
e, expansive phase
EM, epaxial muscles
GHA, geniohyoideus anterior
GHP, geniohyoideus posterior
HY, hypaxial muscles
LAP, levator arcus palatini
LO, levator operculi
p, preparatory phase
SH, sternohyoideus

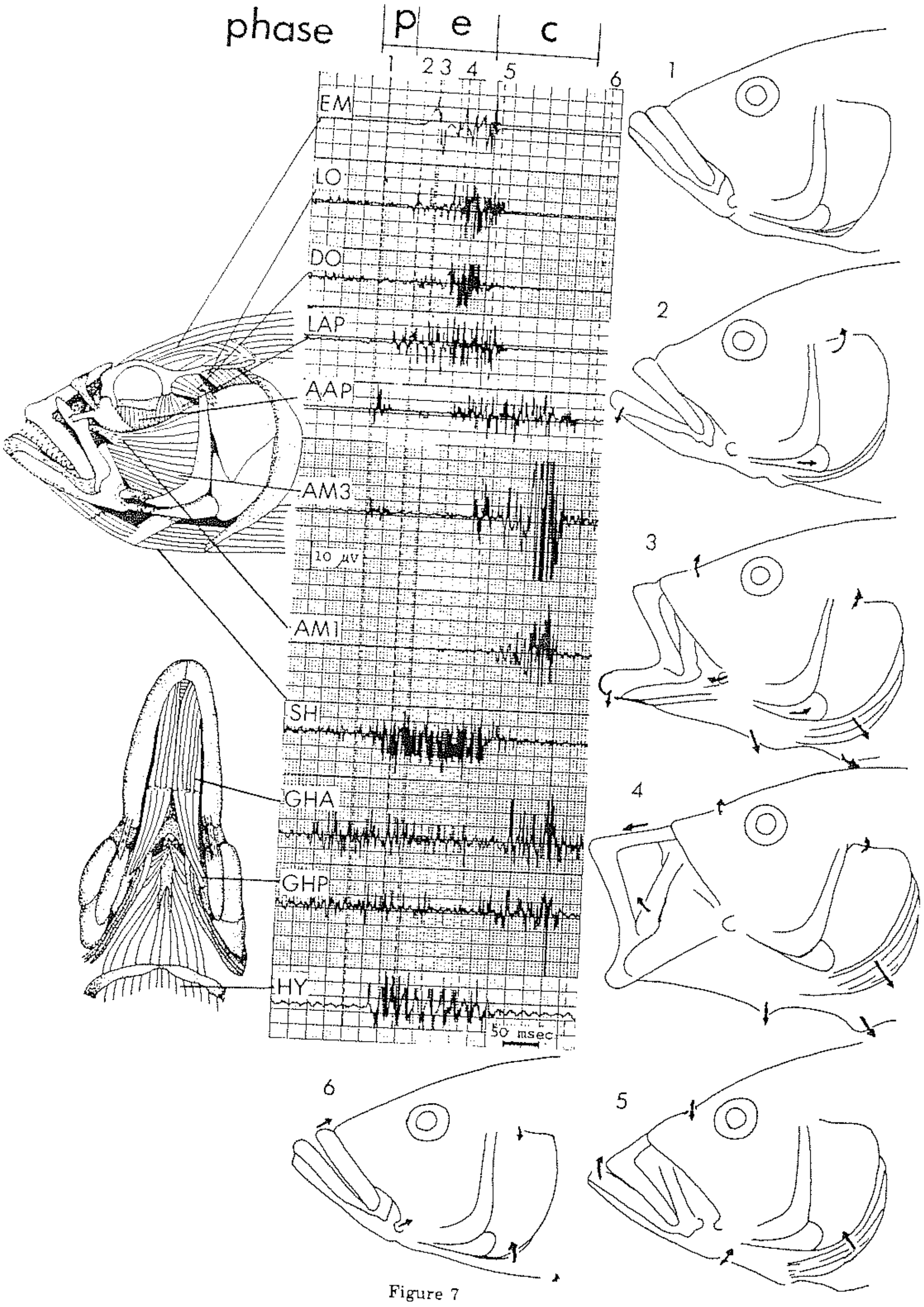

Figure 7

Numerous bilateral recordings (fig. 8) reveal that the electromyographic and kinematic profiles of prey capture by pursuit hunters are symmetrical in regard to pattern as well as time.

Capture of sluggish prey by ambush hunters

Both kinematic and electromyographic profiles closely resemble those of pursuit hunters during capture of sluggish prey (figs. 7, 10), except for the time bases. In general, ambush hunters abbreviate the total duration of the engulfing act, which lasts 140-160 msecs versus 200-250 msecs in pursuit hunters.

The *Preparatory Phase* lasts half as long as that of pursuit hunters. In marked contrast to pursuit hunters, ambush hunters show early activity of the levator arcus palatini, sternohyoideus and hypaxial muscles (fig. 10: LAP, SH, HY). It is difficult to decipher the meaning of activity of such *abductors*, during an essentially *adductive* preparatory phase. The pressure curve (fig. 9) clearly shows that a positive pressure of comparable magnitude to that of pursuit hunters is created during this phase.

The *Expansive Phase* lasts about 75 msec and is characterized by a very steep ascent of the suspensorial abduction curve (fig. 10). However, midway during this phase, there is a

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Abbreviations

AAP,	adductor arcus palatini
AM₂,	A_2 portion of adductor mandibulae
c,	compressive phase
DO,	dilatator operculi
e,	expansive phase
EM,	epaxial muscles
GHA,	geniohyoideus anterior
HY,	hypaxial muscles
LAP,	levator arcus palatini
LO,	levator operculi
p,	preparatory phase
SH,	sternohyoideus

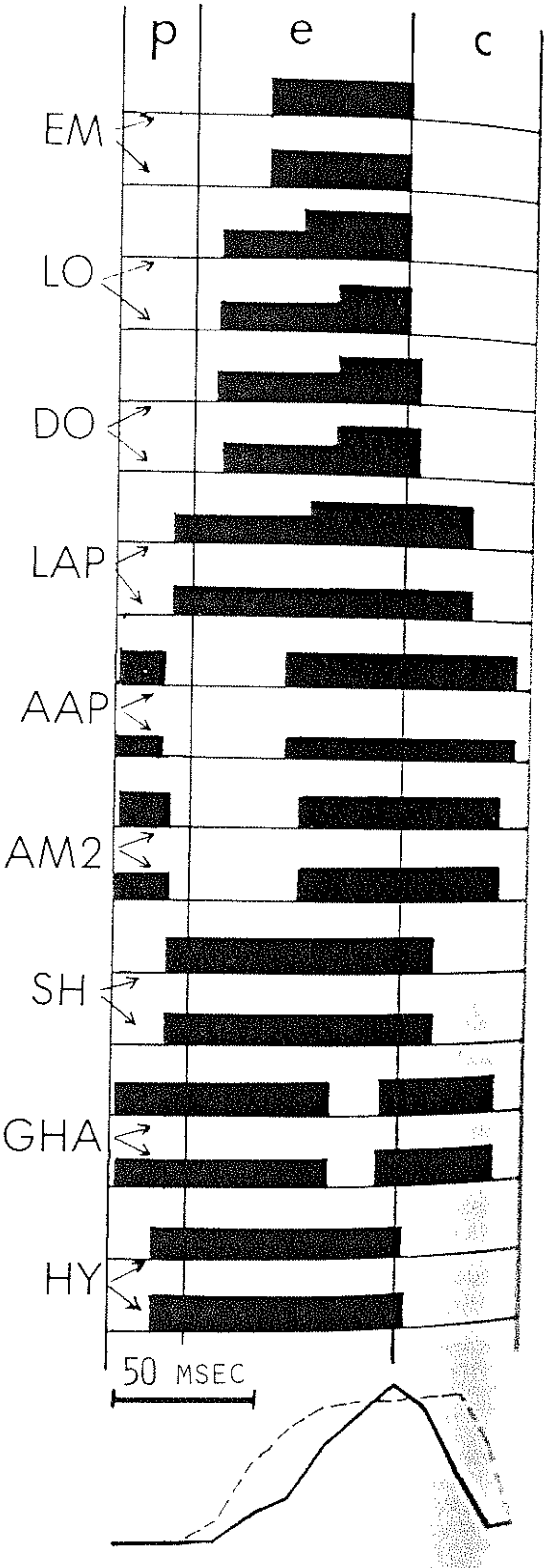

Figure 8

Fig. 8 Diagram summarizing activities of cephalic muscles during the capture of elusive and agile prey (*Fundulus heteroclitus*) by the pursuit hunter *Serranochromis robustus*. Recordings are made from left and right sides. In each couplet, the top represents left side and bottom, the right side. Activity pattern is bilaterally symmetrical. The three phases, preparatory (p), expansive (e), and compressive (c), are indicated at the top and vertical lines. Bottom graphs indicate jaw movement (heavy, solid line) and suspensory movement (broken line). Any deviation from the closed or adducted position, is recorded as a positive figure. Thus the zero line represents closed and adducted positions, while the peaks depict maximal abduction or jaw opening. The last half of the expansive phase is characterized by synchronous firings of all recorded muscles.

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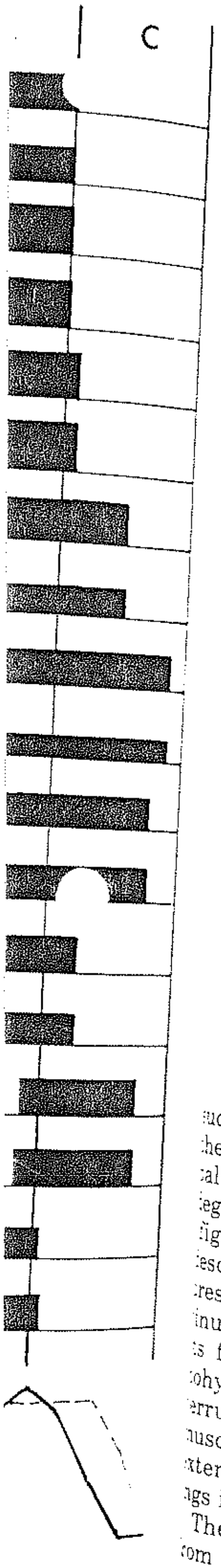

Abbreviations

c, compressive phase
e, expansive phase
p, preparatory phase

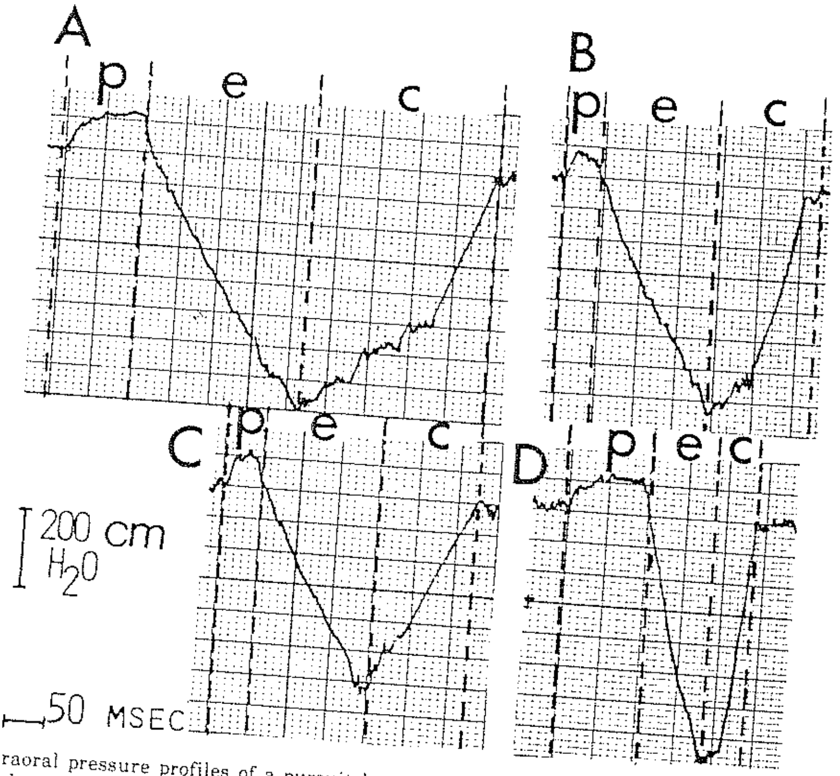

Fig. 9 Intraoral pressure profiles of a pursuit hunter, *Serranochromis robustus* during capture of sluggish (A) and elusive (B) prey. Intraoral pressure profiles of an ambush hunter, *Haplochromis compressiceps* during the capture of sluggish (C) and elusive (D) prey. Recordings obtained from free swimming fish, with plastic tubing passed through an opening drilled through the ethmoid. Plastic tube was secured to the roof of the buccal cavity by flaring the end, and to a clamp fixed to the dorsal spine. Note that magnitude of negative pressure varies only slightly, while velocity is greatly modulated. Preparatory (p), expansive (e), and compressive (c) phases have varying time bases, reflecting patterns of modulation triggered by the behavior the prey.

udden plateau in the curve, correlated with he onset of activity in the adductor arcus alatini. In spite of this sudden change in the egree and velocity of suspensorial abduction ig. 10), the pressure curve continues its steep escent (fig. 9). It is possible that negative ressure within the orobranchial cavity con- inues to build up, because of the lowering of s floor as a result of actions of the ster- ohyoideus and hypaxial muscles and an in- erruption in the firing of the geniohyoideus uscles (fig. 10: SH, HY, GHA). The limited xtent of overlap of antagonistic muscle fir- gs is comparable to that of pursuit hunters.

The *Compressive Phase* varies in duration om 50-75 msec and is characterized by the rtually unopposed action of all adductor muscles (fig. 10: AAP, AM_{1-3}, GHA). It takes 50 msec for the jaws to move from the widest gape to complete closure. Suspensory adduction lags behind jaw closure by a time factor of about 15 msec.

Thus, synchrony of abductors and adductors is limited. The pressure curve exhibits a remarkably close resemblance to that recorded for the pursuit hunter capturing elusive prey (figs. 9B,C).

Capture of elusive prey by ambush hunters

Ambush hunters employ a dramatically different strategy when confronted with elusive and agile prey. The kinematic, electromyographic and pressure profiles are altered fundamentally.

Abbreviations

AAP, adductor arcus palatini
AM_1, A_1 portion of adductor mandibulae
AM_2, A_2 portion of adductor mandibulae
AM_3, A_3 portion of adductor mandibulae
c, compressive phase
DO, dilatator operculi
e, expansive phase

EM, epaxial muscles
GHA, geniohyoideus
HY, hypaxial muscles
LAP, levator arcus palatini
LO, levator operculi
p, preparatory phase
SH, sternohyoideus

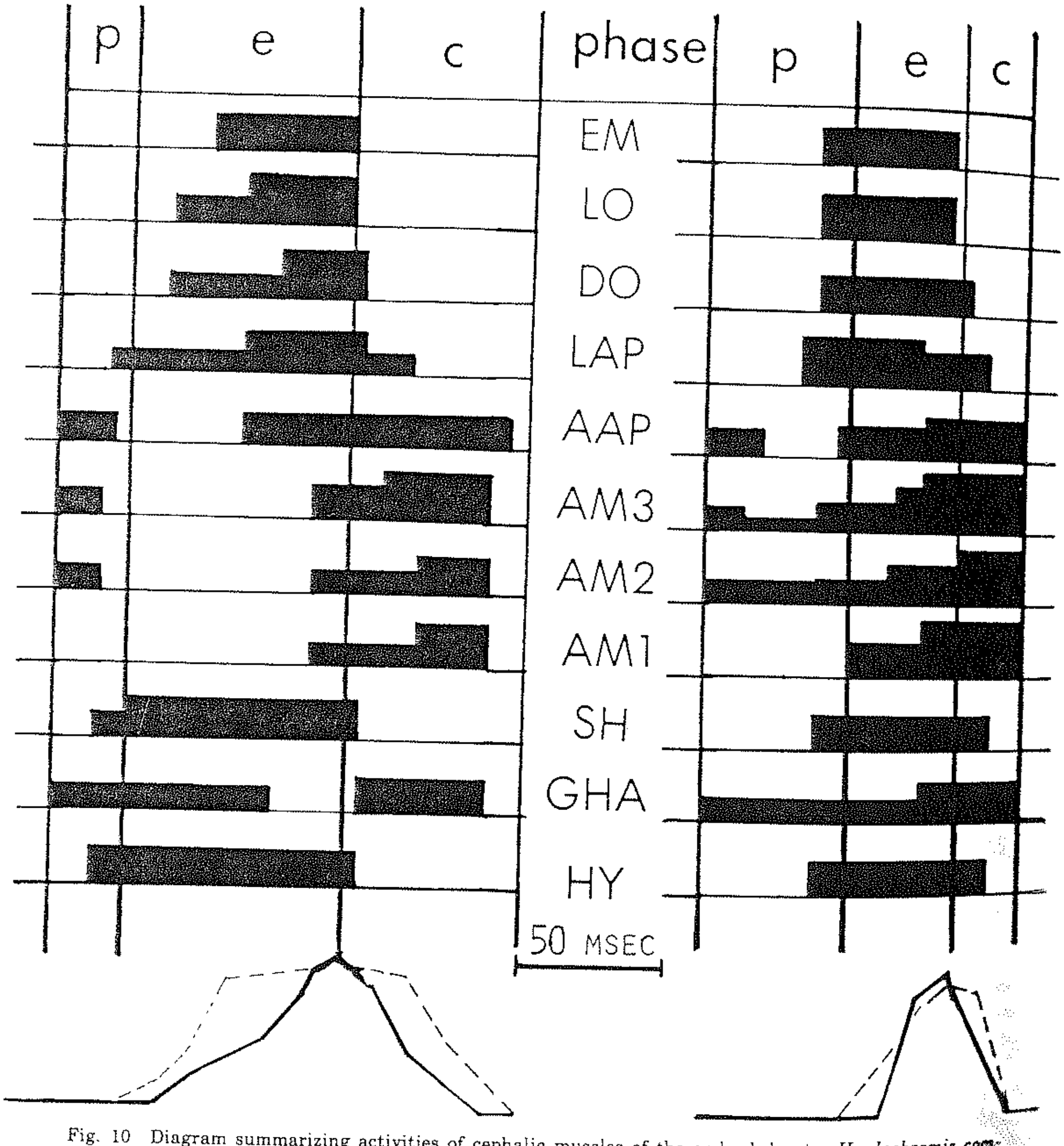

Fig. 10 Diagram summarizing activities of cephalic muscles of the ambush hunter *Haplochromis compressiceps*, during the capture of sluggish (on the left) and elusive prey (on the right). Bottom graphs depict jaw (heavy solid line) and suspensory (broken line) movements, peaks representing either maximum jaw opening or suspensory abduction. When capturing elusive prey, the preprogrammed motor output exhibits complete overlap of firings of all recorded muscles during the expansive phase (e). Note that the preparatory phase during capture of elusive prey is of much longer duration.

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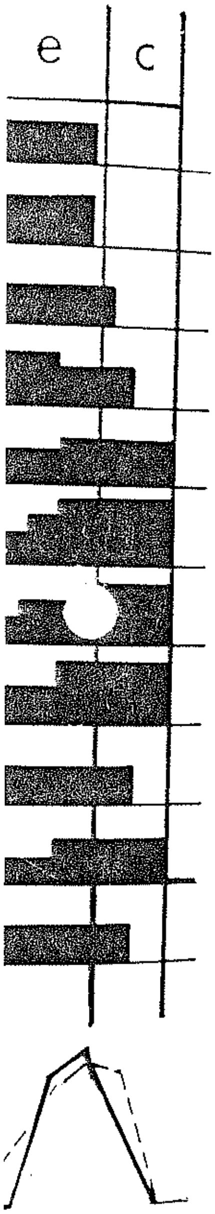

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I sharp contrast to all other feeding pater s of piscivorous cichlids, the *Preparatory Phase* is extended. Toward the end of the preparatory phase, 10 of 11 recorded muscles (fig. 0) shows simultaneous activity. Furthermore, the adductor mandibulae A_2 and A_3 and he geniohyoideus muscles show continued nd extended bursts (fig. 10: AM_3, AM_2, HA), resulting in a distinct rise in intra-robranchial pressure.

T e *Expansive Phase* is greatly abbreviated, ast g less than 50 msec. All 11 recorded mus es (fig. 10) fire synchronously at relatively igh amplitudes. Both suspensorial abduction nd mouth opening proceed at the highest elocity recorded for any cichlid. It is totally nexpected that jaw opening can proceed at his velocity when the jaw adductors (fig. 10: $AM_{1\text{-}3}$) fire at relatively high amplitudes synhronously with the jaw openers (fig. 10: LO, H). Maximal suspensorial abduction is acom ished within 50 msec by relatively high cti y of a pair of clearly antagonistic mus es. he adductor and levator arcus palatini ig. 0: AAP, LAP). The net effect of synronous activity of all recorded muscles dur g the expansive phase is an abrupt decline of least 600 cm H_2O in intraorobranchial pressure (fig. 9D). Thus, the explosive unfolding kes place at a much higher velocity than hen the ambush hunter is capturing slugsh prey.

Th *Compressive Phase* distinguishes itself a xceptional velocity (fig. 10), often less an .5 msec in total duration. When an nbush hunter captures sluggish prey, the mpressive phase often lasts more than twice e time, i.e., over 50 msec (fig. 10). Although act quantification of electromyograms can t be accomplished by the applied techques, one of the most outstanding features is e exceeding high amplitudes of activity of e adductor arcus palatini, adductor mandibae c nplex, and geniohyoideus muscles (fig. A , $AM_{1\text{-}3}$, GHA), all of which are unopsed the last half of the compressive phase. sure of the mouth proceeds at a uniform e, whereas suspensorial abduction reaches peak velocity only in the second half of the ase. Accordingly, the pressure curve makes rapid ascent only in the last half of the ase.

ilateral recordings indicate that muscle ivity is always symmetrical in ambush nte.

Feeding on dead brine shrimp

Under laboratory conditions, some piscivorous species can be forced to feed occasionally on frozen brine shrimp. Among pursuit hunters studied, only the small *Boulengerochromis microlepis* switches from fish to brine shrimp as prey. Other pursuit hunters *(Cichla ocellaris, Serranochromis robustus, Rhamphochromis longiceps, Hemibates stenosoma)* refuse to feed on anything but live fish, in spite of being subjected to long periods of starvation. Most ambush hunters, on the other hand, readily switch from fish to brine shrimp in the absence of the former.

Electromyographic and kinematic profiles differ significantly from those during the capture of fish and are more reminiscent of the patterns in *Tilapia* (Liem and Osse, '75). Yet, one still can distinguish the three phases in most cases (fig. 11) However, the time base, electromyographic and kinematic profiles vary a great deal from one feeding act to another, even within one experimental run. A representative profile, obtained from an experiment with *Haplochromis compressiceps*, is presented here as being characteristic for predaceous cichlids capable of prey switching; in this instance from fish to brine shrimp.

A *Preparatory Phase* of widely varying lengths often, but not always, precedes the main feeding cycle. It can be recognized by distinct bursts of the adductor arcus palatini, adductor hyomandibulae, adductor mandibulae parts A_2, A_3 and A_w, geniohyoideus anterior and posterior, and, surprisingly, the sternohyoideus (fig. 11: AAP, AM_2, GHA, SH). No movements of the jaws and suspensory apparatus are discernable, in spite of the distinct bursts of virtually all adductors and sternohyoideus muscles.

The *Expansive Phase* during the capture of brine shrimp is not only exceptionally attenuated, but also drastically different from the pattern during the capture of fish. In the kinematic profile, mouth opening occurs in two peaks, and four peaks can be distinguished for suspensorial abduction (fig. 11). It is paradoxical that maximal jaw opening coincides with minimal suspensorial abduction, whereas decreased jaw opening occurs when suspensorial abduction reaches one of its four peaks. No clear correlation exists between this peculiar kinematic pattern and the electromyographic profile. The dilemma is compounded by the fact that peaks and valleys in

Abbreviations

AAP, adductor arcus palatini
AM_1, A_1 portion of adductor mandibulae
AM_2, A_2 portion of adductor mandibulae
c, compressive phase
DO, dilatator operculi
e, expansive phase
EM, epaxial muscles
GHA, geniohyoideus anterior
HY, hypaxial muscles
LAP, levator arcus palatini
LO, levator operculi
p, preparatory phase
SH, sternohyoideus

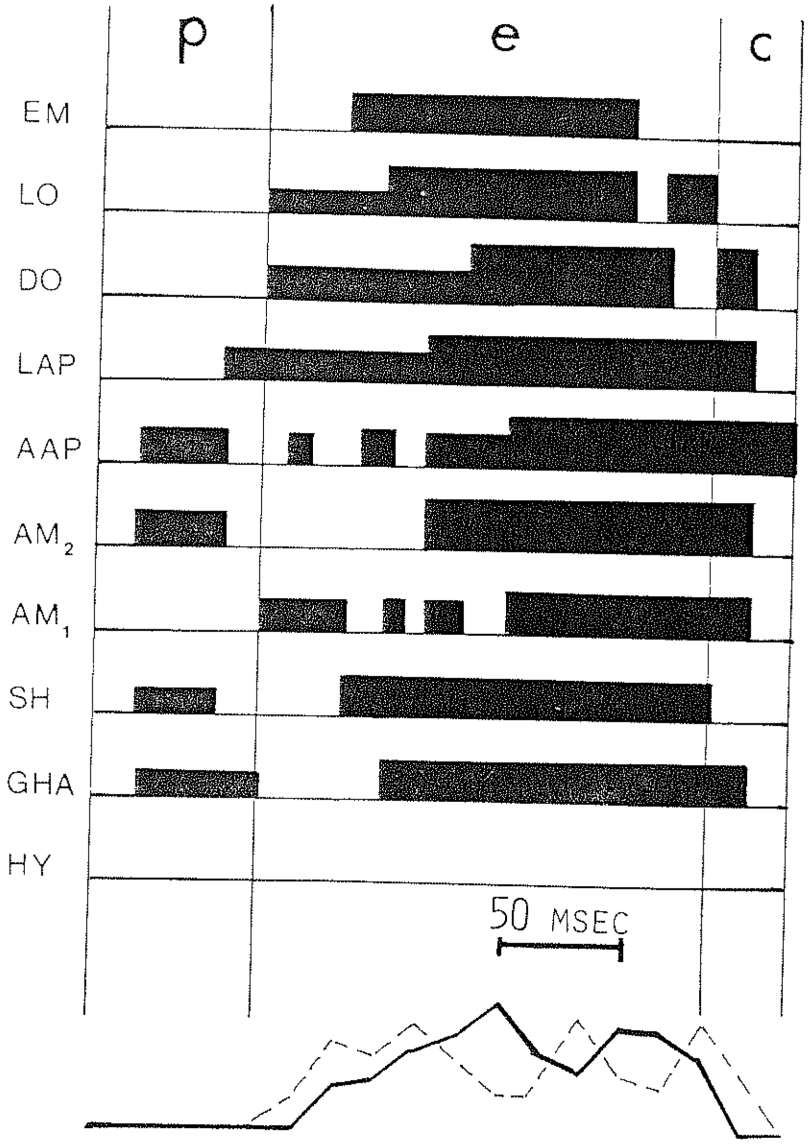

Fig. 11 Representative diagram summarizing activities of cephalic muscles of the ambush hunter *Haplochromis compressiceps* while feeding by inertial suction on brine shrimp *(Gammarus* sp.). Bottom graph depicts jaw (heavy, solid line) and suspensory (broken line) movements, peaks representing either maximal jaw opening or maximal suspensory abduction. The time base during the expansive phase is extremely variable, reflecting the modulated muscle actions. Muscles exhibiting the most variable bursts are the adductor mandibulae part A_1 muscle (AM_1), adductor arcus palatini (AAP) and dilatator operculi muscle (DO). The hypaxial musculature (HY) remains silent throughout the cycle. The preparatory phase (p) does not always occur, while the compressive phase (c) is the least variable.

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mouth opening and suspensorial abduction are accompanied by synchronous activity of all recorded muscles, especially during the last half of the expansive phase (fig. 11). In the beginning of the feeding cycle, there seems to be less synchrony of muscle activity. For example, suspensorial abduction clearly is correlated with unopposed action of the levator arcus palatini. The first two firings of the adductor arcus palatini clearly cause hesitations in suspensorial abduction. As the expansive phase proceeds, suspensorial abduction is regulated by uninterrupted and extended firing of the adductor arcus palatini (fig. 11: AA). A similar pattern can be seen in mouth opening: activity of the levator operculi is correlated with the onset of mouth opening, which becomes more pronounced when the epaxial muscles begin to fire. However, in the second half of the expansive phase, activity in the levator operculi, sternohyoideus, and epaxial muscles are joined by strong bursts of their antagonists (the entire adductor mandibulae complex and the geniohyoideus muscle, fig. 11: AM$_{1-3}$, GHA). Thus, the movements of te jaws are regulated by a complex balancing pattern of synchronous contractions in antagonistic sets of muscles. From the accompanying cinematographic recordings, one can extrapolate that the flow, direction and velocity of the water current containing the food particles are being modulated by means of synchronous action of multiple muscles. The precise control of fluid movement occurs mainly in the later stages of the expansive phase, and regulatory adjustments are associated with decreased feeding speed.

The *Compressive Phase* is perhaps the least modified. Adduction of the jaws precedes suspensorial adduction, and can be correlated with unopposed action of the adductor mandibulae complex and geniohyoideus muscles (fig. 11: AM$_{1-3}$, GHA). Suspensorial adduction is correlated with the termination of firing of the levator arcus palatini and continued activity in the adductor arcus palatini. Thus, the electromyographic and kinematic profiles and the time base resemble those of the compressive phase during the capture of sluggish prey (figs. 8, 10).

It is interesting that the hypaxial muscles do not show any activity during the suction of small suspended food particles. Bilateral recordings reveal a consistent symmetry in muscle activity during the entire feeding cycle.

Comparisons and generalizations

The key functional similarity of the feeding mechanism of piscivorous cichlids is the capacity to generate large and rapid suctions. Explosive expansion of the orobranchial cavity produces the suction so essential to the high speed inertial mode of feeding. In all feeding situations, suction is developed during the expansive phase. Invariably, prey enters the mouth during the last half of the expansive phase and prior to the onset of the compressive phase. Once prey has been sucked into the orobranchial chamber, there is a rapid return of the ambient pressure following even the most forceful compression of the orobranchial cavity (fig. 9D). Positive back pressure causing fluid oscillation within the orobranchial cavity during the compressive phase is prevented by the damping effects of the negative pressure prevailing in the expanding opercular cavities, the volumes of which are regulated by the actions of the dilator operculi (figs. 10, 11: DO), adductor operculi, hyoideus inferior and superior muscles. Thus, the opercular and branchiostegal apparatuses function as an exceedingly effective anti-backwash device capable of damping the effects of a wide range of fluctuations in pressure gradients.

The experiments have established a causal relationship between the behavior of the prey and the bone-muscle activity of the predator. Within a given feeding situation, an extreme regularity of the kinematic, pressure and electromyographic profiles has been recorded both inter- and intraspecifically, although ambush and pursuit hunters exhibit characteristic group differences.

During high speed prey-capture, the kinematic, electromyographic and pressure profiles proceed in three distinct phases with a fixed time base. Such a time constancy (figs. 7, 8, 10, 11) within a given feeding situation seems to support the notion that high-speed inertial suction is a stereotyped motor activity. However, the behavioral responses of the prey can trigger major changes in the time base, and the kinematic, pressure and electromyographic profiles (figs. 8-10). The present experiments demonstrate that the nature and movements of the prey play a paramount role in determining the pattern of prey capture by the piscivorous cichlids. Visual input during the prestrike stalk prior to the preparatory phase concerning the movements and nature of the prey probably is sent to an integration center in the brain. Depending on the visual information, the integrator determines which of the two stereotyped motor activities is recruited (fig. 10). Of course, the resulting pressure profiles of the two patterns do differ significantly (figs. 9C,D). However, it has not been possible to measure the adaptive significance of the different pressure profiles of pursuit and ambush hunters during the capture of sluggish and elusive prey. The consistently steeper slopes of the descents of the pressure curves in the expansive phase during the capture of elusive prey (figs. 9B,D) as contrasted to those during the capture of sluggish prey (figs. 9A,C), seem to indicate that suction at higher speeds enhances agile prey capture. Because the differences in the magnitude of the negative pressure generated during the expansive phase are neither consistent nor significant (fig. 9), I postulate that suction velocity, rather than magnitude of negative pressure, is the key adaptive factor during capture of elusive and agile prey. However, the adaptive meaning of the slower patterns recorded for both ambush and pursuit hunters during the capture of sluggish prey is not clear. In pursuit hunters, the longer duration of the feeding act may be correlated with the use of the kinetic energy gained in the forward swimming motion. On the other hand, in ambush hunters, one may predict that the pattern characteristic for agile prey (fig. 9D) is equally efficient for the capture of sluggish prey. Yet, a slower pattern (figs. 9C, 10) of motor output is recruited. It is postulated that the slower pattern with the least synchrony in muscle activity (figs. 7, 10) may require less energetic cost.

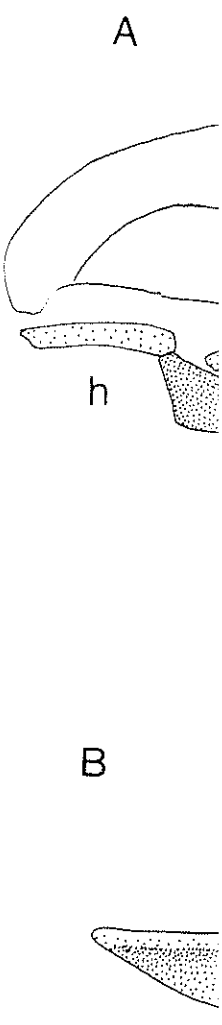
Most ambush hunters, and among pursuit hunters the juveniles of *Boulengerochromis microlepis*, can switch to a low-speed mode of inertial suction feeding, when sucking in small food items from either midwater or the bottom. The low-speed strategy deviates dramatically from the two preprogrammed patterns so characteristic of high-speed inertial feeding. During the low-speed inertial suction feeding, the timebase varies greatly from one feeding act to another within one experimental run and there is a pronounced irregularity of movement patterns (fig. 11). At times, the preparatory phase is eliminated. The strikingly variable timebase and high irregularity of both the electromyographic and kinematic patterns (fig. 11) imply that continuous adjustments of the pressure profile are accomplished by a peripheral sensory feedback mechanism modulating the motor output. Sight does not seem to trigger modulation. Presumably sensory feedback originates from mechanoreceptors within the joints and ligaments, and chemoreceptors of the orobranchial apparatus and is triggered by the nature, density, and location of the small food items. The precise control of water movement is a key factor in effective aquatic feeding on small food particles by fishes. Experimental data presented here (fig. 11) suggest that precise regulation of the water current is brought about by synchronous activity of virtually all recorded muscles (fig. 11). Although reliable techniques for quantifying electromyograms are still unavailable, we may hypothesize from the data gathered on fluctuations in amplitudes that within the generally synchronous pattern the degree of muscle contractions are regulated continuously to achieve the precise control of water flow.

Anatomy of the macerating and swallowing apparatus

All cichlid piscivores masticate, macerate, lacerate and triturate their prey extensively by moving the strong, but often fine teeth of the upper and lower pharyngeal jaws against the prey. Convergence in pharyngeal tooth shape of piscivorous cichlids is truly remarkable. For example, *Lamprologus compressiceps* and *Haplochromis compressiceps,* which belong to two distinct phyletic lineages endemic in Lake Tanganyika and Lake Malawi, respectively, possess an amazingly similar pharyngeal dentition (fig. 18). Many of the pointed teeth have sharply-edged anterior (in the lower pharyngeal jaw) or posterior edges (in the upper pharyngeal jaws), that are either serrated or possess a second specialized pointed cusp (figs. 12, 18). The functional efficiency of the pointed cusps and serrated sharply-edged margins of the teeth in rasping the flesh from the prey can be demonstrated by the much more extensive state of laceration of freshly ingested fishes recovered from the stomachs of piscivorous cichlids compared with those swallowed by cichlids possessing flattened *(Pseudotropheus elongatus),* blunt-cusped (e.g., *Corematodus taeniatus:* Liem, '74) or molariform *(Haplochromis placodon:* Liem, '74) pharyngeal teeth.

1. Osteology

The anatomy of the unique pharyngeal jaw apparatus of cichlids has been described ear-



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Abbreviations

ap,	apophysis for basipharyngeal joint
bb,	basibranchial
bpj,	basipharyngeal joint
cb,	ceratobranchial
cb_5,	fifth ceratobranchial (lower pharyngeal jaw)
eb,	epibranchial
h,	hyoid
hb,	hypobranchial
l,	ligament connecting lower pharyngeal jaw to basibranchial
lp,	lower pharyngeal jaw
mp,	muscular process
nc,	neurocranium
pb2-4,	second-fourth pharyngobranchials (upper pharyngeal jaw)
pg,	pectoral girdle
up,	upper pharyngeal jaw

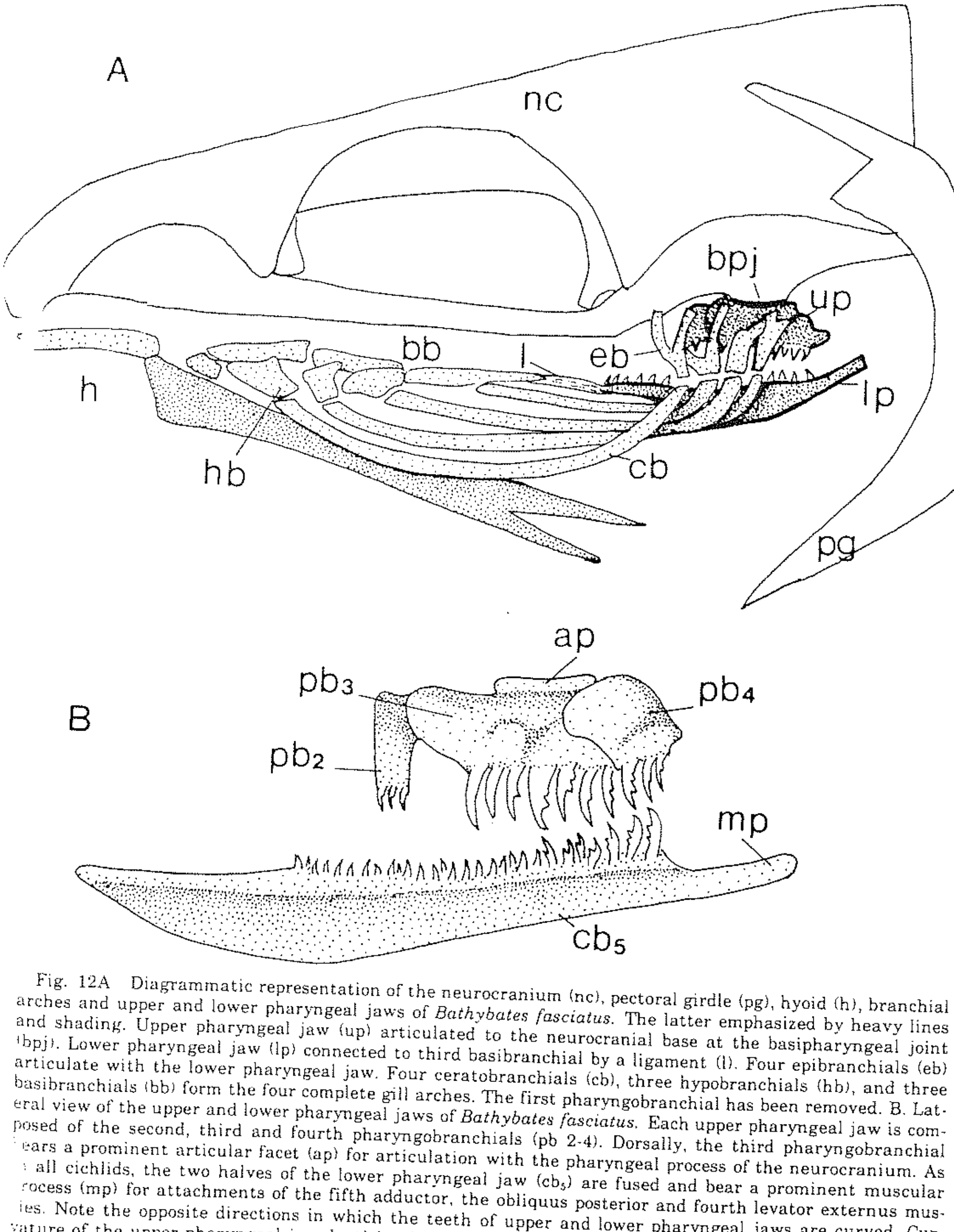

Fig. 12A Diagrammatic representation of the neurocranium (nc), pectoral girdle (pg), hyoid (h), branchial arches and upper and lower pharyngeal jaws of *Bathybates fasciatus*. The latter emphasized by heavy lines and shading. Upper pharyngeal jaw (up) articulated to the neurocranial base at the basipharyngeal joint (bpj). Lower pharyngeal jaw (lp) connected to third basibranchial by a ligament (l). Four epibranchials (eb) articulate with the lower pharyngeal jaw. Four ceratobranchials (cb), three hypobranchials (hb), and three basibranchials (bb) form the four complete gill arches. The first pharyngobranchial has been removed. B. Lateral view of the upper and lower pharyngeal jaws of *Bathybates fasciatus*. Each upper pharyngeal jaw is composed of the second, third and fourth pharyngobranchials (pb 2-4). Dorsally, the third pharyngobranchial ears a prominent articular facet (ap) for articulation with the pharyngeal process of the neurocranium. As all cichlids, the two halves of the lower pharyngeal jaw (cb_5) are fused and bear a prominent muscular rocess (mp) for attachments of the fifth adductor, the obliquus posterior and fourth levator externus mus-ies. Note the opposite directions in which the teeth of upper and lower pharyngeal jaws are curved. Cur-vature of the upper pharyngeal jaw dentition is conducive for the transport of the prey into the esophagus, while that of the lower pharyngeal jaw is not. The upper pharyngeal jaw plays a dominant role during swallowing (fig. 16).

lier (Liem, '74; Goedel, '74b; Barel et al., '76). Thus, the information given here is restricted to selected, salient features that are either characteristic for piscivorous cichlids or important in understanding function.

The principal bony elements that constitute the upper pharyngeal jaws are the second, third and fourth pharyngobranchials (fig. 12). Dorsally, the third pharyngobranchial bears a prominent articular facet (fig. 12: ap) to form the basipharyngeal joint with the pharyngeal process of the neurocranial base (figs. 1, 12). Because of the strong interconnections between the third and fourth pharyngobranchials of both sides, the entire complex functions as one mechanical unit.

The lower pharyngeal jaw is composed of fused fifth ceratobranchials (fig. 12: cb$_5$). Although the pharyngeal jaws are associated with the branchial basket, their mobility is relatively independent. An important ligamentous connection (fig. 12) exists between the lower pharyngeal jaw and the third basibranchial, whereas the branchial basket is anchored to the hyoid apparatus. Movements of the urohyal and hyoid rami will be transferred to the branchial basket, which in turn will elicit movements of the lower pharyngeal jaw. Thus, mechanically, we are dealing with a "hyoid-basibranchial-lower pharyngeal jaw coupling." In sharp contrast, the upper pharyngeal jaws are much more independent, although movements of epibranchials 1-3 can cause the upper pharyngeal jaws to move because of the mechanically intimate nature of the epibranchial-pharyngobranchial joints. Motions of the upper pharyngeal jaws therefore are correlated closely with actions of muscles that are attached directly to the pharyngobranchials and epibranchials; however, movements of the lower pharyngeal jaw can be elicited not only by muscles directly attached to the lower pharyngeal jaw but also by muscles associated with the hyoid apparatus because of the "hyoid-basibranchial-lower pharyngeal jaw coupling."

2. Myology

The branchial musculature of piscivorous cichlids is surprisingly uniform and unspecialized. Throughout the adaptive radiation of piscivorous cichlids the full complement of branchial muscles is retained in a configuration resembling that of more generalized cichlids as *Tilapia* (Goedel, '74b) and *Haplochromis burtoni* (Liem, '74).

The tripartite *transversus dorsalis* anterior and a single, well-developed transversus dorsalis posterior (fig. 13: tda, tdp) represent the transversus dorsalis complex. The transversus dorsalis posterior (tdp) inserts tendinously on the dorsal tubercles of the fourth epibranchials overlying the junction of the third and fourth pharyngobranchials. The transversus dorsalis anterior muscle is complex (fig. 13: tda): (1) the first and most anterior head runs transversely between the anterior surfaces of the second pharyngobranchials; (2) the second head forms the bulk of the muscle mass of which the more ventral fibers run uninterruptedly between the anterior surfaces of the second pharyngobranchials, while the dorsal fibers originate from the parasphenoid in front of the pharyngeal process; and (3) finally, the third head is tendinous in the center, while its attachments are confined to the anterodorsal surfaces of the second epibranchials.

Two dorsal oblique muscles generally are present; the *obliquus dorsalis* is best developed and constant, being a prominent muscle located in the fossa of the third pharyngobranchial lateral to the pharyngeal apophysis. Its parallel fibers insert laterally on the joint of the third and fourth epibranchials (fig. 13: od). In sharp contrast, the *obliquus posterior* (fig. 13: op) is either weakly developed or absent in piscivorous cichlids. When present, it runs between the tubercle representing the junction between the third and fourth epibranchials and the muscular process of the fifth ceratobranchials just anterior to the attachment of the fifth adductor and caudal to

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Abbreviations

ad, adductor
ap, articular process of upper pharyngeal jaw
cb$_5$, lower pharyngeal jaw
eb$_{1-4}$, first-fourth epibranchial
es, esophagus
le, levator externus
le$_4$, fourth levator externus
lem$_4$, fourth levator externus
li, levator internus
lp, levator posterior
od, obliquus dorsalis
op, obliquus posterior
rd, retractor dorsalis
tda, transversus dorsalis anterior
tdp, transversus dorsalis posterior

Fig. 13 Dorsal view of dissected and isolated branchial apparatus and muscles. A. *Bathybates minor.* B. *Boulengerochromis microlepis.*

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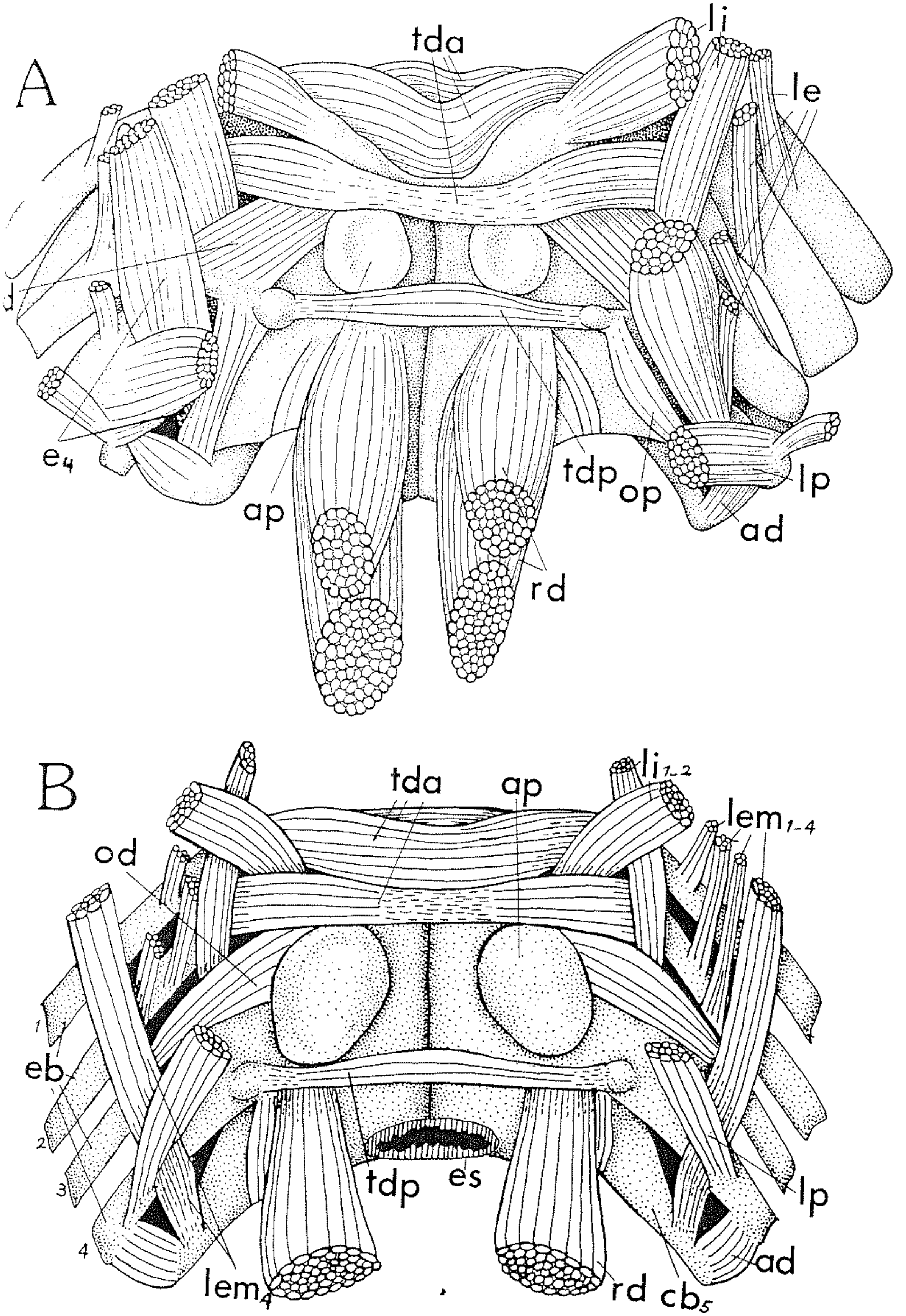

Figure 13

the insertion site of the fourth levator externus.

As in most cichlids, the *retractor dorsalis* (figs. 13, 14: rd, RP) is well developed and originates from the ventral processes of either the third or fourth vertebra and inserts on the posterodorsal aspect of the fourth pharyngobranchials. Additional fibers originating from the second and first vertebra enlarges the muscle mass significantly. Occasional subdivisions in the retractor dorsalis are differentiated (e.g., in *Boulengerochromis*, fig. 13: rd).

The remaining dorsal branchial muscles are the seven pairs of levatores: 4 externi; 2 interni and 1 posterior (figs. 13, 14: le, li, lp). All four levatores externi originate from a prominent concave, shell-shaped *prootic process* (hyomandibulad process of Barel et al., '76) situated on the prootic posterodorsal to the trigeminofacial chamber and ventral to the anterior socket for the head of the hyomandibular (figs. 1, 13: pp. le$_4$, le, lem$_{1\text{-}4}$, li, li$_{1,2}$). Originating from the lateral rim of this process are the first, second, third and fourth levatores externi in succession from anterior to posterior. Both the first and second levatores externi possess cylindrical tendinous insertions, whereas the origins of the third and fourth levatores externi are more extensive; the latter occupies most of the posteromedial surface of the prootic process. All levatores externi are parallel-fibered and increase progressively in length from anterior to posterior. In all piscivores, the fourth levator externus is the longest and bulkiest of the series. The first three of the series insert tendinously on the dorsal aspect of the epibranchials. As in all cichlids, the fourth levator externus is composed of a small lateral straplike head inserting on the dorsolateral process of the fourth epibranchial (fig. 14: le$_4$); the large medial head passes ventrally to insert tendinously on the muscular process of the fifth ceratobranchial, just anterior to the attachment of the fifth adductor muscle (fig. 14: ad).

Originating from the anteromedial aspect of the prootic process are the equally developed cylindrical *levatores interni 1* and *2* (figs. 13, 14: li$_{1,2}$) that insert on the dorsal aspect of the second pharyngobranchial and on the junction of the third epibranchial and third pharyngobranchial respectively.

Posterior to the adductor operculi (fig. 14: ao) is a long, vertical, parallel-fibered, straplike muscle, the *levator posterior* (fig. 14: lp), that originates from the pterotic and inserts on the fourth epibranchial just posterior to the insertion of the lateral head of the fourth levator externus.

Ventrally, three pairs of muscles are associated with the lower pharyngeal jaw: the pharyngocleithralis externus and internus and the pharyngohyoideus (fig. 14: PCE, PCI, PH). The *pharyngocleithralis externus* (fig. 14: PCE), is an almost vertical, parallel-fibered and straplike muscle originating from the anteroventral aspect of the cleithrum. Laterally it is partially covered by the sternohyoideus (fig. 14: SH). Its tendinous insertion is on the ventral crista of the lower pharyngeal jaw and restricted to part of the anterior half of the bone. Immediately medial to this site, is the tendinous insertion of the spindle-shaped *pharyngocleithralis internus* (fig. 14: PCI) that runs horizontally and posteriorly to a fleshy attachment on the medial surface of the cleithrum, dorsal to the origin of the pharyngocleithralis externus. Anterior to the insertion site of the pharyngocleithralis is the tendinous attachment of the elongate pharyngohyoideus muscle, of which the fibers run obliquely to attach to the dorsal process of the urohyal. Often, the fibers are interrupted by one or two tendinous inscriptions; the condition varies interspecifically. Goedel ('74b: p. 348) misinterpreted my discussion on the pharyngohyoideus in nandids (Liem, '70: p. 59). Nowhere have I ever implied a homology between the teleostean pharyngohyoideus and the mammalian digastricus muscle!

Functional analysis of the macerating and swallowing apparatus

Cineradiographic and electromyographic analyses of the macerating and swallowing mechanism of *Cichla ocellaris, Serranochromis robustus, Rhamphochromis longiceps, Hemibates stenosoma, Haplochromis compressiceps* and *Haplochromis livingstoni* have revealed characteristic biomechanical and electromyographic profiles.

1. Kinematic profile

In the species studied, the macerating cycle is composed of two power strokes separated by a transitional stroke (figs. 14-16). Thus, the cycle commences with the first power stroke followed by a transitional stroke and ending in a second power stroke.

Power stroke I. This stroke is characterized by protraction of the upper pharyngeal jaw (fig. 15), which pivots around the basipharyngeal joint in such a way that its an-

A_5, fifth ad
AO, adduct
CB, ceratob
CB_5, lower p
CL, cleithru
EB, epibran
ES, esophag

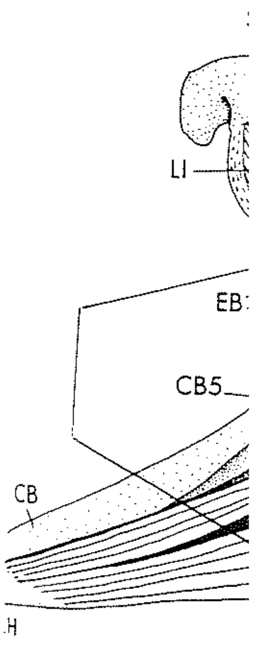

Fig. 14 On left is the lat
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Abbreviations

A_5, fifth adductor
AO, adductor operculi
CB, ceratobranchial
CB_5, lower pharyngeal jaw
CL, cleithrum
EB, epibranchial
ES, esophagus
LE_4, fourth levator externus
LI, levator internus
LP, levator posterior
PCE, pharyngocleithralis externus
PCI, pharyngocleithralis internus
PH, pharyngohyoideus
PS I, Power Stroke I
PS II, Power Stroke II
RP, retractor dorsalis
SH, sternohyoideus
SPH, sphenotic
ST, pterotic
TS, transitional stroke
UH, urohyal

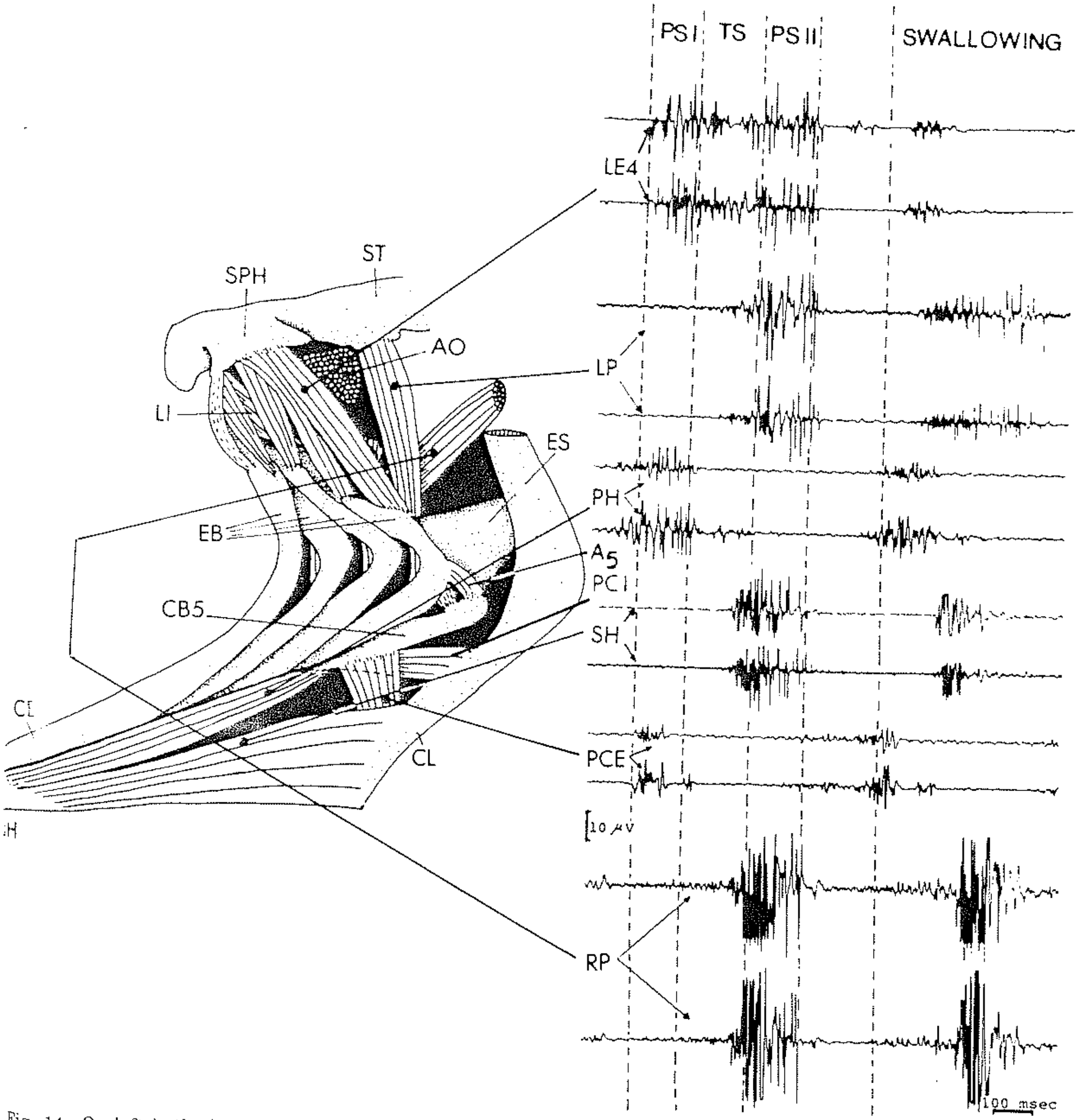

Fig. 14 On left is the lateral view of the branchial apparatus and muscles after removal of operculum, suspensory pparatus, gills, gill rakers and mucous membrane of *Hemibates stenosoma*. On right are bilaterally recorded myograms uring a maceration cycle and swallowing. Vertical interrupted lines delineate the boundaries of the three strokes durng each masticatory cycle: PS I (Power Stroke I), TS (Transitional stroke) and PS II (Power Stroke II). Myograms are resented in couplets, with the top myogram representing the left side and the bottom the right side. Firing sequences re bilaterally symmetrical. During swallowing the patterns of firings become quite variable.

Abbreviations

lj, lower pharyngeal jaw
nc, neurocranium
pg, pectoral girdle
uh, urohyal
uj, upper pharyngeal jaw

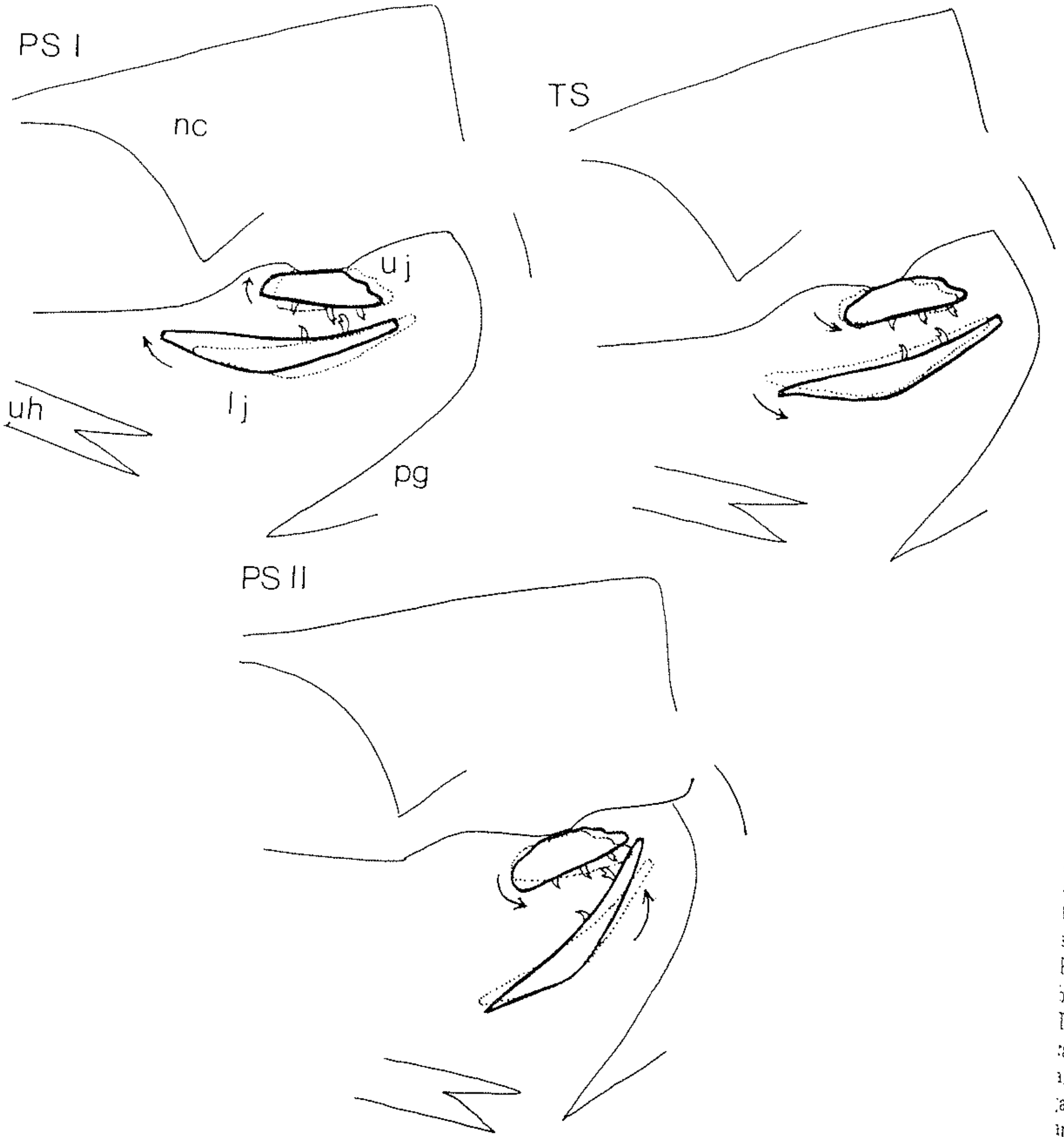

Fig. 15 Diagrammatic representation of kinematics of the pharyngeal jaws of *Bathybates fasciatus*, MCZ 49288 during maceration of a gold fish. Diagrams are based on tracings of a cineradiographic film obtained with an Eclair GV-16 camera attached to a Sirecon image intensifier on a Siemens radiographic instrument at 200 frames per second. Kodak Plus-X Reversal film was exposed at 120 mA and 40 kv. Heavy solid lines depict positions of the jaws (uj, upper pharyngeal jaw; lj, lower pharyngeal jaw) of the frame representing the most extreme position of the particular stroke, while the dotted lines indicate the positions of the jaws ten frames *preceding* the most extreme position of the corresponding stroke. PS I, Power Stroke I; TS, Transitional Stroke; PS II, Power Stroke II. The positions of the neurocranium (nc), pectoral girdle (pg), and urohyal (uh) represent those of the most extreme position of the corresponding stroke only. Dentition is indicated by only a very few representative teeth on each jaw.

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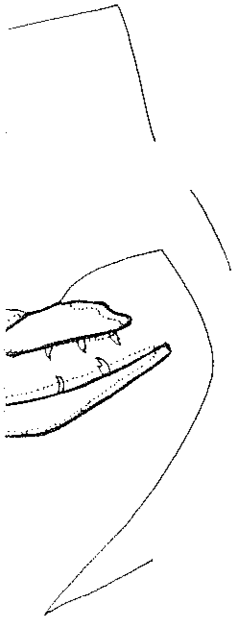

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terior end moves anterodorsally. In a synchronous motion the lower pharyngeal jaw is strongly protracted while rotating clockwise around its transverse axis to approximate the upper pharyngeal jaw (fig. 15).

The *transitional stroke* is weakly retrusive. During this stroke, the upper pharyngeal jaw is retracted slightly while it is rotating anticlockwise around its transverse axis to resume a more or less horizontal position (fig. 15). The lower pharyngeal jaw moves posteriorly and also rotates anticlockwise around its transverse axis (fig. 15). In this way, the upper and lower pharyngeal jaws move apart.

ower stroke II. The upper pharyngeal jaw is strongly retracted while its anterior end moves to the most extreme posteroventral position (fig. 15). Synchronous with this motion is the strong anticlockwise rotation of the lower pharyngeal jaw around its transverse axis. As a result, the posterior half of the lower pharyngeal jaw approximates the upper pharyngeal jaw (fig. 15).

Shearing and massive maceration occurs during Power Strokes I and II. Both actions are concentrated toward the posterior halves of the upper and lower pharyngeal jaws. Accordingly, the posterior pharyngeal teeth are stouter than the anterior ones. During Power Stroke I, the major macerating action is the result of the clockwise rotation around the transverse axis of the lower pharyngeal jaw, of which the posterior teeth are curved anteriorly and possess sharply-edged serrated anterior margins (figs. 12, 18). This rasping action of the lower pharyngeal jaw against the prey is strongly enhanced, because the prey is stabilized by the posteriorly curved teeth of the protracted upper pharyngeal jaws. Massive macerating action also occurs during Power Stroke II, by the cooperative effort of both the upper and lower pharyngeal jaws. The prey is cut by the sharp-edged and serrated posterior margins of the teeth of the anticlockwise pivoting upper pharyngeal jaw, and the lower pharyngeal jaw rotates anticlockwise around its transverse axis to optimize the macerating effects of the sharp-edged and serrated anterior margins of the teeth (fig. 15) located on the posterior half of the jaw.

During the transitional stroke, the prey is either shifted posteriorly toward the gullet or repositioned. This is accomplished by variable retrusive movements of both the upper and lower pharyngeal jaws.

2. Electromyographic profile

Maceration is caused by cyclical action of muscles the pattern of which is correlated faithfully with the kinematic profile.

Power stroke I. The principal muscle responsible for protraction and clockwise rotation of the upper pharyngeal jaw around its transverse axis is the levator internus 1 (anterior) muscle, which shows high amplitude activity consistently (fig. 16: LI_1). In concert, the geniohyoideus anterior and posterior, and the fourth levator externus fire strongly and synchronously (figs. 14, 16: GH, LE_4). Activity of the geniohyoideus and fourth levator externus muscles pull the lower pharyngeal jaw anteriorly and dorsally to exert an anteriorly directed force that is applied to the prey via the sharp-edged cranial margins of the anterior curved teeth.

Transitional stroke. Power Stroke I is followed immediately by a transitional stroke during which both the levator internus and geniohyoideus muscles cease to fire, although the fourth levator externus continues its activity although at a much lower level. During this transitional phase the levator posterior and retractor dorsalis (figs. 14, 16: LP, RD) become increasingly more active, retracting and rotating the upper pharyngeal jaw anticlockwise so that it assumes a more or less horizontal position. Ventrally, actions of the pharyngocleithralis internus and fourth levator externus muscles make the lower pharyngeal jaw move back and tilt in such a way that its anterior tip moves posteroventrally.

Power stroke II. More muscles are active during this phase than in the previous strokes. High amplitude, synchronous bursts have been recorded from the fourth levator externus, levator posterior, pharyngohyoideus, sternohyoideus, retractor dorsalis and pharyngocleithralis externus muscles (figs. 14, 16: LE_4, LP, PH, SH, RD, PCE). Anticlockwise rotation around the basipharyngeal joint of the upper pharyngeal jaw is effected by synchronous action of the levator posterior and retractor dorsalis muscles (fig. 16: LP, RD). In close coordination with the anticlockwise rotation of the upper pharyngeal jaw, the lower pharyngeal also is rotated anticlockwise around its transverse axis when the fourth levator externus (LE_4), pharyngohyoideus (PH), sternohyoideus (SH) and pharyngocleithralis externus (PCE) fire in concert, presumably generating large forces against the posterior half of the lower pharyngeal jaw (fig. 15).

Abbreviations

GH, geniohyoideus
LE$_4$, fourth levator externus
LI, levator internus
LP, levator posterior
PCE, pharyngocleithralis externus
PCI, pharyngocleithralis internus
PH, pharyngohyoideus
RD, retractor dorsalis
SH, sternohyoideus

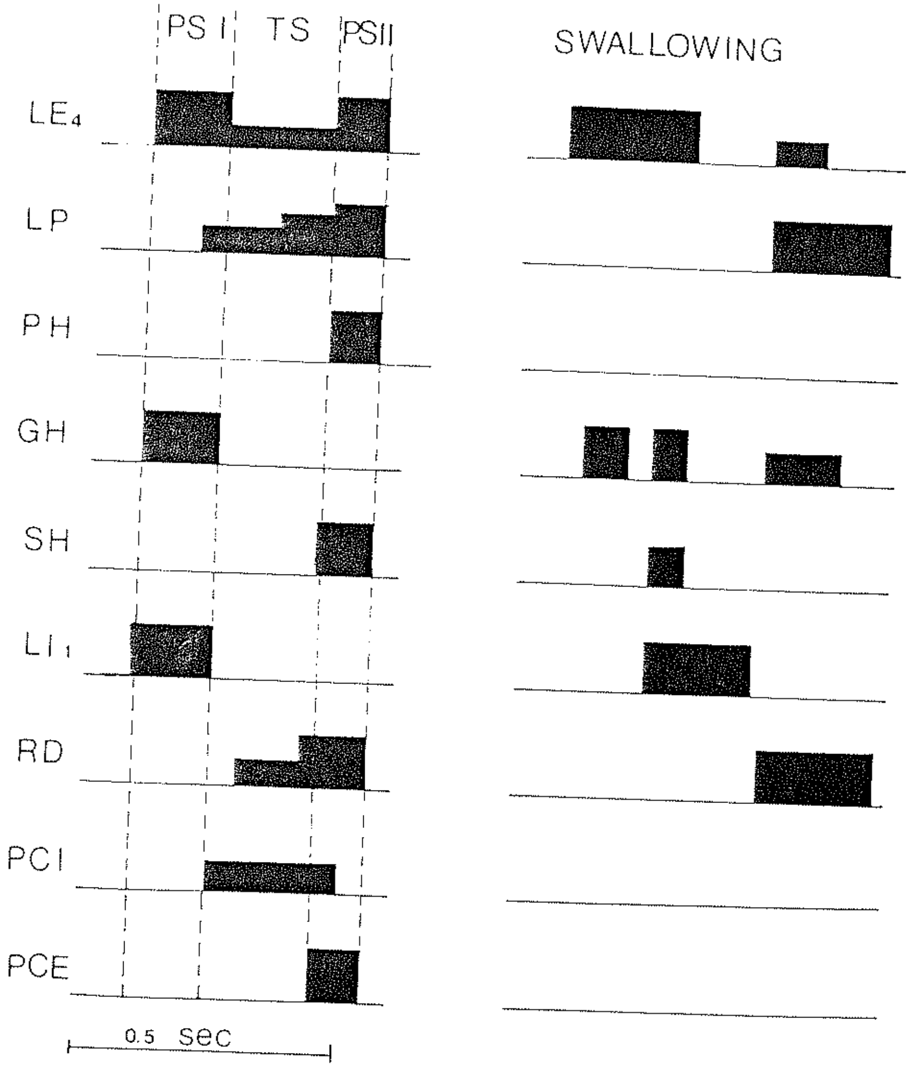

Fig. 16 Diagram summarizing activities of pharyngeal muscles of *Haplochromis compressiceps* during a maceration cycle and swallowing. Vertical lines delineate three stages of a cycle (PS I and PS II are Power Strokes I and II, and TS Transitional Stroke). Note that during Power Stroke II, numerous muscles are active; the combined actions of the fourth levator externus and the pharyngohyoideus and pharyngocleithralis externus produce a powerful force couple. During swallowing the firings of the muscles become quite variable, although the upper pharyngeal jaw together with the levator posterior (LP) and retractor dorsalis (RD) become the dominant components. Note that the curvature of the dentition of the upper pharyngeal jaw is conducive for the swallowing act (fig. 12B).

Maceration is typically cyclical at 2-3 cycles/sec in *Cichla ocellaris*, *Serranochromis robustus*, and *Hemibates stenosoma*. Bilateral recordings in these species, all belonging to the pursuit hunters, seem to indicate that the activity pattern essentially is bilaterally symmetrical (fig. 14). However, in *Haplochromis compressiceps* (an ambush hunter)

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and in *Rhamphochromis longiceps* (a pursuit hunter), both the lower and upper pharyngeal jaws are capable of "opening," "closing," retraction, protraction and lateral translation. In addition, the lower pharyngeal jaw can rotate in three axes, providing supplementary shredding of the prey, which is impaled on the sharp cusps of the upper pharyngeal jaw.

Asymmetrical electromyographic profiles are relatively common in the ambush hunters, especially when macerating larger prey. Following Kallen and Gans ('72), muscular activities are referred to as ipsilateral if they involve muscles of the active side and contralateral when they involve the opposite one. When macerating large prey, *Haplochromis compressiceps* may switch from the symmetrical pattern described above to the following asymmetrical profile. During the asymmetrical electromyographic profile there are no silent periods (fig. 17). As a logical, yet arbitrary, starting point I consider the onset of firing of the left fourth levator externus. In concert with this event, there is ipsilateral activity in the geniohyoideus and levator internus muscles (figs. 17: GH, LI). During the transitional stroke, when the ipsilateral levator externus shows a reduced amplitude and the ipsilateral geniohyoideus and levator internus cease to fire, the following contralateral muscles start to fire: Levator externus, geniohyoideus and levator internus (fig. 17: LE, GH, LI), while the ipsilateral levator posterior and retractor dorsalis (LP, RD) begin their activity. When the ipsilateral levator externus undergoes a sharp increase in the activity level during Power Stroke II, it is accompanied by ipsilateral peak activity of the levator posterior and retractor dorsalis, and distinct bursts of the contralateral geniohyoideus and levator internus muscles. Cessation of the activity in the ipsilateral fourth levator externus coincides with a sharp increase in relative amplitude of its contralateral counterpart. Simultaneously the contralateral levator posterior and retractor dorsalis fire while all muscles of the originally ipsilateral side become silent. Thus, during the asymmetrical pattern silent periods are eliminated by the wide overlap of the firing sequences of the ipsilateral and contralateral muscles (fig. 17).

Since our records of the movements accompanying asymmetrical muscle activity are too sketchy, it is impossible to offer a precise description. However, a few hypotheses can be formed on the basis of the new data presented here. Asymmetrical maceration proceeds at 2-3 cycles/sec. Thus there is no difference in speed between bilaterally symmetrical and asymmetrical maceration. Furthermore, symmetrical and asymmetrical patterns often alternate, although the former is, in general, the

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Abbreviations

GH, geniohyoideus
LE_4, fourth levator externus
LI, levator internus
PH, pharyngohyoideus
RD, retractor dorsalis

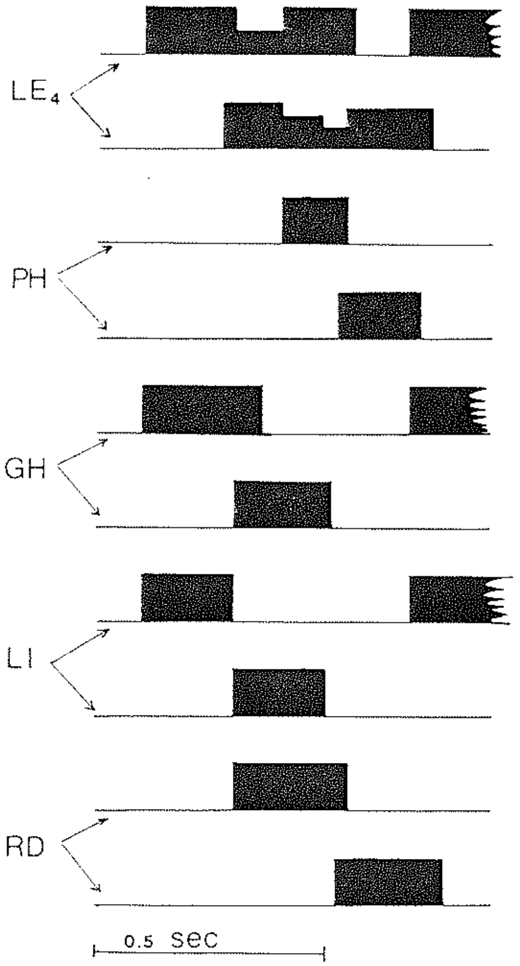

Fig. 17 Diagram summarizing activities of the pharyngeal muscles of *Haplochromis compressiceps* during a maceration cycle. Muscles are presented in couplets, with the top representing the left side and the bottom the right side. Corresponding muscles from left and right sides show different firing sequences. Periods of activity overlap forming a continually-modified muscular sling. The pattern does return to a symmetrical one after a variable number of cycles.

more common. Translational movements of the upper and especially the lower pharyngeal jaws do occur as a result of bilaterally asymmetrical muscle activity. Both upper and lower pharyngeal jaws rotate around three axes, undergo protrusion, retrusion and translational movements. More importantly all of these processes occur simultaneously.

Swallowing is accompanied by variable firings of muscles associated with the upper pharyngeal jaw. In general, muscles attached to the lower pharyngeal jaw are relatively silent during the swallowing act. In most instances the swallowing act is preceded by an interruption in the cyclical pattern so characteristic for maceration (figs. 14, 16). Strong bursts of the retractor dorsalis and levator posterior muscles represent the dominant features of the electromyographic pattern during the swallowing act. During the swallowing of larger prey, the electromyographic pattern is repeated, with the activity of the first levator internus alternating with that of the retractor dorsalis and levator posterior. Variations in the electromyographic profile of the fourth levator externus, geniohyoideus, sternohyoideus, and pharyngocleithralis externus muscles (figs. 14, 16: LE$_4$, GH, SH, PCE) in the stage prior to the swallowing act may be correlated with position and size of the prey.

3. Generalizations on the macerating and swallowing mechanisms

Anatomically the pharyngeal jaw apparatus of piscivorous cichlids deviates slightly from that of generalized insectivorous cichlids. Both the upper and lower pharyngeal jaws are more elongate and less robust, but muscular specializations can be considered minimal. The effectiveness of the macerating apparatus is enhanced by modifications in the dentition. Thus the posterior margins of the teeth of the upper pharyngeal jaws become sharp-edged and serrated, often by the development of a specialized accessory cusp in addition to the main cusp (fig. 12), whereas in the teeth of the lower pharyngeal jaw the sharp-edged serrated margin is the anterior one (figs. 12, 18). Thus among teeth, bones and muscles, dentitional characteristics have the most predictive value for piscivory. However, the experimental results, presented here, clearly indicate that the best descriptive comparative anatomy can offer is a statement of functional possibilities. Functional analysis permits decision of which among the broad spectrum of possible actions do actually exist.

Pharyngeal movements of piscivorous cichlids are triphasic, with two power strokes that are separated by a transitional stroke. During Power Stroke II, the lower pharyngeal jaw is acted upon simultaneously by the fourth levator externus and the combination of sternohyoideus and pharyngohyoideus. Bilateral and synchronous contractions of these three muscles are summated setting up a powerful force couple against the prey. At the same time the prey is acted upon by the upper pharyngeal jaw that is retracted and rotated by the retractor dorsalis. Power Stroke I is a protrusive one, during which the teeth of the upper and lower pharyngeal jaws approximate each other resulting in trituration. Thus the prey, wedged between the upper and lower pharyngeal jaws is being acted upon throughout the cycle because of the wide overlap of the firing sequences of its component muscles. The efficiency of this process is attested by the fact that fish remains that are recovered from a cichlid piscivore's gut are so lacerated that it is generally impossible to identify the species (e.g., Greenwood, '74: p. 31). The basic triphasic pattern is apparent in all the piscivorous cichlid species studied, although a rather broad spectrum of interspecific variations on the triphasic theme has been found.

In some piscivorous cichlids, the anatomically symmetrical muscular system of the pharyngeal apparatus can act asymmetrically. Because the articular surfaces of the basipharyngeal joint are relatively flat, they afford freedom for lateral and anteroposterior gliding movements of the upper pharyngeal jaw. The lower pharyngeal jaw can rotate around three axes and undergo protraction and retraction. Asymmetrical muscle action causes simultaneous protrusion, retrusion, opening, closing and transverse movements of both the upper and lower pharyngeal jaws. These complex movements clearly represent an adaptive feature and cannot be regarded as fabricational noise (sensu Seilacher, '74) of a design of a system for a major movement. Any translational motion while the teeth are in close approximation provides supplementary shredding of the prey.

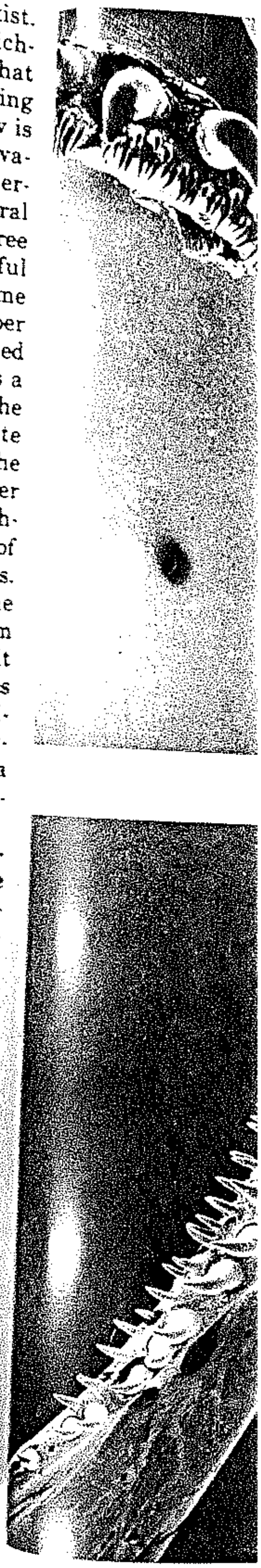

Fig. 18 Scanning electron micrographs of the dentition of the mandible of *Haplochromis compressiceps* (A) and *Lamprologus compressiceps* (B); SEM's of dentition of the lower pharyngeal jaw of *Haplochromis compressiceps* (C) and *Lamprologus compressiceps* (D). Note the striking convergence in shape of the dentition of these two unrelated lineages.

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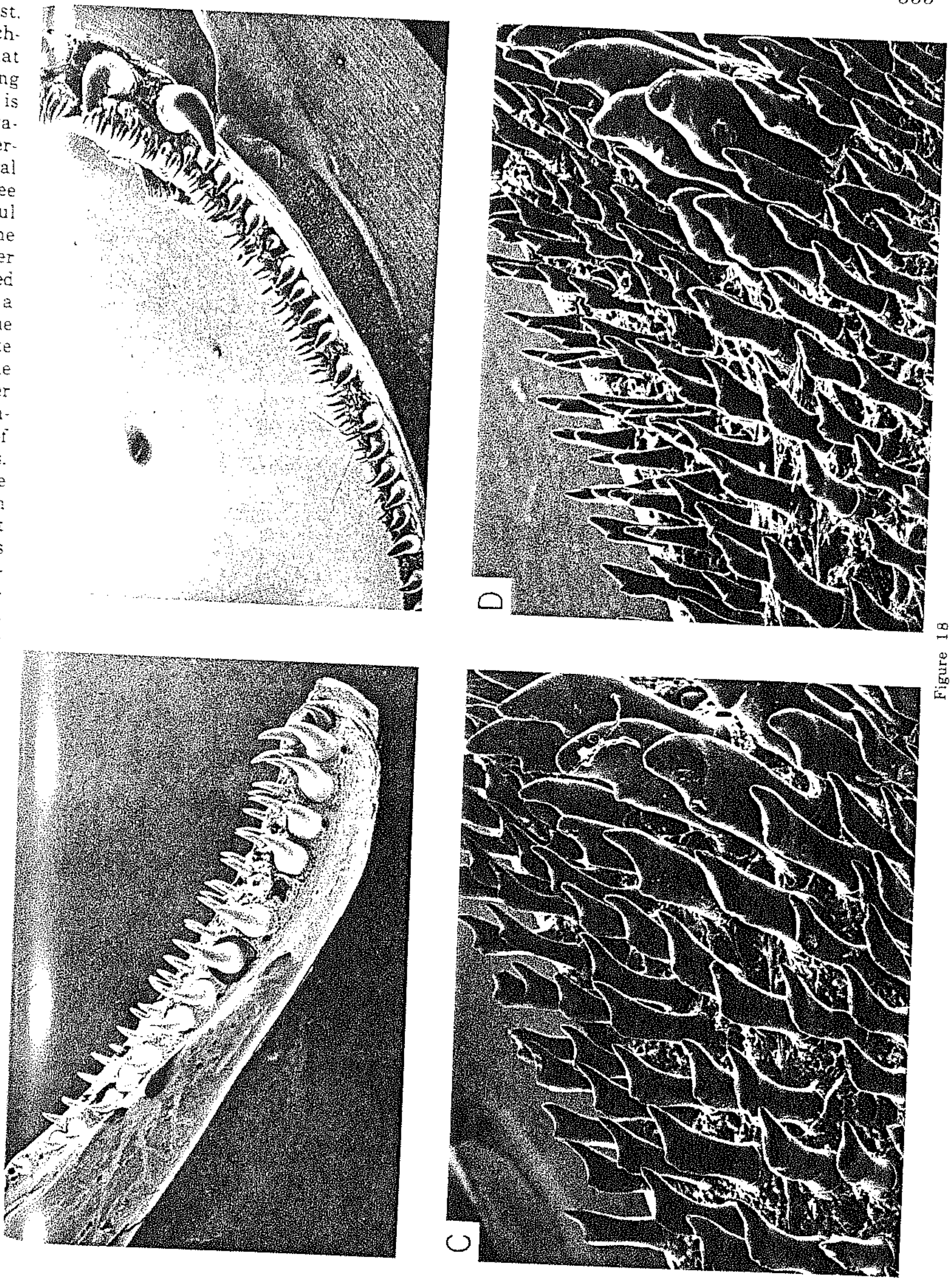

Figure 18

Perhaps the most important concept emerging from this experimental study is that the lower pharyngeal jaw is suspended in a muscular sling, part of which is always in tension because of the extensive overlap of the activity sequences of its component muscles. Functionally, this design is comparable to the jaw apparatus of bats and goats as elucidated by Kallen and Gans ('72) and DeVree and Gans ('76). The muscular components of the lower pharyngeal jaws of piscivorous cichlids may be considered parts of a muscular sling that suspends the moving bony element. The principal components making up the muscular sling of the lower pharyngeal jaw of cichlids are the following pairs of muscles: Medial heads of the fourth levator externus; pharyngohyoideus; pharyngocleithralis internus and externus. As proposed by Kallen and Gans ('72) and DeVree and Gans ('76) a continuously variable muscular sling provides considerable advantages to mastication. Rapid adjustments can be made in response to struggling prey of various sizes, and unilateral force couples can be alternated with bilateral force couples to maximize shearing and shredding of the prey.

According to the cineradiographic data, the main masticatory actions are confined toward the posterior halves of the upper and lower pharyngeal jaws. During both power strokes, the teeth of the posterior halves of the upper and lower pharyngeal jaws approximate each other and protrusive, retrusive and translational motions will cause extensive laceration to the prey. Teeth of the anterior halves of the jaws mainly are engaged in the transport and positioning of the prey. A faithful morphological reflection of this biomechanical profile is the fact that teeth located in the posterior halves of the pharyngeal jaws of cichlids are generally the more specialized ones.

DISCUSSION

Behavioral influences of the prey on the internal oscillator of the predator

Experimental evidence presented here has established consistent differences between ambush and pursuit hunters in respect to electromyographic, biomechanical, pressure and behavioral profiles during prey capture. Nyberg ('71) is the first worker to record two types of feeding in the predaceous largemouth bass *(Micropterus salmoides,* Centrarchidae). In the first mode of feeding, the bass swims over the prey at high speed with fully opened mouth, whereas in the second mode the bass moves more slowly and uses suction developed during opening of its mouth to suck in the prey. Nyberg further hypothesized that smaller bass approach their prey at lower speed, using greater suction velocity than larger bass. It is possible that the smaller bass studied by Nyberg are actually subadults. Juveniles of pursuit hunters are either invertebrate eaters or cryptic ambush hunters (Sohn, personal communication). Thus Nyberg's two feeding types, which are correlated with size, actually may reflect the differences between pursuit and ambush hunters. Previous studies (e.g., Osse, '69; Liem, '70; Nyberg, '71) dealing with high speed inertial suction feeding in teleosts have not considered the possible influence of the behavior of the prey on the mode and strategy of feeding by the predator.

In this study I have shown that each piscivorous cichlid studied, regardless whether ambush or pursuit hunter, possesses a repertoire of two patterns of HSIS during prey capture (fig. 10). The patterns are characteristic for the particular behavioral group and independent of phylogenetic status of the taxon. For example, *Cichla ocellaris* of South America, *Hemibates stenosoma* of Lake Tanganyika and *Serranochromis robustus* of a Zambian river all exhibit identical patterns characteristic for pursuit hunters, whereas juveniles of *Boulengerochromis microlepis* from Lake Tanganyika and *Haplochromis compressiceps* from Lake Malawi share strikingly similar patterns, that set ambush hunters apart from pursuit hunters. In all cases, the nature and locomotory behavior of the prey determines which of the two patterns is recruited. Each pattern is characterized by an extreme regularity of the kinematic, pressure, electromyographic and behavioral profiles. Thus we may conclude that HSIS feeding is basically a preprogrammed motor activity controlled by an internal oscillator. Visual input during the prestrike stalk is relayed to the integrator that determines which one of the two preprogrammed motor outputs is recruited. Size, swimming velocity and the nature of movement patterns of the prey play a paramount role in determining the pattern of prey capture. Once a particuar preprogrammed motor output has been deployed, it is not or cannot be modified during the strike. The two stereotyped motor activities do differ significantly within a species. Important dif-

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Important differences exist between the stereotyped motor activities of ambush and pursuit hunters. As a rule, in pursuit hunters prey capture is accomplished by jaw movements at lower speeds if compared with those of ambush hunters in comparable feeding situations (figs. 7, 8, 10).

High suction velocity and overlap of muscle activity

Agile and elusive prey will elicit stereotyped motor activities producing the greatest suction velocities by ambush as well as pursuit hunters (figs. 8-10). It is paradoxical that the greater the overlap of firing sequences of jaw opening and closing muscles, the greater the velocity of jaw movements (fig. 10). For example, the levator operculi muscle, a jaw opener, fires synchronously with the adductor mandibulae A_2 and A_3, both jaw closers (fig. 10). Yet the mandible is depressed at an extraordinary velocity; maximal depression of the mandible occurring within 25 milliseconds. Anker ('74) has constructed an elegant 4-bar linkage model of the levator operculi-opercular apparatus-mandible coupling (Liem, '70). This model expresses the ratio of output-rotation (of the mandible) and input-rotation (of the gill cover) and predicts the optimal value at which the torque transmission is maximal. Although Barel et al. ('77) claim that the model has been proven mathematically and the physiological range of rotation of the mandible has been proven deductively, empirical tests of the model's predictive value must still be executed. The mathematical derivation of the kinematic transmission-coefficient presupposes that the operculomandibular, operculo-interopercular, and quadratomandibular joints, and the insertion sites of the interoperculomandibular ligaments are in one plane. In piscivorous cichlids this is certainly not the case. Furthermore, the model assumes that the action of the levator operculi muscle is unopposed by the adductor mandibulae muscles. Electromyography of the high velocity strike of an ambush hunter clearly shows synchronous activity of the two antagonistic muscle complexes. The model predicts that pursuit hunters have a more favorable torque transmission than ambush hunters, yet the latter have been measured to move the mandible at a much higher velocity (25 msec versus 75 msec) during the capture of agile and elusive prey. A disparity between model and empirical data gethered from high-speed cinematography may reflect the inherent problems of the application of optimality arguments ("minimum principle") in biological systems, or the disregard of synchronous firing sequences of antagonistic muscle groups and elastic properties of ligaments and tendons associated with the levator operculi-opercular apparatus-mandible coupling. Presently, the significance of the extensive overlap of the firings of antagonistic muscles during high speed inertial-suction feeding remains unknown.

Opercular and branchiostegal mechanisms as anti-backwash devices

Intraorobranchial pressure profiles (fig. 9) during high speed inertial suction feeding reveal the key functional role of the opercular and branchiostegal apparatuses in preventing fluid oscillation within the oropharynx. Thus the emergence of the opercular and branchiostegal apparatuses in the palaeoniscoids during the Permian may be regarded as an important adaptation for the predator feeding regime since it functions as an exceedingly effective and versatile anti-backwash device. Once a wide range of fluctuations in pressure gradients can be damped by the opercular and branchiostegal mechanisms, high volumes and velocities of suction can be generated to optimize feeding by HSIS.

The muscular sling and the cichlid lower pharyngeal jaw

Perhaps the most important functional consequence of the insertion of the greater bulk of the fourth levator externus on the muscular process of the lower pharyngeal jaw (Liem, '74) is that the latter has become suspended in a muscular sling (Kallen and Gans, '72; "Muskelschlinge" of Tittel, '63), part of which can be kept in continuous tension because of the extensive overlap in the firing sequences of its component muscles during the masticatory cycle (figs. 14, 16, 17). Such an organization facilitates the control of protrusion, retrusion, lateral translations as well as rotation about three axes of the lower pharyngeal jaw. In piscivorous cichlids, the fourth levator externus (exerting an anterodorsally directed force at the posteriorly located muscular process), and the pharyngocleithralis externus and pharyngohyoideus (in combination creating a posteroventrally directed force at the anterior end of the lower pharyngeal jaw), form a powerful force couple during the Power Stroke II (figs. 14-16: LE_4, PCE, PH) maximizing the lacerating effects on the prey. Any translational motion while the posterior teeth are near occlusion during Power Stroke II results in additional shredding of the prey. Higher nervous control beyond simple reflexes seems necessary to explain the varying firing intensities and patterns of the component muscles of the muscular sling during different masticatory actions influenced by the nature, size, and position of the prey. Because the tension of the muscular sling can be continuously modified, the lower pharyngeal jaw of cichlids can be considered a key evolutionary innovation of maximum versatility or plasticity (Liem, '74). Only slight reconstructions of the structures making up the lower pharyngeal jaw and its muscular sling are necessary for successful and rapid adaptation to drastic shifts of trophic niches. The inherent functional versatility (flexibility or plasticity) of the muscular sling can be demonstrated even more convincingly in experiments dealing with nonpiscivorous cichlids (Liem, in preparation).

Origin and evolution of piscivorous cichlids

Greenwood ('74) has estimated that 30% of all *Haplochromis* species in Lake Victoria are piscivorous predators. Next to insects, fishes are perhaps the trophic resource most extensively exploited by cichlids. This phenomenon probably is correlated with the great abundance of fishes as prey items and the fact that only slight deviations in physiology and anatomy are required to shift from the generalized insectivorous to the piscivorous feeding regime. The available empirical data do not support the traditional thought that would attribute the abundance, taxonomic diversity and persistence of good functional and anatomical design of piscivorous cichlids to highly developed parental care. Of course, there is empirical evidence that parental care, territoriality, arena behavior, the establishment of personal bonds, and other sociobiological aspects of cichlids can greatly accelerate speciation events (Wilson, '75; Fryer, '77). Actually it was more than two decades ago since Dobzhansky ('51) suggested that evolution proceeds most rapidly in those groups that practice parental care. Cichlids possess a phenomenal ability to speciate (Fryer and Iles, '72; Greenwood, '74) producing the stochastic variability from which the punctuational pattern (sensu Gould and Eldredge, '77) of cichlid evolution can be derived. In t perspective, speciation, brought about stochastic genetic events, provides the r and random material for macroevoluti (Mayr, '63: p. 621) of cichlids. In my vie cichlids owe their evolutionary success terms of trophic exploitation not only to the phenomenal ability to speciate stochasticall but also to their inherently versatile fun tional design (Liem, '74), in which optim solutions in the Newtonian mechanical sen can be evolved rapidly. Thus adaptive chang can evolve by saltation with a minimum nu ber of compromises after the stochastic even leading to speciation have been complete Piscivorous cichlids illustrate this princip well. Electromyographically, inertial suctio by piscivores (figs. 7, 10, 11) and such ge eralized cichlids as *Haplochromis burtoni* an *Tilapia melanopleura* (Liem and Osse, '75) d not differ much. The salient specialization i piscivores is their ability to reduce the feedin cycle temporally. Many insectivorous cichlid and ambush hunters are facultative an opportunistic feeders possessing versatil behavioral repertoires. Even the laceratin actions of the pharyngeal jaw apparatus o piscivores can be derived easily from that o insectivores. Thus the essential difference between the electromyographic profile of insectivores (Liem, '74: p. 430: fig. 8) and that of piscivores (figs. 7, 10, 11) is the shift of the firing of the retractor dorsalis from Power Stroke I and Transitional Stroke to Transitional Stroke and Power Stroke II. Of course, during swallowing, the retractor dorsalis firing patterns exhibit an amazing array, demonstrating built-in ability to modify its firing sequences.

The switch of the teeth of the outer row of the jaws from being bicuspid (characteristic for insectivores) to unicuspid (almost unique for piscivores) occurs quite late during postmaturation growth of the individual (Greenwood, '74). Furthermore, the principal pharyngeal dental specialization in piscivores is basically the progressive lateral compression of most teeth (fig. 18). Therefore the entire functional and anatomical switch from insectivory to piscivory and vice versa can be accomplished by surprisingly simple and saltationary mechanisms. Actually, if we abandon our propensity to formulate models on the basis of optimal design and, instead, compare the full ranges of the total functional repertoires, we can observe a considerable overlap of the feeding mechanisms of insectivorous and piscivorous cichlids.

It is not surprising that great difficulties are encountered in the attempts to determine whether intralineage groups of piscivorous cichlids of Lake Victoria are true, hierarchically evolved, sister groups, or whether they represent gradal assemblages of polyphyletic ancestry (Greenwood, '74). A priori bias toward phyletic gradualism, which is basically an outgrowth of Linnaeus' notion *"natura non facit saltum"* (nature does not make leaps) has led to intensive searches for perfect intermediates or links between insectivorous and piscivorous cichlids. From a punctuational view, it is predictable that such searches generally have failed.

Piscivorous cichlids may not have arisen by orthoselection in gradually-changing lineages, but represent the differential success of subsets from a potentially random pool of speciation events. Adaptive features identified in this paper as characteristic for piscivory could have evolved in multiple and independent lineages at a punctuational tempo (sensu Gould and Eldredge, '77), which seems to be the dominant mode of cichlid evolution. As a result, the homogeneity of specialized morphological features in piscivorous cichlids, which exhibit a confusing web of parallelism, is making the problem of determining monophyletic lineages on the basis of shared combinations of specialized morphological characters extremely difficult.

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