

## Biological Versatility, Evolution, and Food Resource Exploitation in African Cichlid Fishes

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**SYNOPSIS.** Increased potential versatility in form and function of the feeding apparatus of cichlid fishes has led to a prodigious proliferation in the number of possible functional solutions to an increasing variety of biological problems. Optimal utilization of every conceivable trophic resource in lacustrine environments by just one fish family, the Cichlidae, has been achieved by eruptive evolutionary radiation within the characteristically cichlid body plan producing mechanisms which partition the diverse food resources with extraordinary efficiency therefore minimizing resource sharing. There is a direct relationship between the effectiveness of trophic resource exploitation and the functional integration of the cichlid body plan in which a minimum number of adaptive compromises are necessary to evolve optimal anatomical solutions by rapidly realizable changes.

Anatomical data presented here reveal that cichlids possess a specific kind of mosaic in which the basic percoid jaw apparatus permits unparalleled optimal adaptations by simple morphogenetic changes while unique and dramatically diverse patterns of muscular coordination involving degrees of synchrony and extensive modulating capabilities of antagonistic muscle groups have been discovered electromyographically. At the same time the highly integrated pharyngeal jaw apparatus is sufficiently specialized providing complete freedom for the jaws to evolve into refined collecting devices.

The exceptional evolutionary success of lacustrine cichlids demonstrates how rare and very specific kinds of biologically versatile morphological mosaics represent the best preadaptations for the ancestors of major new taxa. Given identical ecological conditions and temporal factors, a group of organisms possessing such rare mosaics, in which optimal biological versatility is realizable by simple evolutionary mechanisms, will dominate newly formed environments to the detriment of taxa not so endowed.

Recently, it has been proposed that a key innovation in cichlids has played an important role in giving the family a significant competitive advantage over other fish families in the rapid colonization of African lakes (Liem, 1973). It has also been dem-

onstrated that the functional integration of the key innovation, i.e., the pharyngeal jaw apparatus, is so basic and its potential adaptive versatility so rich that it is maintained throughout the adaptive radiation even though numerous nondisruptive evolutionary changes do take place. Vermeij (1973*a,b*) has proposed that the potential versatility of a given higher taxon or body plan is determined by the number and range of independent parameters controlling form. In Vermeij's (1973*c*) study on gastropods it has been shown that the range of possibilities in gastropod shell form has increased through geologic time as the result of an increase in the number of controlling parameters. It is axiomatic that concomitant with increased potential versatility in form there will be a proliferation in the

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possible functional solutions not only to any given mechanical problem but also to an increasing variety of biological problems.

This paper deals with a functional-anatomical analysis of the body plans of a rather generalized perch-like fish, *Perca fluviatilis*, and some African representatives of the somewhat related and more specialized family Cichlidae. In this comparison we will attempt to determine and evaluate the differences in realized and potential versatility in form and function of the cephalic regions of the two body plans. We will also discuss the question whether the novel integration of structures of the pharyngeal apparatus in the Cichlidae may have increased the number of independent parameters controlling form so that fewer adaptive compromises are made and more functions can be optimized without detriment to other structures and functions. Finally we will try to correlate the increased potential for complex functional integra-

tion of structures in cichlid fishes with their effectiveness of exploitation of continuously available trophic resources in lacustrine habitats.

#### GENERAL ASPECTS OF THE JAW MECHANISM

Our studies reported here are based on comprehensive anatomical data integrated with electromyographic findings (Fig. 1) synchronized with either light motion pictures or cineradiography (see Osse, 1969; Osse et al., 1972; Liem, 1973).

The head of a fish serves as a bow of a streamlined body while simultaneously protecting the brain and sense organs and performing respiratory, coughing, yawning, and feeding movements. Our experiments reveal that the greatest movements of bony elements and highest muscle activity occur during feeding, which can therefore be considered the dominant function affecting almost all parts of the head. The

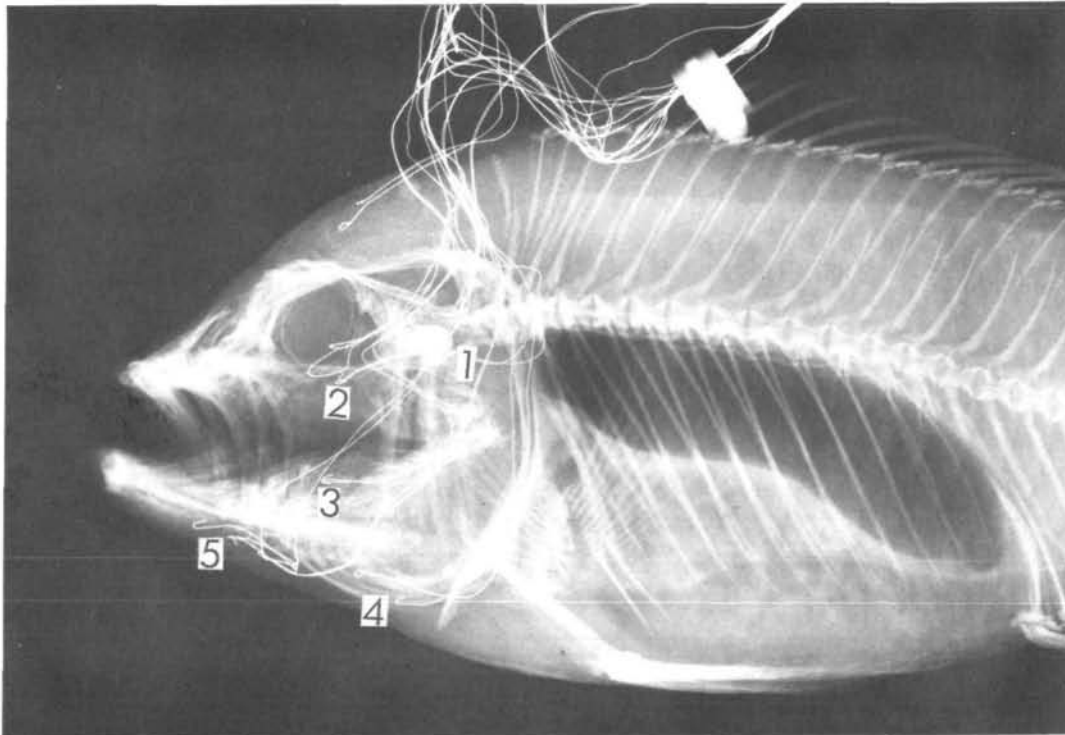


FIG. 1. Lateral radiogram of the head of live *Haplochromis burtoni* with wire electrodes in epaxial muscles, dilator operculi (1), adductor arcus palatini (2), adductor mandibulae  $A_3$  (3), sternohyoideus (4) and

geniohyoideus anterior (5). Wires are bundled and attached to a dorsal spine with a clamp from where the color coded electrodes are led into the amplification system.

functional demands imposed by feeding must therefore have had a decisive influence on the integration of the structural elements of the fish head. However, certain constraints are imposed on the degree of feeding adaptations by other functions, such as respiration.

### Suction

The perch and cichlids do create a suction to produce a current for both respiratory and feeding functions. Suction is created by the following major mechanisms:

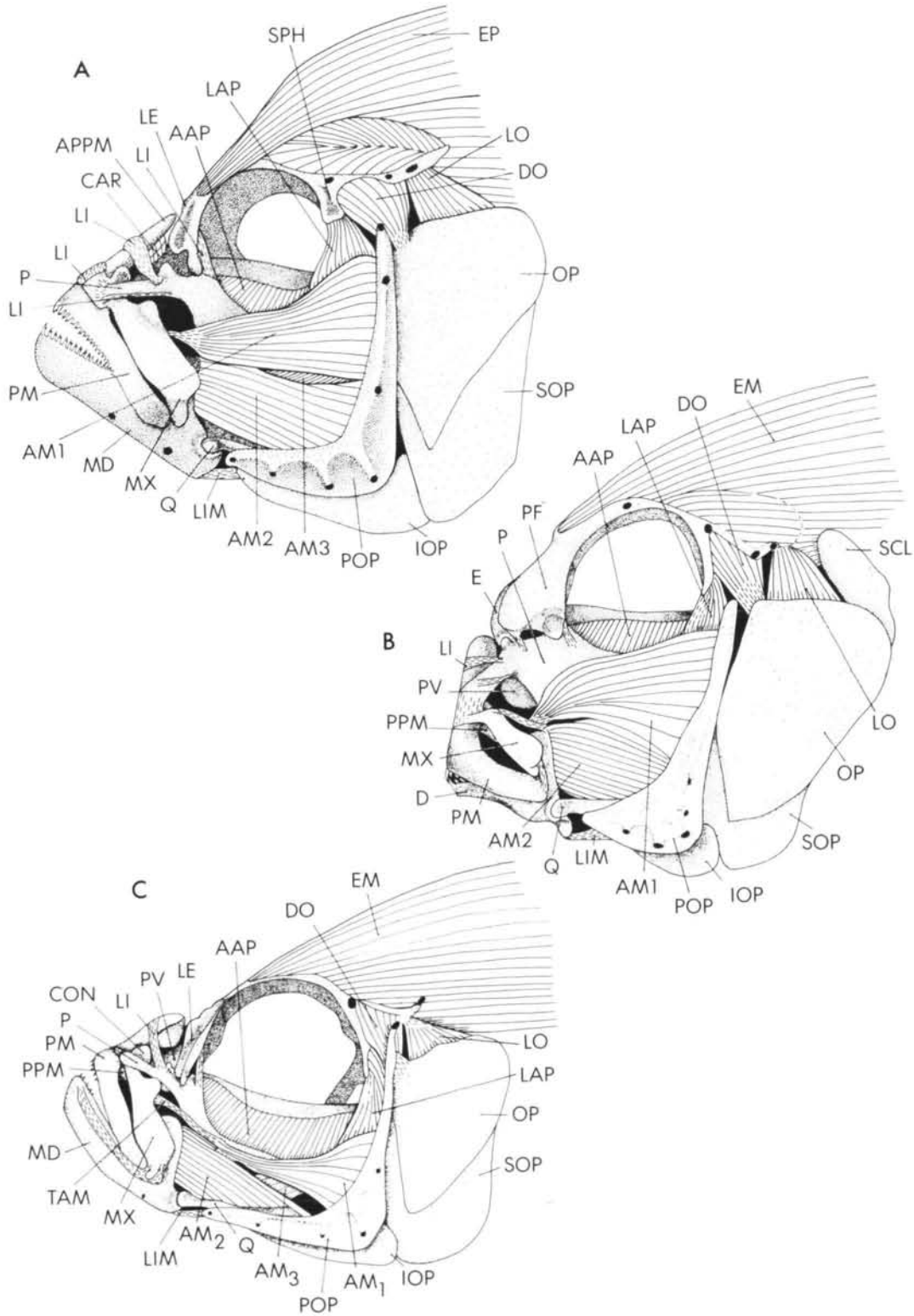
*Suspensory abduction.* The suspensory apparatus (Fig. 16) is composed of the hyomandibular (HM), preopercular (POP), symplectic (SY), quadrate (Q), entopterygoid (ENT), metapterygoid (MPT), and palatine (P). It is roughly a V-shaped complex of which the tip of the anterior leg (represented by the palatine) possesses a cartilage-lined depression accommodating the dorsolateral ball-like process of the lateral ethmoid of the neurocranium. This joint allows mediolateral movements of the suspensorium in relation to the neurocranium. The tip of the posterior leg (represented by the hyomandibular) is a long crest differentiated into a rostradorsal ball-like articular head. The hyomandibular articulates with the neurocranium by means of the rostradorsal ball-and-socket, synovial joint and with a dorsal articular crest which fits in an elongate fossa on the ventral aspect of the pterotic (Fig. 15:ST). During suction, the levator arcus palatini (Fig. 2:LAP), which originates from the postorbital process of the neurocranium and inserts on the lateral surfaces of the hyomandibular, and metapterygoid, is the first muscle to contract, thereby moving the suspensorium laterally (Fig. 3:m. lev. arc. pal.). Indirectly suspensorial abduction will result in (i) opercular abduction because the opercular articulates with the opercular process of the hyomandibular (Fig. 16A:O) and (ii) abduction and retraction of the hyoid rami because the angle between the two hyoid rami widens causing considerable caudal movement of the hyoid symphysis (Fig. 4).

*Abduction and posteroventral movement of the hyoid rami.* This mechanism is activated a few milliseconds after the onset of suspensorial abduction in the perch (Fig. 3:m. sternoh.) during which time the sternohyoideus generates a caudally and ventrally directed force on the hyoid apparatus (Fig. 4). In cichlids these two events show remarkably different patterns (Figs. 8, 9:m. 1. a. p., m. st.). During this activity, the sternohyoideus is not only aided by the levator arcus palatini but also by the hypaxial muscles (Fig. 3:ventral body musc.) which rotates the cleithrum, i.e., the origin of the sternohyoideus, backwards facilitating retraction and depression of the urohyal, i.e., the insertion of the sternohyoideus (Fig. 13:UH,SH). Because of the ligamentous connections of the basi-branchial elements to the hyoid, posteroventral movement of the latter will cause dorsoventral enlargement of the branchial basket. It is important to note that the geniohyoidei anterior and posterior muscles (Fig. 3:m. genioh. ant., m. genioh. post.; Fig. 13:GHA,GHP) exert forces on the hyoid and mandible. When the mouth is being opened, and the hyoid is retracted by the levator arcus palatini and sternohyoideus, the working line of the geniohyoideus posterior (first burst in Fig. 3:m. genioh. post.) moves ventral to the quadratomandibular joint causing mandibular depression.

*Lifting of the neurocranium.* Increase in the volume of the buccal cavity is partially accomplished by dorsal rotation of the neurocranium (in the perch over an angle of about 20°) brought about by contraction of the epaxial muscles (Fig. 2: EM, EP; Fig. 3:dorsal body musc.). Indirectly, lifting of the neurocranium will aid mouth opening and protrusion, and dorsoventral expansion of the branchial basket.

*Opercular abduction and rotation.* The opercular is strongly abducted by the dilatator operculi (Fig. 2:DO), which is aided indirectly by suspensorial abduction. Concurrently, the levator operculi (Fig. 2:LO; Fig. 3:m. lev. operc. ant.) lifts up the opercular by rotating the bone around the joint with the hyomandibular.

*Mandibular depression.* The mandible is



depressed over varying angles (in the perch up to 80°). The depression is initiated by the levator operculi muscle (Fig. 2:LO; Fig. 3:m. lev. oper.) and aided by all ventral cephalic and hypaxial muscles (Fig. 3:m. sternoh., m. hyoh. inf., m. genioh. post. and ant. first bursts, ventral body musc.). Contraction of the levator operculi moves the interconnected opercular, subopercular, and interopercular (Fig. 2:OP, SOP, IOP) posterodorsally. This movement is transmitted to the posteroventral tip of the mandible by the interoperculomandibular ligament (Fig. 2:LIM, MD, D). Because this force is applied ventral to the quadratomandibular joint (Fig. 2:Q) the anterior tip of the mandible will drop. In the perch the distance between the quadratomandibular joint and the anterior tip of the mandible is seven times the distance between the quadratomandibular joint and the insertion site of the interoperculomandibular ligament. Consequently, the caudal displacement of the interopercular caused by opercular lifting is enlarged seven times with respect to the anterior tip of the mandible. The presence of a ligament between the interopercular and the epihyal of the hyoid provides a potentially effective coupling whereby the sternohyoideus and hypaxial muscles can also pull the interopercular caudally and dorsally to depress the mandible (Liem, 1970).

*Upper jaw protrusion.* A consistent relationship exists between mandibular rotation and upper jaw protrusion (Liem, 1970). High speed cinematography in *Perca* (Fig. 5) reveals that maximal mandibular depression consistently coincides with maximal rotations of the maxilla and premaxilla, both of which turn at a faster rate than the mandible. This consistent correlation which has also been recorded in cichlids and nandids (Liem, 1970) indicates a causal re-

lationship between mandibular rotation and upper jaw protrusion. Anatomically this linkage is realized by the dentomaxillary and anterior mandibulomaxillary ligaments (Fig. 6:MML) which run, respectively, between a point near the symphysis of the dentary and the anterior side of the ventral tip of the maxilla, and between the coronoid process of the mandible and the medial aspect of the broad ventral part of the maxilla.

*Expansion of the branchiostegal apparatus.* The ventrolateral enlargement of the opercular cavity is accomplished by contraction of the inferior hyohyoideus (Fig. 13:HH, HH1-3) and the short muscle bundles between the branchiostegal rays and the ceratohyal which spread the rays.

*Generalization.* The above mentioned events leading to a sudden enlargement of buccal and opercular activities do take place in a definite and consistent sequence although some synchrony occurs (Fig. 3). Preceding the expansion phase there is a brief period of activity of the adductors of the jaws [adductor mandibulae A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub> (Fig. 2:AM<sub>1-3</sub>)], the suspensorium—adductor arcus palatini (Fig. 2:AAP), opercular (adductor operculi), and branchiostegal apparatus (hyohyoideus superior). These muscular activities diminish the initial volume of the cavities prior to the sudden enlargement optimizing the gape-and-suck function.

#### *Adduction, retraction, and contraction*

Rapid closing and retraction of jaws, adduction of the suspensory apparatus and the opercular, and compression of the branchiostegal apparatus take place sequentially.

*Adduction of the suspensorium.* The adductor arcus palatini muscle (Fig. 2:AAP)

FIG. 2. Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball. A, *Haplochromis burtoni*; B, *Tropheus moorii*; C, *Haplotaxodon microlepis*. AAP, adductor arcus palatini; AM<sub>1</sub>, A<sub>1</sub> portion of adductor mandibulae; AM<sub>2</sub>, A<sub>2</sub> portion of adductor mandibulae; AM<sub>3</sub>, A<sub>3</sub> portion of adductor mandibulae; APPM, ascending process of premaxilla; CAR, rostral cartilage; CON, cranial condyle, D, dentary; DO, dilatator operculi; E, ethmoid; EM and EP,

epaxial muscles; IOP, interopercular; LAP, levator arcus palatini; LE, lateral ethmoid-prefrontal; LI, ligaments; LIM, interoperculomandibular ligament; LO, levator operculi; MD, mandible, MX, maxilla; OP, opercular; P, palatine; PF, prefrontal; PM, premaxilla; POP, preopercular; PPM, premaxillary condyle of maxilla; PV, prevomer; Q, quadrate; SCL, supraethrum; SOP, subopercular; SPH, sphenotic; TAM, tendon of A<sub>1</sub> portion of adductor mandibulae.

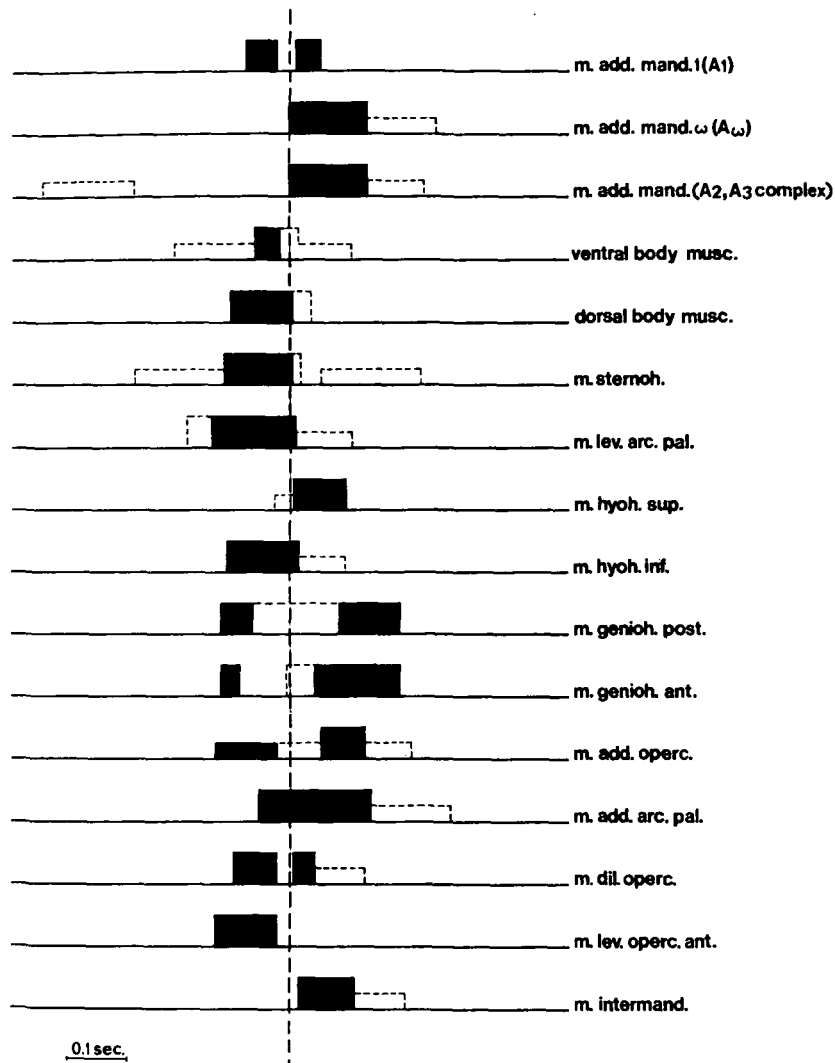


FIG. 3. Diagram of the active periods of the muscles of *Perca fluviatilis* during feeding. Dashed lines indicate frequent variations in the periods. The vertical dashed line indicates the onset of activity in the A<sub>2</sub>, A<sub>3</sub> complex; dorsal body musc., dorsal body muscles; m. add. arc. pal., adductor arcus palatini; m. add. mand. ω (A<sub>ω</sub>), intramandibular portion of adductor mandibulae; m. add. mand. 1 (A<sub>1</sub>), A<sub>1</sub> portion of adductor mandibulae; m. add. mand. (A<sub>2</sub>, A<sub>3</sub> complex), A<sub>2</sub> and A<sub>3</sub> portions of adductor mandibulae; m. add. operc.,

adductor operculi; m. dil. operc., dilatator operculi; m. genioh. ant., geniohyoideus anterior; m. genioh. post., geniohyoideus posterior; m. hyoh. inf., hyohyoideus inferior; m. hyoh. sup., hyohyoideus superior; m. intermand., intermandibularis; m. lev. arc. pal., levator arcus palatini; m. lev. operc. ant., levator operculi anterior; m. sternoh., sternohyoideus; ventral body musc., ventral body muscles. (From Osse, 1969.)

shows considerable activity during suction (Fig. 3:m. add. arc. pal.) indicating its important role in regulating the degree and velocity of suspensorial abduction in coordination with its antagonist, the levator arcus palatini (Fig. 3:m. lev. arc. pal.; Fig. 2:LAP). However, once the levator arcus palatini seizes its activity, the adductor

arcus palatini adducts the entire suspensory apparatus at a high velocity.

*Adduction of the opercular.* In close coordination with the dilatator operculi, the adductor operculi functions as a regulator of opercular abduction (Fig. 3:m. add. operc.). However, in the absence of activity of its antagonist, i.e., dilatator operculi, the

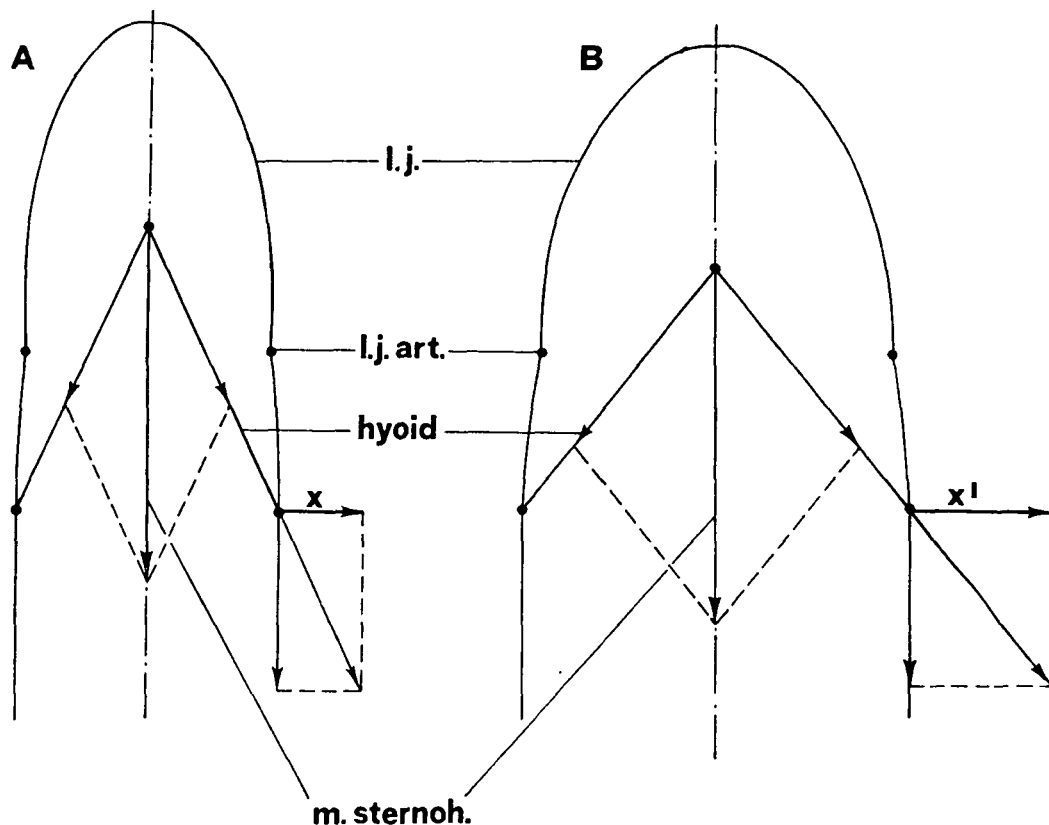


FIG. 4. Diagram indicating the consequences of suspensorial abduction for the lateral component  $x$  of the force of the *m. sternohyoideus*. *A*, weak abduction; *B*, stronger abduction. *l.j.*, lower jaw; *l.j. art.*, lower jaw

articulation; *m. sternoh.*, sternohyoideus;  $x$ , lateral component of sternohyoideus during weak abduction;  $x'$ , lateral component of sternohyoideus during strong abduction. (From Osse, 1969.)

adductor operculi compresses the opercular cavity.

*Closing and retraction of jaws.* The adductor mandibulae (Fig. 2:AM<sub>1</sub>, AM<sub>2</sub>, AM<sub>3</sub>; Fig. 6:IAM) elevate the mandible (Fig. 3:*m. add. mand. ω*, *m. add. mand. 1*, *m. add. mand. A<sub>2</sub>*, *A<sub>3</sub>* complex). In *Perca*, there is no overlap between the activity of the adductor complex and the jaw opens (Fig. 3). Because the depression of the mandible is considerable, the adductor complex has a considerable leverage, which is realized by the great length of the muscle fibers inserting on a very short tendon close to the quadratomandibular joint (Fig. 6:A<sub>3</sub>, TAM). The tendon passes through the very narrow, vertical slit between mandible and suspensorium and inserts on the mandible very close to the quadratomandibular joint so that its excursions are quite restricted although the mandible undergoes very

large movements.

The "superficial" head, the adductor mandibular A<sub>1</sub> has a tendon on the medial aspect of the maxilla (Fig. 6:TAM<sub>1</sub>) caudoventral to the articulation with the palatine. The tension in the tendon as a result of contraction of A<sub>1</sub> will indirectly reduce the velocity with which the mandible is depressed, and will press the cranial condyle of the maxilla (Fig. 6:CC, CON, MX) against the prevomer (Osse, 1969). Because the insertion site is caudoventral to the palatomaxillary joint, A<sub>1</sub> will pull back the maxilla to its resting position. The caudodorsal movement of the ventral end of the maxilla around the palatomaxillary joint is transmitted to the premaxilla causing retraction of the upper jaw. Slack in the ligaments connecting the upper jaw with the mandible causes retraction to fall behind jaw adduction. Alexander (1967)

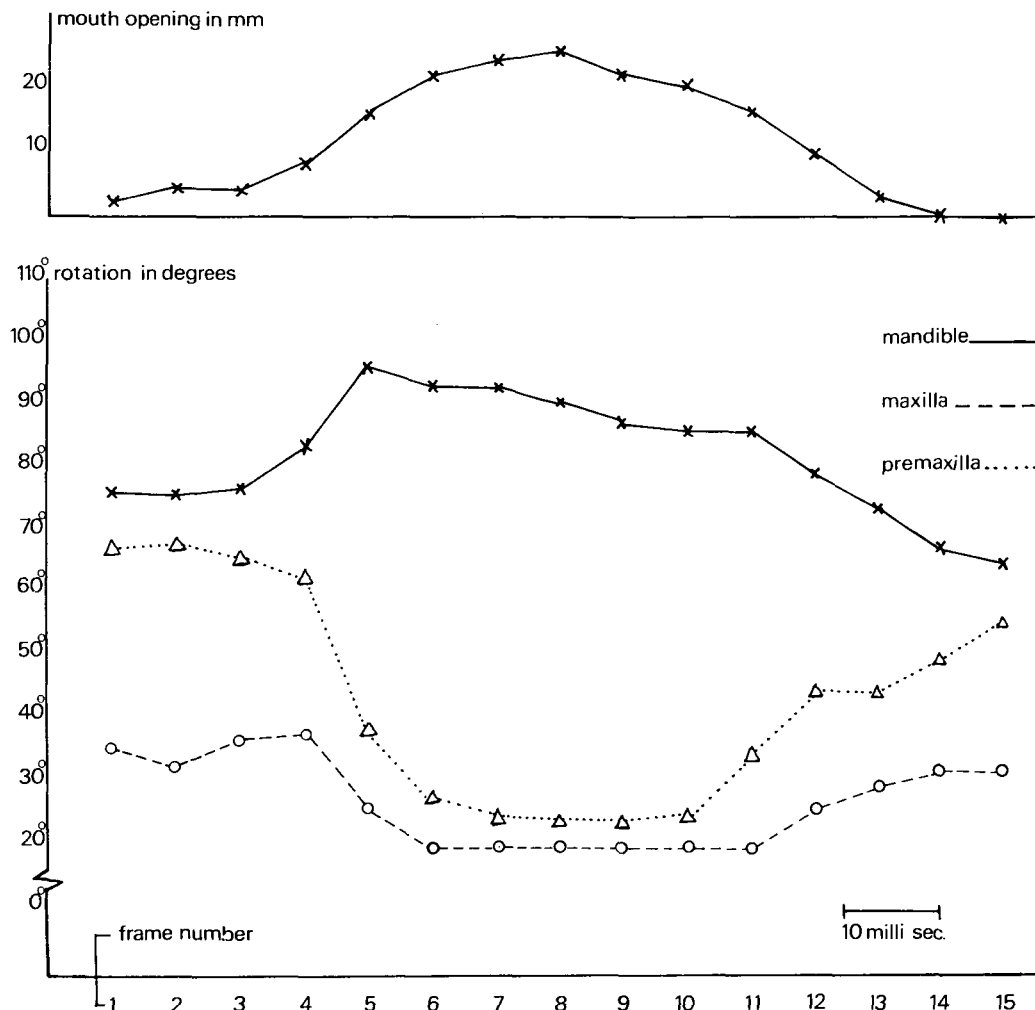


FIG. 5. Graphic representation of the rotation of mandible, premaxilla, and maxilla in *Perca fluviatilis*

during mouth protrusion, as measured from separate frames of a 150 frames/sec 16 mm motion picture.

proposed a mechanism to prevent retraction of the premaxillae during suspensorial abduction involving the moving of the anterior ends of the palatine medial to the cranial maxillar condyles, but our preliminary cineradiographic studies on cichlid fishes have not revealed such a movement.

*Protraction of the hyoid.* Although the geniohyoidei anterior and posterior muscles (Fig. 3:m. genioh. ant., m. genioh. post.; Fig. 13:GHA, GHP) play a major role in depressing the mandible, they perform a drastically different function when the mandible is fixed by the adductor mandibulae muscles. Simultaneous contraction of the geniohyoidei muscles (second bursts

in Fig. 3:m. genioh. ant., m. genioh. post.) leads to protraction of the hyoid when the mandible is fixed by activity of the adductor mandibulae complex.

*Contraction of the branchiostegal apparatus.* The branchiostegal rays are moved dorsally by the hyohyoideus superior muscle resulting in a drastic decrease of the broad base of the cone shaped opercular cavity.

#### FEEDING CHARACTERISTICS OF *PERCA*

Although the major features of the above jaw mechanisms are applicable to both the perch (*Perca fluviatilis*) and the cichlids, there are important differences between



the two groups.

*Perca fluviatilis* neither bites nor grinds the food with its jaws. Instead, the upper and lower jaws function as braces of a folded and laterally compressed apparatus which unfolds and expands at a high velocity into a wide hollow cylinder (Fig. 7). During this rapid unfolding the transverse sections of the buccal cavity is transformed from an inverted V into a circle. The perch can be considered a typical gape-and-suck feeder. The sudden expansion of the jaw apparatus occurs in less than 50 msec and generates a large suction force of more than 300 cm water (Alexander, 1967). The adaptive significance of the circular mouth opening (Fig. 7) is that it combines a maximal surface area with a hydrodynamically preferential minimal circumference. Although the generated suction force acts on both prey and predator, the latter's mass is so much larger that it has to swim forcefully to overtake the prey. In the perch, prey is sucked into the esophagus with minimal participation of the jaw teeth and the pharyngeal jaw apparatus. Food preparation or mastication does not occur in the numerous observations in the laboratory.

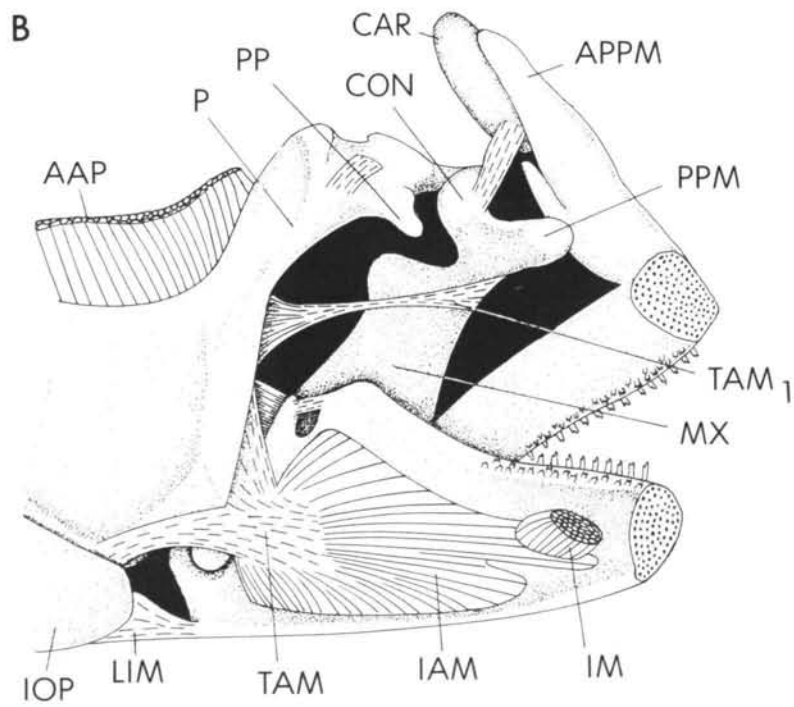
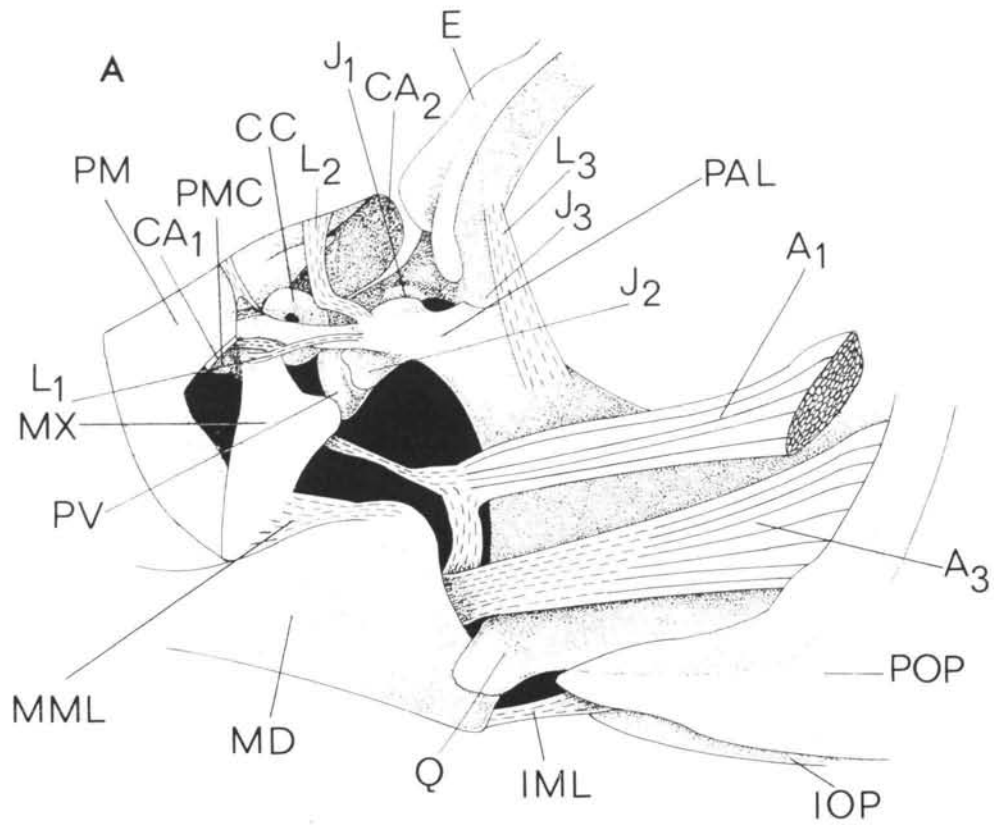
Being a typical gape-and-suck feeder, the perch's pharyngeal jaw apparatus is involved in neither food preparation nor food transport (Osse, 1969), although it may play a minor role in deglutination of some foods during unusual conditions. The anatomical configuration of the pharyngeal jaw apparatus of *Perca* corresponds with that of *Pristolepis* (see Liem, 1973) in the following salient features: (i) the dorsal branchial muscles such as the fourth levatores externi and levatores posterior insert on the dorsal branchial elements, i.e., fourth epibranchials; (ii) the absence of an articulation between the upper pharyngeal jaws and the skull base; (iii) the left and right lower pharyngeal jaws remain separate. Although no electromyographic data are available, the morphological pattern in *Perca* is sufficiently close to that of *Pristolepis*, that we may assume that the pharyngeal jaws possess a very limited functional versatility.

FEEDING CHARACTERISTICS OF SOME CICHLIDS

In sharp contrast with the condition in *Perca* (Osse, 1969), the nandids (Liem, 1970), and *Cyprinus carpio* (Ballintijn, 1969), the jaw movements of the cichlids studied exhibit a much greater variety within a given individual fish. In cichlids, jaw movements can be adjusted to the specific demands of a particular environmental situation. The nature of the exceptionally versatile jaw movements and the controlling mechanisms have been analyzed by motion analysis and electromyography of *Haplochromis burtoni* (Fig. 1), *H. polystigma*, *Tilapia nilotica*, *T. melanopleura*, *T. mariae*, and *Petrotilapia tridentiger*.

Contrary to the condition in *Perca* in which the jaws function to elongate and enhance the sucking mechanism, the protrusible premaxillaries and mandibles of cichlids are highly coordinated and versatile collecting devices. The electromyograms made during the feeding movements show consistent differences in the timing and duration of activity and amplitude of the involved muscles. Such differences are correlated with the nature, size, and location of the food.

In *Haplochromis burtoni* the main activities of the sternohyoideus (Fig. 8:m. st.) and levator arcus palatini muscles (Fig. 8:m. 1. a. p.; Fig. 2:LAP; Fig. 13:ST) are always synchronous and, mostly, precede those of the levatores operculi (Fig. 8:m. 1. o.; Fig. 2:LO) by a period varying between 0 and 80 msec. A suction force can therefore be created before the mouth opens, depending on the location and nature of the food and the substrate. Suction is employed when food is taken from the surface or midwater. Tubifex worms, on the other hand, are carefully extracted from the sand and gravel by the premaxillaries and dentaries by synchronous activity of the jaw openers, i.e., levator operculi and the adductor mandibulae complex. By modulating the intensity of contractions of the synchronously active antagonists, *H. burtoni* is able to regulate the velocity and degree of protrusibility and gape of the jaws. Such a controlling mechanism is especially well developed in the algae scraper *Petrotilapia tridentiger* (Liem, unpublished), which is capable of accommodating its tooth bands



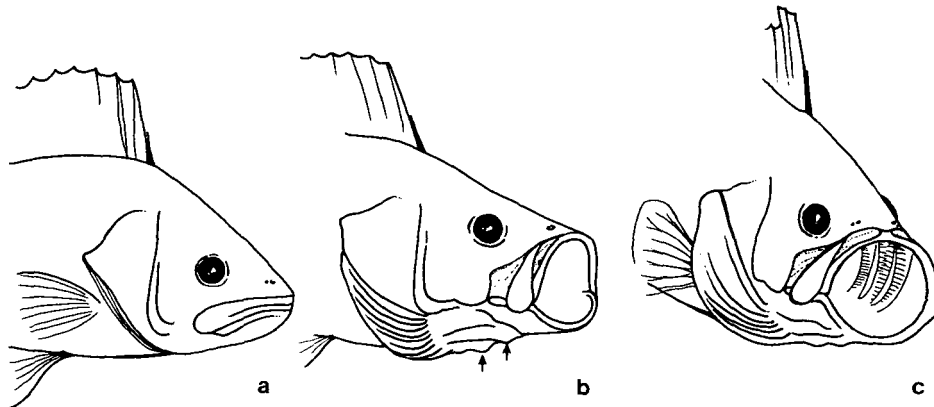


FIG. 7. Representative tracings of the head of *Perca fluviatilis* during feeding from a 16 mm movie at 64 fr/sec. *a*, Rest position; *b*, lateral view of the unfolded

tubelike jaw apparatus, note the protruding hyoid apparatus (arrows); *c*, frontal view of condition in *b* to show the position of the branchiospinae.

to irregularities of the rock surface. The geniohyoideus anterior and posterior muscles (Fig. 8:m. g. a., m. g. p.; Fig. 13:GHA, GHP) exhibit the typical double bursts and are synchronous with the adductor mandibulae muscles. In some situations *H. burtoni* produces a series of low amplitude suction movements by alternating contractions of the sternohyoideus and geniohyoideus anterior muscles causing respectively retractive and protractive movements of the hyoid rami. Some foods are transported caudally by long drawn out activity periods of the adductor mandibulae muscles accompanied by a strong burst of activity in the dilator operculi muscle.

In the *Tilapia* species studied, the mouth is opened before suspensorial and opercular abduction. Considerable protrusion of the upper jaw is often accompanied by only slight mandibular depression. Electromyographically these movements are characterized by the early activity of the levator operculi muscle (Fig. 9:m. l. a. p.;

Fig. 10:m. lev. op.), which precedes the main bursts of the sternohyoideus and levator arcus palatini muscle (m. st., m. l. a. p., m. sternohy., m. lev. arc. pal.). One can also recognize a distinct preparatory phase during which all adductor muscles are active. In *Tilapia*, the A<sub>1</sub> part of the adductor mandibulae muscle, which is inserted by a tendon to the maxilla (Fig. 6:A<sub>1</sub>-TAM<sub>1</sub>) is active synchronously with the levator arcus palatini muscle (Fig. 9:m. a. m. l., m. l. a. p.). It seems that cichlids, in general, are regulating the velocity and degree of jaw protrusion by synchrony of the A<sub>1</sub> part of the adductor mandibulae muscles with its antagonists. Such a mechanism may be responsible for the important fact that *Tilapia melanopleura* can depress its mandible fully without protruding the upper jaws. A similar observation has been made on *Pterophylum* (Alexander, 1967) as it feeds from the bottom. C. Noomen (University of Leiden, personal communication to J. W. M. O.) has suggested that in *Haplochromis* abduction of

FIG. 6. *A*, Lateral aspect of preorbital region of *Tilapia nilotica* to show articulations and joints between jaws, neurocranium and suspensorium. *B*, Medial aspect of jaws and associated muscles and ligaments in *Haplochromis burtoni*. A<sub>1</sub>, A<sub>1</sub> portion of adductor mandibulae; A<sub>2</sub>, A<sub>2</sub> portion of adductor mandibulae; AAP, adductor arcus palatini; APPM, ascending process of premaxilla; CA<sub>1</sub>, cartilaginous disc of premaxillary condyle underlying premaxilla; CA<sub>2</sub> and CAR, rostral cartilage; CC and CON, cranial condyle; E, ethmoid; IAM, intramandibular portion of adductor mandibulae; IM, intermandibularis; IML, interoper-

culomandibular ligament; IOP, interopercular; J<sub>1</sub>-J<sub>3</sub>, palatal joints with prevomer, lateral ethmoid and prefrontal; L<sub>1</sub>, palatomaxillary ligament; L<sub>2</sub>, palatopalatine ligament; L<sub>3</sub>, craniopalatine ligament; LIM, interoperculomandibular ligament; MD, mandible; MML, maxillomandibular ligament; MX, maxilla; P and PAL, palatine; PM, premaxilla; PMC, premaxillary condyle; POP, preopercular; PP, prevomerine process of palatine; PPM, premaxillary condyle of premaxilla; PV, prevomer; Q, quadrate; TAM<sub>1</sub>, tendon of A<sub>1</sub> portion of adductor mandibulae; TAM<sub>2</sub>, tendon of A<sub>2</sub> portion of adductor mandibulae.

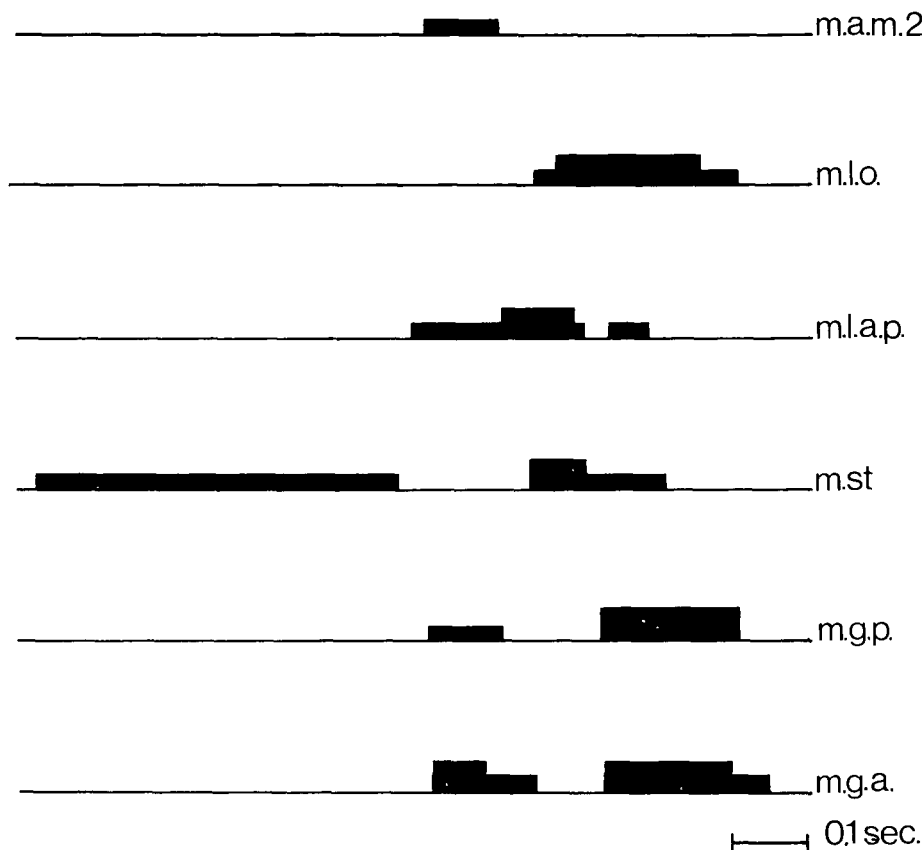


FIG. 8. Diagram of activity periods of head muscles during one feeding cycle in *Haplochromis burtoni*. Note the synchronous activity of the adductor mandibulae (m. a. m. 2) and both the geniohyoid muscles (m. g. a., m. g. p.) in the preparatory phase. The mouth opens

the suspensorium elicits forces which protrude the premaxillae. The regulatory patterns of cichlid feeding mechanisms are therefore much more complex and varied than previously postulated by Vandewalle (1972) on an anatomical basis.

In non-piscivorous cichlids, the feeding movements are less extreme and of longer duration and the electromyograms exhibit lower amplitudes (Fig. 10) than in the perch (see Osse, 1969). One full suction cycle (including resumption of the resting position) lasts 400 msec in non-piscivorous cichlids, 230 msec in the perch.

Although broad comparative data are not yet available and the functional mechanisms of cichlid jaws remain poorly understood, this study has revealed a previously unknown, functional versatility in

after some activity of abductors and depressors (m. l. o., m. st.). m. a. m. 2, A<sub>2</sub> portion of adductor mandibulae, m. g. a., geniohyoideus anterior; m. g. p., geniohyoideus posterior; m. l. a. p., levator arcus palatini; m. l. o., levator operculi; m. st., sternohyoideus.

the cichlid feeding mechanisms, which differ drastically from those of more generalized percoids such as *Perca* (Osse, 1969), *Sebastes* (Alexander, 1967), and nandids (Liem, 1970).

The cichlid pharyngeal jaw apparatus represents a morphological key innovation, which has freed the premaxillary and mandibular jaws to evolve numerous specializations (Liem, 1973). The morphological novelty involves the development of a synarthrosis between the two lower pharyngeal jaws, a strategic shift of insertion of the dorsomedial heads of the two fourth levatores externi muscles, and the specialized synovial joints between upper pharyngeal jaws and basicranium (Fig. 11:CB<sub>5</sub>; LE<sub>4</sub>). In all cichlids the fourth levator externus retains a varying but

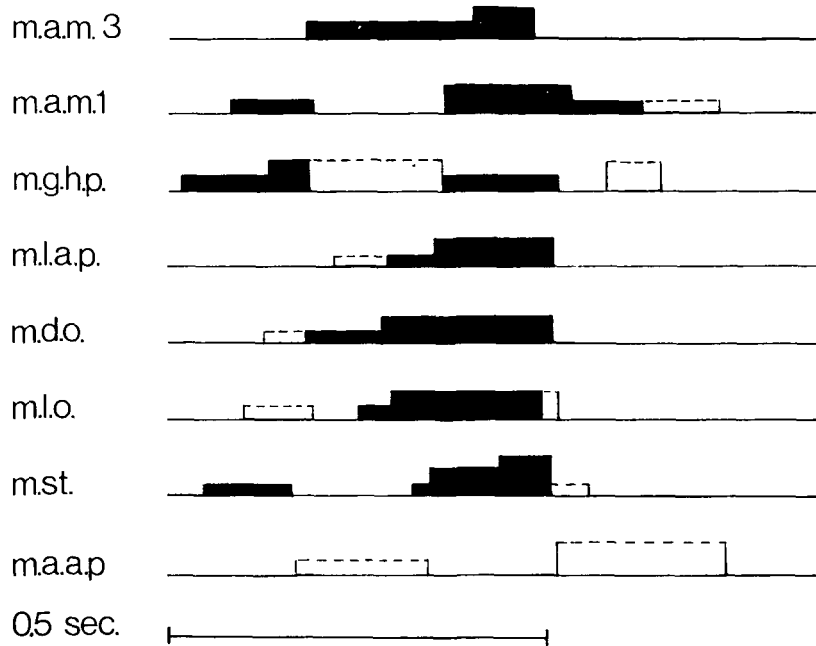


FIG. 9. Diagram of activity periods of head muscles during feeding based on six feeding acts in *Tilapia melanopleura*. Levels indicate amplitude of emg. Activity indicated by dashed lines occurred only in one of the six feeding acts. m. a. a. p., adductor arcus palatini;

m. a. m. 1, A<sub>1</sub> portion of adductor mandibulæ; m. a. m. 3, A<sub>3</sub> portion of adductor mandibulæ; m. d. o., dilatator operculi; m. g. h. p., geniohyoideus posterior; m. l. a. p., levator arcus palatini; m. l. o., levator operculi; m. st., sternohyoideus.

mostly vestigial lateral component which maintains the original, but aponeurotic insertion on the dorsolateral aspect of the fourth epibranchial. Such a lateral head is especially well developed in *Cichla ocellaris* and several other taxa indicating that the prominent medial part has evolved by splitting of the original fourth levator externus as postulated by Liem (1973). However, we disagree with Goedel (1974b) who regards the dominant medial head inserting on the lower pharyngeal jaw as the protractor arcuum branchialium muscle which allegedly has arisen *de novo* as a functional antagonist of the retractor pharyngeus. Electromyographic evidence (Liem, 1973, and unpublished) disproves such a function. This conversion of preexisting elements into the unique adaptive complex has furnished the Cichlidae with a most efficient mechanism to transport, manipulate, and prepare an exceptionally wide variety of foods (Liem, 1973). Because the functional integration of the cichlid pharyngeal jaw apparatus is so basic and its potential adaptive versatility so rich,

it is maintained throughout the adaptive radiation even though numerous nondisruptive evolutionary changes do take place. However, in spite of the seemingly endless spectrum of evolutionary variations in the adaptive expressions of the pharyngeal jaw mechanisms of cichlids, we have found strikingly identical solutions to the same functional problem in taxa from distinctly different ancestral origins. Common in African lakes is the snail *Melanoides tuberculata* which possesses a very thick and tightly-coiled elongate shell which is particularly resistant to crushing. Yet this snail is crushed and broken by the pharyngeal apparatus of the mollusc-eating *Astatoreochromis alluaudi alluaudi*, *Haplochromis placodon*, *Lamprologus tredocephalus*, and *Haplochromis vanderhorsti* respectively from Lakes Victoria, Malawi, Tanganyika, and the East African Luicha river. All are characterized by the following specializations (Fig. 11): highly developed pharyngeal jaws and dentition; hypertrophied fourth levator externus (LE<sub>4</sub>) and posterior (LP), retractor pharyngeus (RP), transversus ventralis

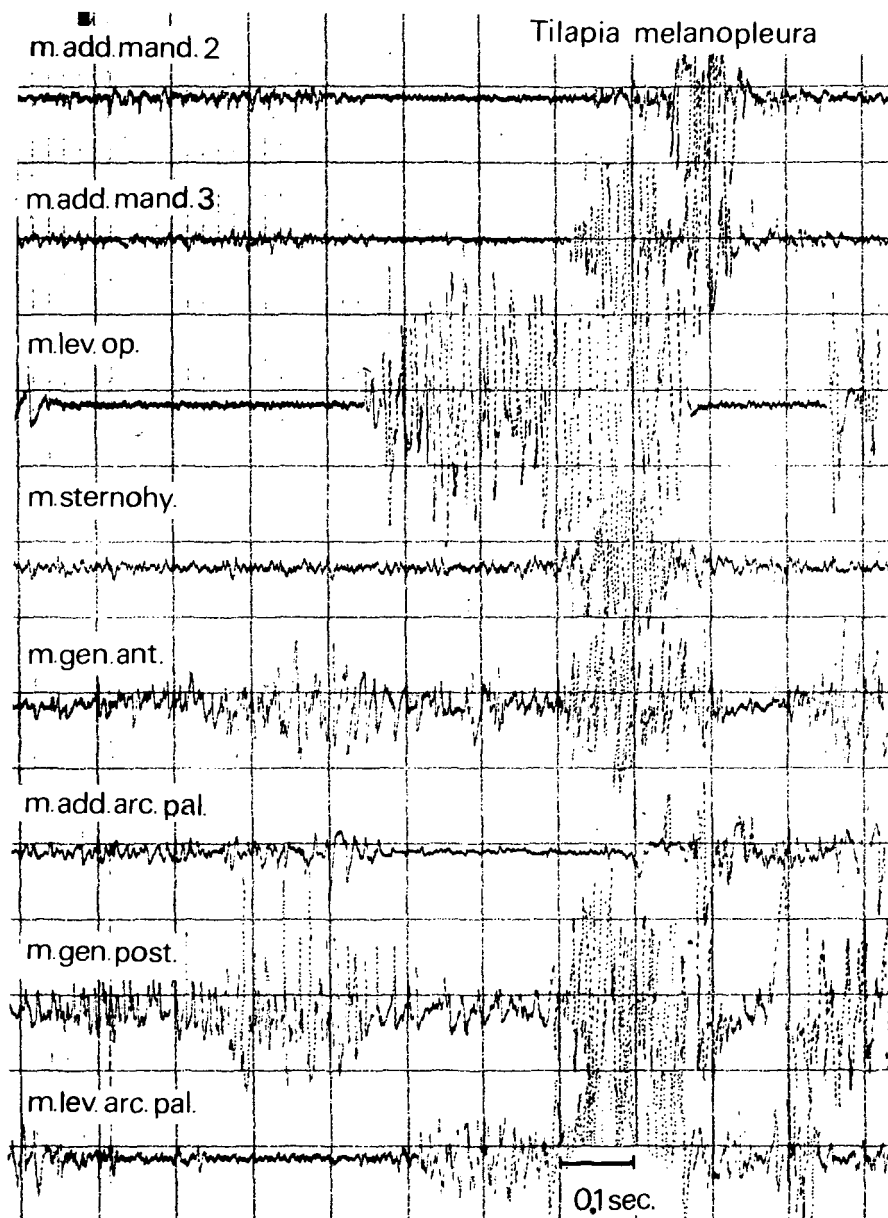


FIG. 10. Pattern of muscle activity of *Tilapia melanopleura* feeding on Tetramin flakes on the bottom. Note the preparatory phase (left side) with synchronous activity of adductor muscles, the early activity of the levator operculi and the nearly synchronous activity of abductor and adductor muscles (right side) (during high activity the base line is lost and the individual

spikes are hardly distinguishable). m. add. arc. pal., adductor arcus palatini; m. add. mand. 2 and m. add. mand. 3, respectively, A<sub>2</sub> and A<sub>3</sub> portions of the adductor mandibulae; m. gen. ant., geniohyoideus anterior; m. gen. post., geniohyoideus posterior; m. lev. arc. pal., levator arcus palatini; m. lev. op., levator operculi; m. sternohy., sternohyoideus.

(TV), pharyngocleithralis externus (PHCE) and internus (PHCI) and fifth adductor muscles (AD); reduced adductor operculi muscle (AO); a shift of the insertion of the pharyngohyoideus muscle (PH

to a much more caudal site on the lower pharyngeal jaw (CB<sub>5</sub>); the levator posterior (LP) has split into two distinct heads, the anterodorsal having the original insertion on the fourth epibranchial whereas the

posteromedial head joins the tendon of the fourth levator externus (Fig. 11B) to attach on the muscular processes of the lower pharyngeal jaw (CB<sub>5</sub>). There is unequivocal evidence that the four allopatric taxa which share these far reaching morphological and functional specializations represent separate phyletic lines (Greenwood, 1954, 1956, 1964; Fryer and Iles, 1972). Other unrelated mollusc-feeding cichlids sharing the specialization are *H. ishmaeli*, *H. pharyngomylus*, *H. obtusidens*, *H. humilior*, and *Tylochromis polylepis*. Different gene complexes have therefore produced one efficient solution to exploit molluscs as a food resource. Once these specializations have evolved, they will be retained in their basic configuration although degenerative changes do occur when environmental demands are relaxed under either laboratory conditions (Greenwood, 1965a) or in nature as exemplified in Lake Nakavali by *Astatoreochromis alluaudi occidentalis* (Fig. 11A,B) in which the fourth levator externus, levator posterior, and retractor pharyngeus (LE<sub>4</sub>, LP, RP) are less developed than in *alluaudi alluaudi*. However, the second head of the levator posterior, although reduced, is retained (Fig. 11B:LP).

In sharp contrast to the Cichlidae, in the perch (*Perca*) and the percoids—e.g., the Nandidae (Liem, 1970), *Pristolepis* and *Badis* (Liem, 1973)—the upper pharyngeal jaws are either “freely-floating” or slide along the cranial base through mediation of a cartilaginous cushion and the lower pharyngeal jaws are paired with muscular associations the nature of which creates considerable functional constraints. Consequently, in *Perca* the pharyngeal jaws mainly function to prevent the prey from escaping, while in the nandidae they are involved in deglutination of large prey *in toto*.

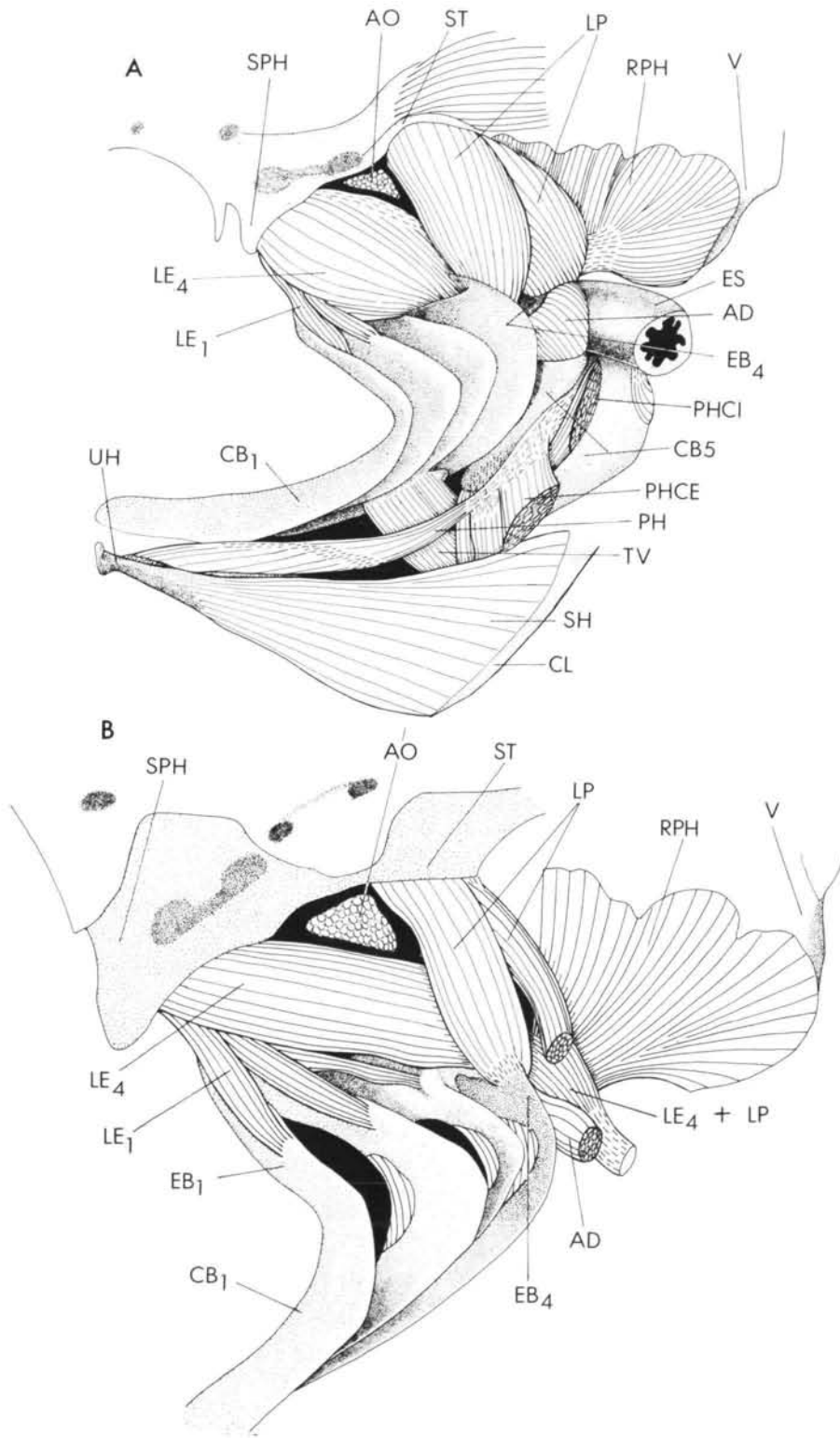
#### CICHLID RESPIRATORY MECHANISMS

During active ventilation, the pattern of activity of muscles in cichlids (Fig. 12) is comparable to that of the perch (cf. Osse, 1969) and the carp (cf. Ballintijn, 1969). The inspiratory muscles are the levator operculi (m. l. o.), sternohyoideus (m. st.),

geniohyoideus posterior (m. g. h. p.), and dilatator operculi (m. d. o.), whereas the adductor arcus palatini (m. a. a. p.), the adductor mandibulae complex (m. a. m. 3), and geniohyoideus anterior (m. g. h. a.) are active during expiration. The contrasting functions of the anterior and posterior heads of the geniohyoideus (Fig. 13:GHA, GHP) as first described in the perch (Osse, 1969) are also characteristic for cichlids (Fig. 12:m. g. h. a., m. g. h. p.) invalidating the functional collective term protractor hyoideus as proposed by Holmquist (1910) and Liem (1967, 1970). Shortly after recovery from tricaine methanesulfonate anesthesia the amplitudes of the electromyograms of all muscles, except those of the branchial arches, are high, but they decrease rapidly, disappearing in the noise after 20 hr. After 4 to 5 hr, only one muscle, the adductor mandibulae part A<sub>3</sub> remains rhythmically active. During low intensity ventilation in cichlids, suction is generated solely by elastic recoil following compression by the adductor mandibulae part A<sub>3</sub> muscle resulting in an extraordinarily efficient respiratory mechanism requiring minimal energy.

Although Chardon and Vandewalle (1971) and Goedel (1974a,b) have found morphometric differences between oral-incubating and substrate-spawning species of *Tilapia*, we have obtained consistently identical patterns in the electromyograms of the respiratory muscles of *T. nilotica* (oral incubator) and *T. melanopleura* (substrate spawner). The morphometric differences found by Chardon and Vandewalle (1971) and Goedel (1974a,b) are reflections of differences in differential growth rates of specific regions, which may be correlated with feeding rather than with oral breeding mechanisms. An increase in volume of the buccal and pharyngeal cavities is not always a prerequisite for oral incubation since some species, e.g., *Tropheus moorii*, carries no more than 7 eggs, whereas *Tilapia esculenta* may have as many as 711. Both are oral incubators and will have very different relative volume requirements.

We have found an important difference between the respiratory patterns of *Haplochromis burtoni* on one hand and the *Tilapia*





species on the other. In *Tilapia* the sternohyoideus is consistently nonactive whereas the levator arcus palatini shows great activity. In *H. burtoni* the reverse is true in seven of the eight experiments. During the respiratory phase, contraction of the sternohyoideus primarily lowers the floor of the mouth, whereas the levator arcus palatini abducts the sidewalls. Ballintijn (1972) has shown experimentally that a teleost fish can regulate ventilation by either varying the intensity of a particular muscle or varying the number of active muscles without altering the nature of movements and hence the hydrodynamic efficiency of the respiratory apparatus. Although one of the experimental *H. burtoni* was apparently capable of switching from sternohyoideus to levator arcus palatini breathing, there is a clear preferential inspiratory motor pattern with an active sternohyoideus for this species. The adaptive significance of the preference for the use of one of the two muscles to enlarge the buccal cavity is unknown. It is conceivable that a somewhat dorsoventrally flattened buccal cavity can be more favorably enlarged by movements of the floor of the mouth (sternohyoideus activity) whereas a mouth with a greater depth may benefit from lateral movement of the sidewalls (levator arcus palatini). However, in the percoids *Acerina*, *Perca*, and *Stizostedion* the sternohyoideus muscle is never active during respiration although the cross sectional shapes of the buccal cavities range from deep to dorsoventrally flattened.

During oral incubation in *H. burtoni* and *T. nilotica*, the female carrying the brood has the floor of her mouth greatly depressed, with the branchiostegal apparatus displaced ventrally and the operculars abducted. Only very slight respiratory movements are discernible. The only tangible feature adaptive to oral incubation seems to

be the initial permanent activity of the sternohyoideus after anesthesia. Such a non-phasic continuous activity of the sternohyoideus keeps the urohyal and, hence, the floor of the mouth in a more ventral position mimicking the condition in a female carrying eggs. A depressed urohyal not only increases the volume of the buccal cavity through the respiratory cycle but also facilitates suspensorial abduction because of the resulting lateral force exerted on the epihyals (Fig. 4). This mechanism could optimize the respiratory functions in an oral-brooding female. Yet continuous activity of the sternohyoideus seems to be an unnecessary energy drain. However, in the total reproductive effort of the species oral incubation may well represent optimum fitness.

#### OPTIMAL FOOD RESOURCE EXPLOITATION BY LACUSTRINE CICHLIDS

Cichlid adaptive radiation is essentially one of trophic specializations (Fryer, 1959; Greenwood, 1973). Major adaptive radiations among animals generally occur in the presence of competition (Stanley, 1973) because it provides a powerful centrifugal force for the occupation of new niches (Mayr, 1963). In exceptional cases, e.g., Darwin's Finches, the Hawaiian Honeycreepers, and the cyprinids of Lake Lanao (Myers, 1960), freedom from competition has indeed contributed to the emergence of adaptive radiations. However, "...the cichlids of the African lakes have undergone even greater radiation than these groups in spite of the presence of competitors" (Fryer and Iles, 1972, p. 520). When the lacustrine environments were formed, potential competitors of cichlids such as the Mochocidae, Bagridae, Characidae, and Cyprinidae entered the Rift Valley Lakes (Victoria, Tanganyika, Malawi) simultaneously with the non-

FIG. 11. Lateral view of branchial apparatus and muscles after removal of opercular, suspensory apparatus, gills, gill rakers, and mucous membrane. *A*, *Astatoreochromis alluaudi alluaudi*; *B*, *A. alluaudi occidentalis* with the lower pharyngeal jaw, hyoid and associated muscles removed. AD, fifth adductor; AO, adductor operculi; CB<sub>1</sub>, first ceratobranchial; CB<sub>s</sub>, lower pharyngeal jaw (fifth ceratobranchial); CL,

cleithrum; EB<sub>1</sub> and EB<sub>4</sub>, first and fourth epibranchial; ES, esophagus; LE<sub>1</sub> and LE<sub>4</sub>, first and fourth levator externus; LP, levator posterior; PH, pharyngohyoideus; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; RPH, retractor pharyngeus superior; SH, sternohyoideus; SPH, sphenotic; ST, pterotic; TV, transversus ventralis; UH, urohyal; V, vertebra.

specialized riverine cichlids. For example, the cyprinid *Labeo cylindricus* of Lake Malawi was almost certainly present in the lake before such specialized cichlid competitors as *Labeotropheus* and *Pseudotropheus* evolved (Fryer and Iles, 1972). In the presence of competitors and predators, the cichlids have evolved an incredibly large number of endemic specialists exploiting every conceivable food resource in the lakes. The patterns of optimal food resource exploitation exhibited by lacustrine cichlids seem to support Cody's (1974) model in which high resource abundance, dissimilar resources and coexistence of exploiting competitors, favor a wide range of specialists over generalists. The dramatically diverse foods being efficiently exploited by cichlid specialists fall within the following major categories: phytoplankton, sedimented planktonic algae, epilithic algae, periphyton, higher plants, molluscs, benthic arthropods, insects, zooplankton, fish scales and fins, whole fishes, fish eyes, fish eggs, embryos, and larvae. During early intralacustrine evolution, intense competitive interactions between taxa have accelerated the rate of clear-cut partitioning of the trophic resources producing progressive specializations into diversified subzones, in which prodigious ramifications cover a breadth of total adaptations that are unparalleled by any other vertebrate family.

Food resource partitioning in cichlids has been accomplished through accentuated and accelerated functional and morphological divergence during speciation. In Lake Nabugabo, which was cut off from Lake Victoria only about 4000 years ago, the 10 cichlid species show the early stages of food partitioning among closely related species (Greenwood, 1965*b*). Similarly ill-defined partitioning phenomena may occur occasionally in the relatively young (Late Pleistocene) Lake Victoria as demonstrated by several related species with strikingly similar feeding habits coexisting in identical habitats (Fryer and Iles, 1972, pp. 303-308). Intense competitive interactions may potentially occur between the less-specialized taxa feeding on the same foods, although the niches tend to fill rapidly and

abut one another. A wealth of indirect evidence testifies to the operation of intense interspecific competition in the early evolutionary history of lacustrine cichlids. In the "older" and therefore more specialized and complex cichlid communities of Lakes Malawi and Tanganyika (Late Pliocene), food preferences of the various taxa are, in general, very distinct. Even in those cases in which various taxa seem to exploit the same food resource, more detailed observations have revealed a well-defined partitioning into subzones as exemplified by *Tilapia esculenta* and *T. variabilis* from Lake Victoria. Both exploit phytoplankton, but the former collects the material from suspension whereas the latter gathers the sedimented phytoplankton (Lowe-McConnell, 1956). In the crater lake Barombi Mbo in West Cameroon, both *Sarotherodon lohbergeri* and *S. steinbachi* feed on organic debris, but *S. lohbergeri* collects it from the surfaces of rocks and plants while *S. steinbachi* gathers it mainly from sandy areas (Trewavas et al., 1972). Numerous cichlid species depend on the layer of algae growing on the rocks in Lake Malawi as a food resource. Some use the algae directly, but others specialize to exploit the associated microfauna composed of insect larvae and crustaceans (Fryer, 1959). The food resources on the rocks have been partitioned so that species feeding on one kind of food do not compete directly with those using a different food.

Optimal utilization of available food supplies by lacustrine cichlids has been achieved by eruptive evolutionary radiation within the characteristically cichlid body plan producing mechanisms which partition the trophic resources with extraordinary efficiency. The net effect of such ecological differences between taxa, elicited by competition during the early evolutionary stages, is a drastic reduction or even elimination of trophic competition. In more complex communities, such as the cichlids living in association with the algae-covered rocks of Lake Malawi, we do find mixed species assemblages of high population density feeding on identical algae. Such a coexistence of taxa with identical food requirements has been attributed to a

superabundance of food. These coexisting species have been regarded as iconoclastic associations whose members flagrantly defy Gause's principle by living as individuals in a mixed indivisible society rather than as species with distinct niches (Fryer and Iles, 1972, pp. 286-290). However, the possible existence of competition for shelter and territory in the presence of superabundance of food cannot be dismissed until detailed ethological studies prove otherwise, since Smith and Tyler (1973) have demonstrated by direct observations that territorial and spatial requirements play a dominant role in coral reef fish communities. For mammals, Stanley (1973) has shown that advanced mobility and behavior have permitted the evolution of aggressive interactions and territoriality in species living under conditions in which food is not usually in limited supply.

It is theoretically possible to postulate that intralacustrine evolution of cichlids has been generated by the specialized sexual and reproductive behavior, parental care, territoriality, and other subtle means such as exceptionally efficient communication, ability to change color rapidly, and superior intelligence (Fryer and Iles, 1972). While such mechanisms may accelerate the evolutionary process and may produce morphological differences which reflect stochastic factors and differences in environment, they cannot account for the dramatic degree of divergence demonstrated by lacustrine cichlids. We agree with Fryer (1959), Greenwood (1964, 1973), and Lowe-McConnell (1969) that intralacustrine cichlid radiation is essentially one of trophic specialization. Even in the relatively young crater lake Barombi Mbo which dates from the late quarternary, most species of cichlids differ in their diets so much that no two species are likely to come into direct competition for food (Trewavas et al., 1972). Food resource partitioning is the rule, while trophic resource sharing is the rare exception in lacustrine cichlid communities.

#### MORPHOLOGICAL VERSATILITY AND OPTIMIZATION OF TROPHIC FUNCTIONS

The extraordinary effectiveness of food

resource exploitation by lacustrine cichlids is based on a greater mechanical efficiency and versatility of the feeding apparatus.

#### *Consequences of a versatile key innovation*

With the emergence of the pharyngeal jaws as a key innovation, the cichlids gained a distinct selective advantage over potential competitors in their quest for exploitative domination of trophic resources in lacustrine environments. The novel and complex integration of the basicranium, the levatores externi and posterior muscles, sutural connection of the fifth ceratobranchials, new contraction patterns of the pharyngohyoideus, pharyngocleithralis internus and externus, and the levatores externi and posterior muscles, represent a fundamental alteration in body plan (Liem, 1973). In sharp contrast with the condition in generalized percoids, the complex pharyngeal jaw apparatus of cichlids is an exceedingly efficient precision instrument capable of crushing molluscs (Fig. 11), manipulating fish scales into packets to facilitate deglutination, slicing flesh from whole fishes, molding filamentous algae onto more manageable masses, masticating crustaceans and insect larvae, and cutting leaves of higher plants, etc.

In evolving the more complex integration, numerous structures which were previously either independent or governed by independently varying morphogenetic parameters have become dependent upon one another. However, this special kind of integration has increased the potential versatility of the cichlid pharyngeal jaw apparatus because it furnishes multiple functional pathways that can be realized by relatively simple morphogenetic changes. Fundamental functional changes can be produced by: accelerated growth rates of the upper pharyngeal jaws either caudal or cranial to the basipharyngeal joint resulting in important alterations of the lever arms; shifts of muscle attachments sometimes resulting in functional reversals; and alterations in the shape, size, and position of the articular surfaces of the basipharyngeal joint. All such changes are governed by

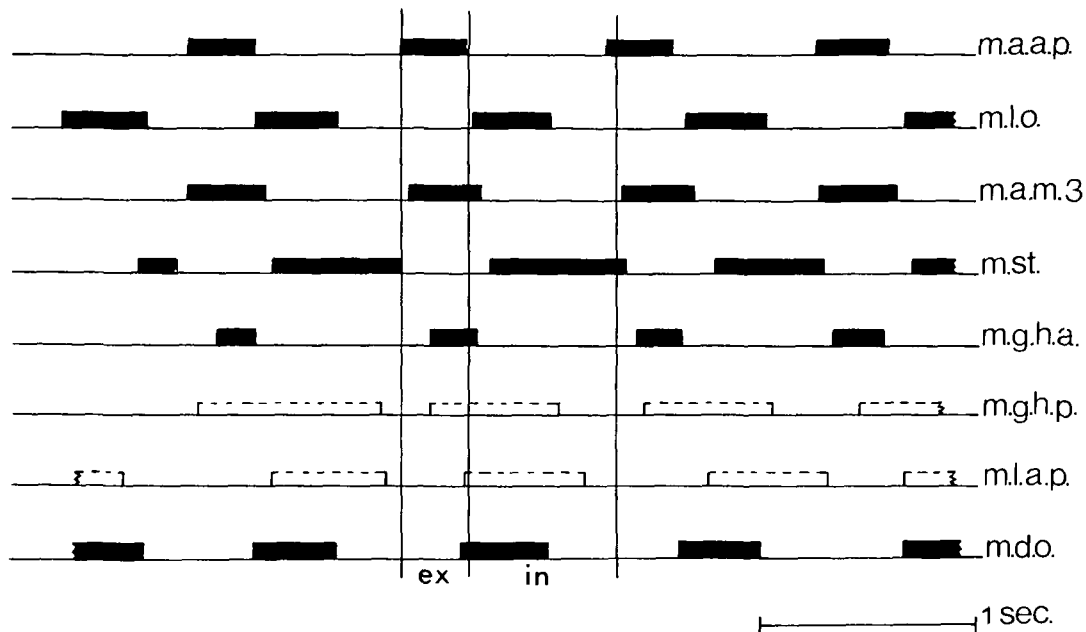


FIG. 12. Pattern of activity periods of some head muscles during respiration in *Haplochromis burtoni*. Expiration and inspiration phases are indicated with respectively ex and in. The open blocks indicate activity in one experiment only. m. a. a. p., adductor arcus

palatini; m. a. m. 3, A3 portion of adductor mandibulae; m. d. o., dilatator operculi; m. g. h. a., geniohyoideus anterior; m. g. h. p., geniohyoideus posterior; m. l. a. p., levator arcus palatini; m. l. o., levator operculi; m. st., sternohyoideus.

simple morphogenetic factors and can, therefore, evolve very rapidly.

#### *Adaptive expressions of the premaxillary and mandibular jaws*

The most important biological meaning of the emergence of the highly integrated cichlid pharyngeal jaw apparatus is the change from mutual dependence to independence of the jaw apparatus (premaxillary, mandibular) and the pharyngeal jaw complex. Once the two "functional units" have become relatively independent, many restrictions on adaptive expressions of form are either relaxed or removed. The jaw complex, including the upper jaw, mandible, suspensorium, opercular, and hyoid units, is released from limitations because of the versatility of the pharyngeal jaw apparatus. By contrast the pharyngeal jaw apparatus of generalized percoids causes numerous adaptive compromises in the entire jaw complex. In cichlids the jaw complex has been freed to evolve into numerous, highly efficient and specialized

food collecting devices in which a minimal number of adaptive compromises are necessary.

The most outstanding features of the total jaw complex of cichlids are its relatively generalized morphological composition (Figs. 2, 6, 14) and the ability to control jaw movements in an exceptionally precise manner by varying the extent of synchrony and modulating the degree of contractions of antagonistic muscle groups (Figs. 8, 9, 10). Throughout the adaptive radiation the basic functional integration of the jaw complex is maintained. Opening of the jaws is initiated by the levator operculi (Figs. 2, 14:LO) through the intermediary of the interopercular (IOP) and the interoperculo-mandibular ligament (LIM) which translates the caudodorsal movement of the interopercular into mandibular depression. In the long bodied *Julidochromis ornatus*, the interoperculo-mandibular ligament has become quite elongate and more horizontal (Fig. 14A:LIM) causing a delay in the transmission of forces to depress the mandible. Speed of mandibular depression

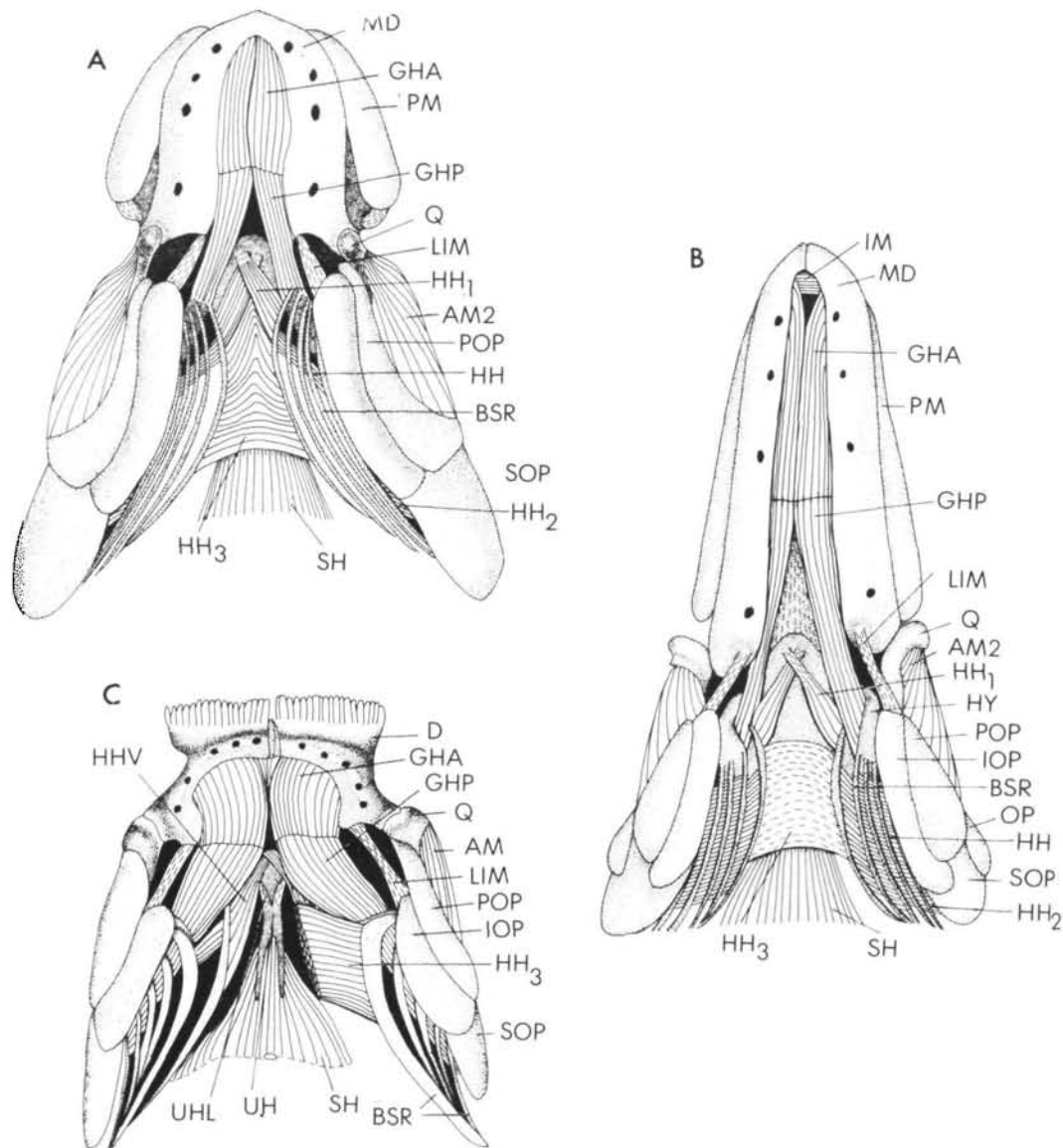


FIG. 13. Ventral aspect of muscles of the head. *A*, *Haplochromis burtoni*; *B*, *Haplochromis (Limnochromis) pfefferi*; *C*, *Tropheus moorii*. AM and AM<sub>2</sub>, A<sub>2</sub> portion of adductor mandibulae; BSR, branchiostegal ray; D, dentary; GHA, geniohyoideus anterior; GHP, geniohyoideus posterior; HH, hyohyoideus; HH<sub>1</sub>, hyohyoideus inferior; HH<sub>2</sub> hyohyoideus superior;

HH<sub>3</sub>, third division of hyohyoideus; HHV, hyohyoideus inferior; HY, hyoid; IM, intermandibularis; IOP, interopercular; LIM, interoperculomandibular ligament; MD, mandible; OP, opercular; PM, premaxilla; POP, preopercular; Q, quadrate; sh, sternohyoideus; SPO, subopercular; UH, urohyal; UHL, urohyalohyohyal ligament.

has been diminished in favor of a hypertrophied adductor complex and levatores arcus palatini muscles for which there is strong selection in connection with its habit of slipping into crevices among rocks where it feeds on diatoms and filamentous algae. Numerous variations have evolved in the

adductor complex: in the algal eating and rock-scraping *Tropheus moorii* and the goby-like *Eretmodus cyanostictus*, which feeds on algae and its microfauna, the A<sub>1</sub> portions of the adductor mandibulae muscles (Figs. 2, 14:AM<sub>1</sub>) play dominant roles not only in regulating the degree of protrusion

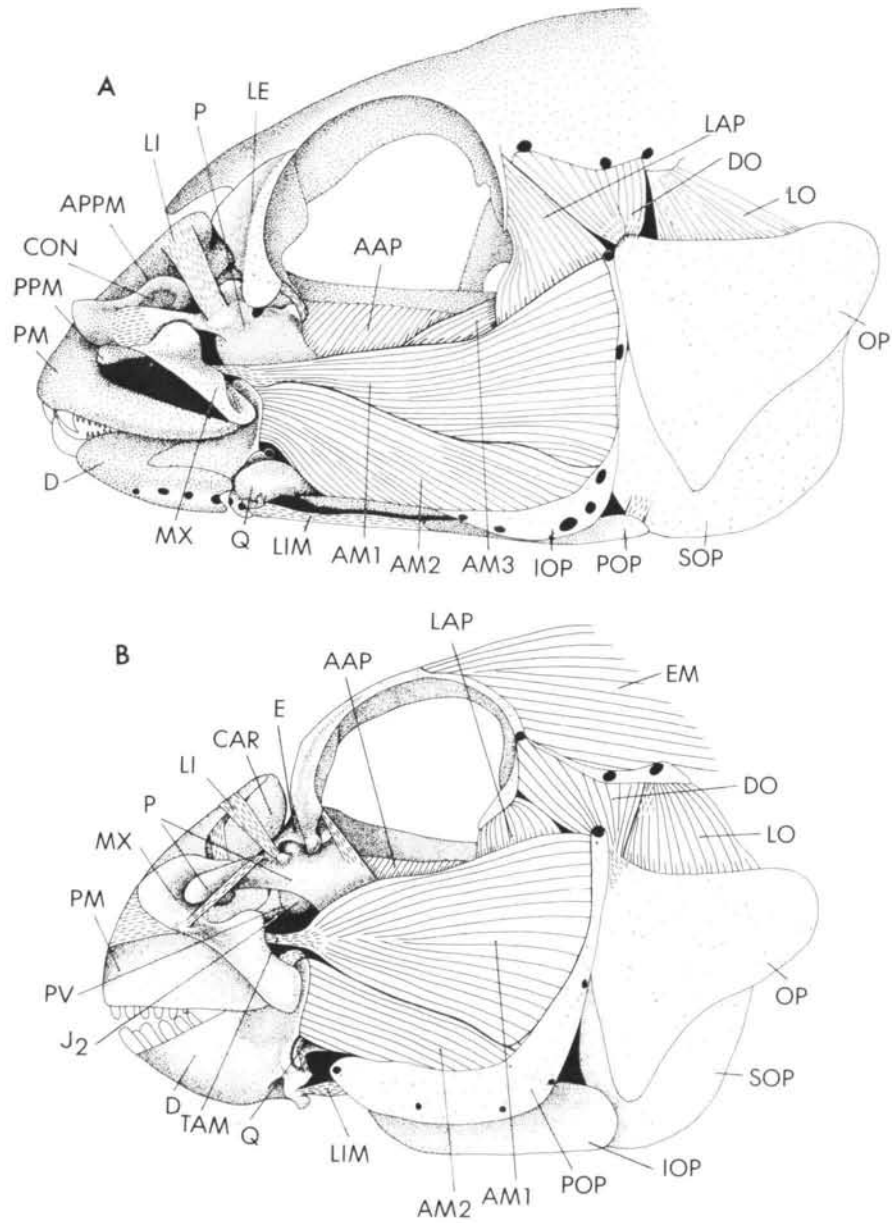


FIG. 14. Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball. *A*, *Julidochromis ornatus*; *B*, *Eretmodus cyanostictus*. AAP, adductor arcus palatini; AM<sub>1-3</sub>, respectively, A<sub>1</sub>-A<sub>3</sub> portions of adductor mandibulae; APPM, ascending process of premaxilla; CAR, cartilage; CON, cranial condyle; D, dentary; DO, dilatator operculi; E, ethmoid; EM, epaxial muscles; IOP, interopercular;

J<sub>2</sub>, palatoprevomerine joint; LAP, levator arcus palatini; LE, lateral ethmoidprefrontal; LI, palatopalatine ligament; LIM, interoperculohyomandibular ligament; LO, levator operculi; MX, maxilla; OP, opercular; P, palatine; PM, premaxilla; POP, preopercular; PPM, premaxillary condyle of maxilla; PV, prevomer; Q, quadrate; SOP, subopercular; TAM, tendon of A<sub>1</sub> portion of adductor mandibulae.

but also in the stability of and total exerted power by the upper jaw; the piscivorous (although copepods are occasionally taken) *Haplotaxodon microlepis* emphasizes the

rapid and extensive unfolding of the jaws, suspensorium, hyoid, and operculars so characteristic of gape-and-suck feeders (Fig. 2). Employing the identical

mechanisms found in the generalized *Haplochromis burtoni*, the gape-and-suck effect in *Haplotaxodon* had been greatly enhanced by increased moment arms of the long-fibered levator arcus palatini (Fig. 2:LAP), dilatator operculi (DO), and sternohyoideus muscles (Fig. 13:SH), respectively, around the craniohyomandibular, operculohyomandibular, and interhyalomandibular joints. The expanding capacity of the jaws is improved by accelerated growth rates of the mandible, premaxilla, and maxilla (Fig. 2C) and by higher mobility in the sliding joints; in *J. ornatus* and *Telmatochromis temporalis* the adductor mandibulae muscles become more massive and increase their fiber lengths by invading on the preopercular so that the sensory canal becomes marginal (Fig. 14A:AM<sub>1</sub>, AM<sub>2</sub>, AM<sub>3</sub>, POP). The gape of the mouth is oblique in the generalized *Haplochromis burtoni* (Fig. 2A), but is horizontal in *J. ornatus* (Fig. 14A), vertical in *Haplotaxodon microlepis* (Fig. 14C), and ventral in *Tropheus moorii* (Fig. 2B). The drastic functional consequences of such radical shifts in position of the oral gape reflect the adaptive versatility of the body plan. These shifts do not involve any modifications in either the angle between the ascending and alveolar processes of the premaxilla which is retained at approximately 90° (Fig. 16:APPM, PM) or the position of the quadratomandibular joint (Figs. 2, 14:Q) in respect to the lateral ethmoid (LE). A vertically directed gape evolves by an accelerated growth of the mandible, alveolar process of the premaxilla, and maxilla (Fig. 16:D, MD, PM, MX), accompanied by decelerated growth of the preorbital region of the neurocranium (Fig. 15B) and ascending process of the premaxilla (Fig. 16:APPM). An elongate mandible is correlated with a very acute angle between the mandibular rami (Fig. 13B:MD) and increased length of the parallel fibers of the geniohyoideus anterior and posterior muscles (GHA, GHP) favoring much greater excursions of the involved elements. The reversed condition, a ventrally located gape of the mouth, is realized by a decelerated growth rate of the mandible, maxilla, and alveolar process of the premaxilla (Fig. 2B:D, MX, PM), while

the preorbital region of the neurocranium is not only shortened but curved ventrally (Fig. 15C). A shortened mandible is correlated with a distinctly obtuse angle between the mandibular rami (Fig. 13C: D) and an increased cross-sectional area of the geniohyoideus anterior and posterior (GHA, GHP) which produces the power necessary to stabilize the mandible against the formidable resistance encountered during the scraping of epilithic algae. The mechanisms underlying these trophically strategic adaptive alterations involve a minimum number of morphogenetic parameters.

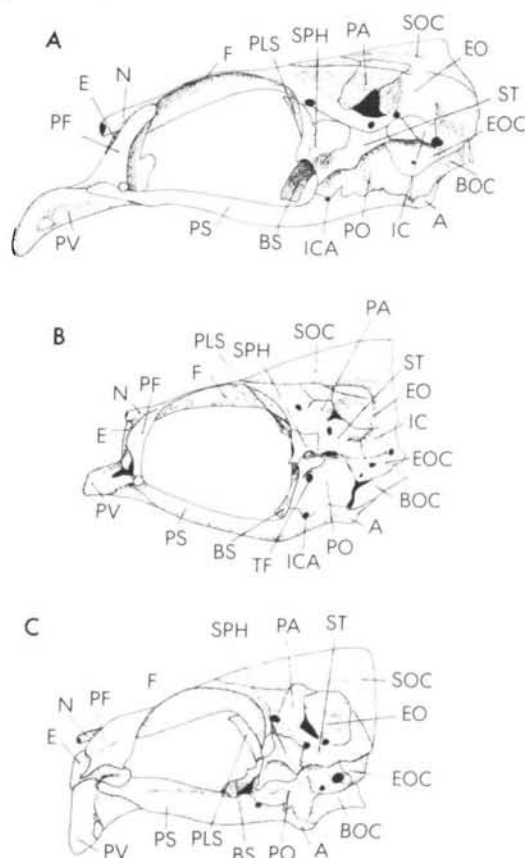


FIG. 15. Lateral aspect of neurocranium. A, *Xenotilapia melanogenys*; B, *Haplotaxodon microlepis*; C, *Tropheus moorii*. A, pharyngeal process (apophysis); BOC, basioccipital; BS, basisphenoid; E, ethmoid; EO, epiotic; EOC, exoccipital; F, frontal; IC, intercalary (opisthotic); ICA, internal carotid artery; N, nasal; PA, parietal; PF, prefrontal; PLS, pleurosphenoid (pterosphenoid); PO, prootic; PS, parasphenoid; PV, prevomer (vomer); SOC, supraoccipital; SPH, sphenotic; ST, pterotic; TF, trigeminofacial chamber.

### *Variations in jaw structure*

Aside from the differences in the proportions between alveolar and ascending processes of the premaxilla, the maxilla undergoes the greatest variation in form. In the generalized insectivorous *Haplochromis burtoni*, the maxilla (Fig. 16B:MX) is a relatively slender bone with a narrow neck and a small head with equal-sized premaxillary (PPM) and cranial condyles (CON). In the bottom-feeding *Xenotilapia sima*, which feeds on chironomid larvae and molluscs, the head and condyles (Fig. 16C:MX, PPM, CON) are greatly enlarged to allow for greater protrusibility with stability of the upper jaw. The body of the maxilla often becomes expanded (Fig. 16C:MX). In the filamentous algae-eating *Telmatochromis temporalis*, the narrow neck of the maxilla is enlarged and the more massive cranial condyle (Fig. 16A:MX, PPM, CON) serves as a brace on the neurocranium. The connections of the maxilla to the premaxilla, suspensorium, and neurocranium as depicted in Figure 6 (PM, PMC, CA, CC, PV, MX, CON, PPM, PAL, P) for *Haplochromis burtoni* and *Tilapia nilotica* are maintained in this basic configuration throughout the adaptive radiation in Lake Tanganyika.

Accelerated growth rates of the mandible often affects the dentary and articular (Fig. 16C:D, A) equally, both of which have well-developed ascending processes (APD, APA) separated by a large gap. In *Telmatochromis* feeding on algae, the mandible is short, with the dentary and articular united much more extensively (Fig. 16A:D, A). In several taxa a special flange, the adductor fossa (Fig. 16C:OF), is developed to increase the insertion site for the A<sub>2</sub> portion of the adductor mandibulae muscle.

### *Adaptive alterations in the suspensory apparatus*

In all cichlids the junction between the metapterygoid and symplectic process of the hyomandibular is maintained (Fig. 16:MPT, HM). The general form varies greatly according to the adaptive requirements. In gape-and-suck feeders, the hyomandibular is a long slender bone with slightly separated cranial condyles and a

very long symplectic process (Fig. 16C:HM) significantly increasing the moment arm of the levator arcus palatini, which in turn enhances the degree and velocity of unfolding. Many algae scrapers, on the other hand, show a trend toward a very broad hyomandibular with widely separated cranial condyles (Fig. 16A:HM) and short symplectic process decreasing the degree and velocity of suspensorial abduction but increasing the space for the adductor mandibulae complex (Fig. 14A). Taxa with great mobility of the upper jaw, possess relatively small palatine bones which are joined to the ectopterygoid only (Fig. 16C:P, ECT), while those with trophic adaptations requiring strength and stability of the upper jaw have large palatines connected to both the ectopterygoid and entopterygoid (Fig. 16A:P, ECT, ENT). Such differences are the results of the differential growth rates of the palatine and entopterygoid. Diminished growth rate of the entopterygoid results in separation of the entopterygoid and palatine favoring a greater freedom of movement for the maxillary head. By means of small variations in the position and shape of articular surfaces of the three joints between palatine and neurocranium (Fig. 6:J<sub>1-3</sub>, PP), the mobility of the anterior part of the suspensorium, and consequently that of the entire upper jaw, can be modified rather drastically.

### *Dental specializations*

More attention has been paid to dentition than to any other aspect of cichlid anatomy. Optimal solutions to diverse mechanical problems are developed in the total jaw complex, including the dentition which exhibits supralimital specializations, which transcend the limits usually found within the order (Myers, 1960). The generalized dentition consists of an outer row of stout, bicuspid teeth, followed by one or two rows of smaller and finer, usually tricuspid, teeth (Greenwood, 1973). A slightly modified condition is found in the Lake Malawi *Haplochromis intermedius* in which the two inner rows of teeth show a trend to become unicuspid by accelerated and decelerated growth rates of, respectively, the center



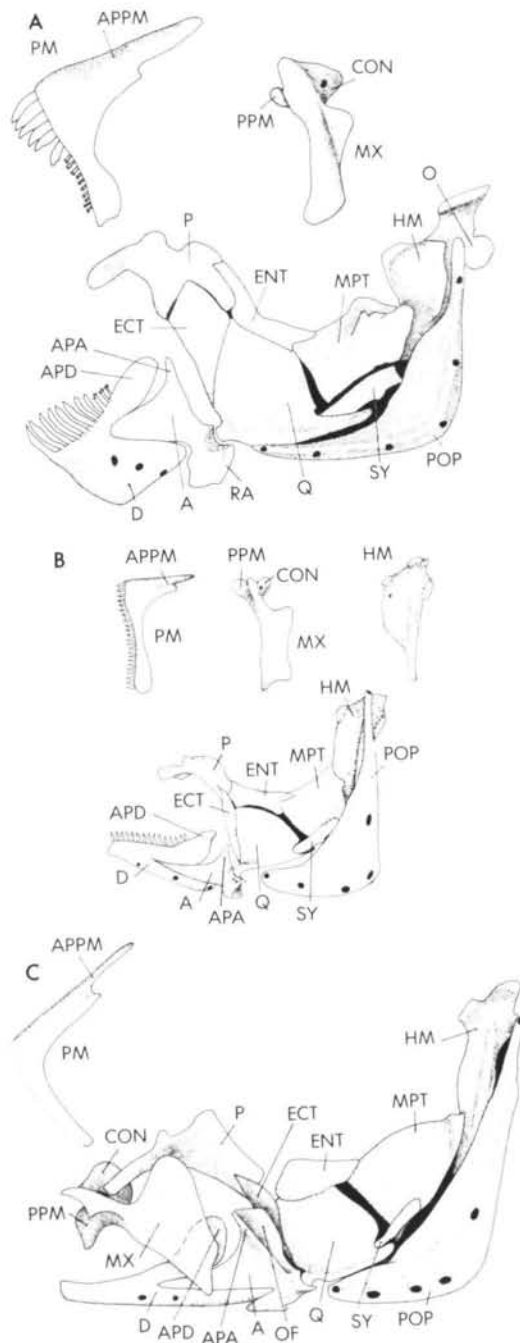


FIG. 16. Lateral aspect of suspensory apparatus and jaws. *A*, *Telmatochromis temporalis*; *B*, *Haplochromis burtoni*; *C*, *Xenotilapia sima*. A, articular (angular); APA, ascending process of articular; APD, ascending process of dentary; APPM, ascending process of premaxilla; CON, cranial condyle; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; HM, hyomandibu-

lar, MPT, metapterygoid; MX, maxilla; O, opercular process of hyomandibular; OF, fossa for adductor mandibulae; P, palatine; PM, premaxilla; POP, preopercular; PPM, premaxillary condyle of maxilla; Q, quadrate, RA, retroarticular; SY, symplectic.

cus and the flanking cusps (Fig. 17B). Although taxa with this generalized dentition are as a rule insectivorous, *H. intermedius* feeds on cladocerans and copepods (Fryer and Iles, 1972). From this generalized morphotype, an amazing array of divergent specialized dentitions evolved. Lepidophagous taxa have developed an increase in the number of inner tooth rows. In *Corematodus taeniatus* (Fig. 17C, D) from Lake Malawi the increased number of tooth rows is accompanied by a change in tooth form into unicuspid (although some are bicuspid), broadened spade-like teeth. Such a broad-toothed surface is the functional equivalent of a file; it is also found in the lepidophagous *Haplochromis welcommei* of Lake Victoria (Greenwood, 1965c), while in Lake Tanganyika entirely different solutions evolved (Poll, 1956). Another adaptation involving a prodigious proliferation of teeth occurs in epilithic algae scrapers, e.g., *Labeotropheus fuelleborni* (Fig. 17A), in which the tooth rows have not increased but all teeth are of the same size and distinctly tricuspid (including those of the first row) with all three cusps equally differentiated. Less profound changes have occurred in the allegedly eye-plucking (Wickler, 1966) *Haplochromis compressiceps* with an outer row of stout unicuspid teeth and an inner row of smaller mostly unicuspid teeth, although some are tricuspid (Fig. 18B). In the mollusc-eating *Haplochromis placodon* all teeth are unicuspid and arranged in a rather haphazard manner rather than in distinct rows (Fig. 18A). These jaw teeth are well adapted to collecting the molluscs which are crushed by the pharyngeal jaws (Liem, 1973). Although in most cases the dental morphology is unequivocally adaptive to specific trophic specializations there are examples in which no such correlation exists. For instance, the zooplankton feeding *Haplochromis chrysonotus* of Lake Malawi (Fryer and Iles, 1972) possesses an outer

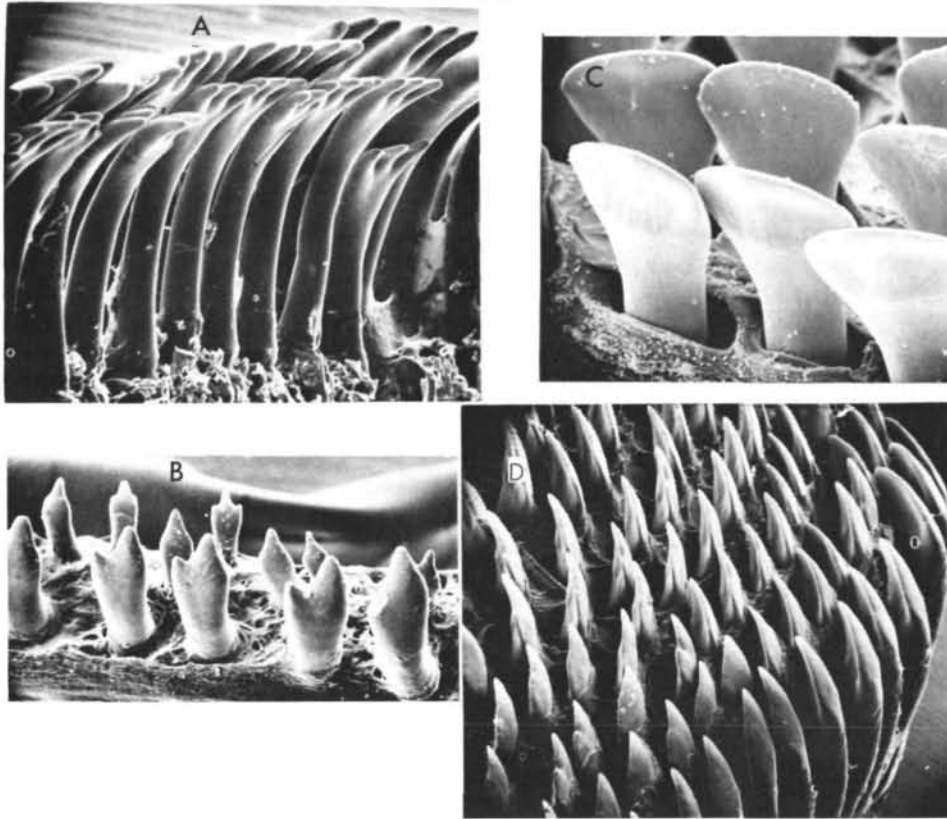


FIG. 17. Mandibular teeth as seen with the scanning electron microscope. A, *Labeotropheus fuelleborni*; B, *Haplochromis intermedius*; C, *Corematodus taeniatus* (pos-

terior view); D, *Corematodus taeniatus* (anterolateral view), note bicuspid teeth on left side.

row of extremely stout, canine-like teeth while the inner rows are composed of smaller, unicuspid, slightly curved sharp teeth (Fig. 18C). Such a configuration seems more appropriate for a fish-eater, and may reflect piscivorous ancestry.

#### CONCLUSION

The potential versatility of the total feeding apparatus of cichlids has been fully realized in the lacustrine forms whose body plan was strongly selected and perfected partially as a result of competition with each other, while the Characidae, Centropomidae, Cyprinidae, Bagridae, Mochocidae, Clariidae, and Mastacembelidae possess less potentially versatile body plans. There is a direct relationship between the effectiveness of trophic resource exploitation and the functional in-

tegration of the cichlid feeding apparatus in which a minimum number of adaptive compromises are necessary to evolve optimal functional anatomical solutions in the exploitation of the dramatically diverse foods. In non-cichlids two major parameters associated with the jaws and the pharyngeal jaws cannot vary independently from each other because the latter lack the necessary building blocks and functional integration and, consequently, the ability to manipulate and prepare a great variety of foods. In cichlids the two parameters can vary independently because the functional integration of the specialized pharyngeal jaws relaxes or removes restrictions on the form and function of the jaws enabling them to evolve into exceptionally efficient food-collecting devices. As pointed out by Vermeij (1973a,b) the more parameters controlling form can

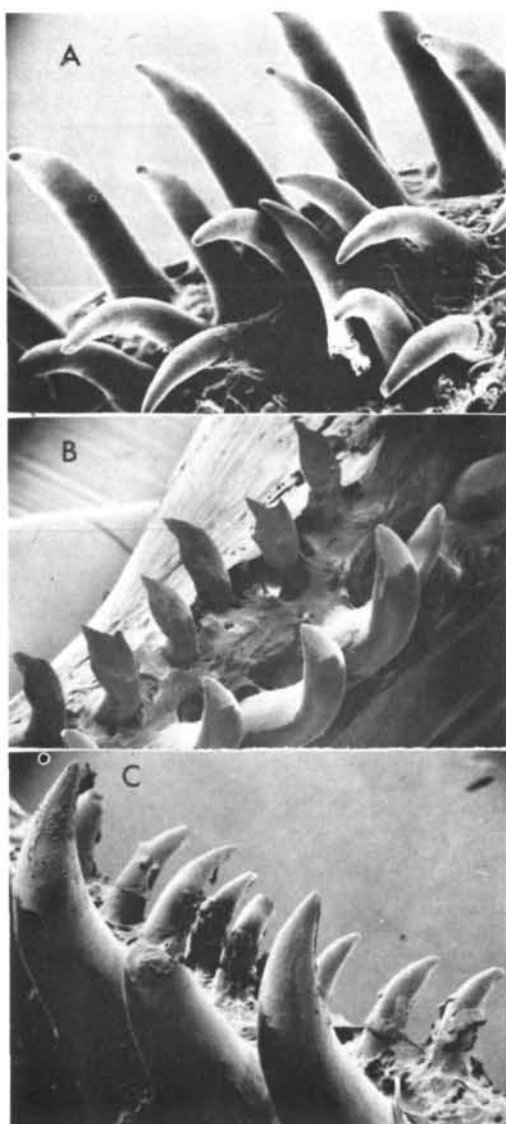


FIG. 18. Mandibular teeth as seen with the scanning electron microscope. A, *Haplochromis placodon*; B, *Haplochromis compressiceps*; C, *Haplochromis chrysonotus*.

vary independently, the greater the diversity of morphological types and the larger the potential adaptive zone. Since the cichlids have given rise to numerous variations upon the same original evolutionary theme, we may consider them to have at least broad, but terminal, evolutionary success (*sensu* Stebbins, 1973), which is based upon the enormous number of alternative possibilities afforded by their jaws and pharyngeal jaws for solving the problem of

exploitation of almost inaccessible food resources. Greenwood (1973) has stressed the basic suitability of the cichlid body plan as a substrate for adaptational modifications since it has reached an anatomical differentiation that is neither too specialized nor too generalized. As shown in this study, cichlids possessed a very specific kind of mosaic evolution in which the basic percoid jaws were conserved while the specialized pharyngeal jaws evolved very rapidly (Liem, 1973). The jaw apparatus, although generalized in its basic configuration, permits adaptive radiation into a great variety of lacustrine habitats by simple morphogenetic changes affecting differential growth rates of various components and dentition and by seemingly endless variations in the patterns of muscle contractions without changing the basic cichlid body plan. At the same time, the highly integrated cichlid pharyngeal jaw apparatus is sufficiently specialized with respect to its muscular and skeletal features so as to provide unchallenged functional versatility which enables the lacustrine cichlids to exploit new food resources in an entirely novel and most efficient way. This extremely rare combination of a less-integrated, generalized morphological complex with a highly integrated key innovation, both of which can vary independently to optimize functional solutions to a great variety of mechanical problems, is compatible with the fact that the cichlids have successfully occupied and dominated all conceivable habitats in the great lakes of Africa. The evolutionary success of lacustrine cichlids demonstrates how specific kinds of biologically versatile morphological mosaics represent the best kinds of preadaptation for the ancestor of major new taxa. Such a proliferation evolves to the detriment of relatively non-versatile taxa given identical ecological conditions and temporal factors in a newly formed environment.

In marine habitats, the Embiotocidae, Labridae, and Scaridae share the unique and complex integration of the pharyngeal apparatus with the Cichlidae in respect to several salient specializations. We postulate that the embiotocids, labrids, and the more

divergent scarids are closer related to the cichlids than to any other living percoids (Liem manuscript). However, the biological role of this shared key innovation in the different marine habitats is still unknown, although a functional anatomical analysis and comparison with cichlids is now in progress.

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