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EVOLUTIONARY STRATEGIES AND MORPHOLOGICAL INNOVATIONS: CICHLID PHARYNGEAL JAWS

KAREL F. LIEM

Abstract

Liem, Karel F. (Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138) 1974. Evolutionary strategies and morphological innovations: Cichlid pharyngeal jaws. Syst. Zool. 22:425-441.—The percoid fish family Cichlidae possesses a phenomenal ability to colonize lakes and to diversify to an extent unmatched by any other vertebrate family in the presence of predator pressure and strong competition. The invading cichlids successfully occupy contiguous and occasionally overlapping adaptive zones and specialize progressively into diversified subzones, ramifying prodigiously and covering a breadth of total adaptation that would have been entirely unpredictable if we were aware only of the rudiments of the evolutionary process. This evolutionary avalanche can be attributed to the cooccurrence of a wide range of prospective adaptive zones in the lacustrine environment, and the presence of a unique morphological key innovation of maximum versatility. The new adaptive complex has been revealed in this study by electromyographic analysis synchronized with cineradiography of the cichlid pharyngeal jaw apparatus. The morphological novelty characterizing the family Cichlidae involves the development of: a synarthrosis between the lower pharyngeal jaws, a strategic shift of insertion of the two fourth levator externi muscles, and synovial joints between upper pharyngeal jaws and basicranium. This specialized, highly integrated key innovation enables the cichlids not only to transport (deglutination) but also to prepare food, freeing the premaxillary and mandibular jaws to evolve numerous specializations dealing with the collection of dramatically diverse foods. The functional integration of the innovation is so basic and its potential adaptive versatility so rich that it is maintained throughout the adaptive radiation even though numerous non-disruptive evolutionary changes do take place, providing prodigious opportunities for explosive evolution during the exploitation of rich resources of food in the lacustrine environment. The conversion of the preexisting elements into a new and significantly improved cichlid adaptive complex of high selective value may have evolved by rapid steps under influence of strong selection pressure acting on the minor reconstruction of the genotype which is involved in evolutionary changes of the pertinent ontogenetic mechanisms. Such relatively simple evolutionary processes are probably the cause for the general phenomenon that only slight reconstructions of existing structures are necessary for successful and rapid adaptation to drastic shifts of adaptive zones.

INTRODUCTION

Cichlid fishes have demonstrated a phenomenal ability to colonize lakes and to diversify to an extent unmatched by any other vertebrate family. In great African lakes cichlids fulfil roles which elsewhere are enacted by members of different families and orders (Greenwood, 1964). Cichlids have undergone their prodigious adaptive radiation in the presence of such potentially competitive and highly successful families as the Cyprinidae, Characidae, Bagridae, Mochocidae, and Clariidae. Their evolutionary success seems to be due to the perfection of their adaptations rather than

to the lack of either competition or predators (Fryer and Iles, 1972). However, the exact nature of the refinements of cichlid adaptations remains poorly known because much attention has been focused on the environmental factors, and the organism tends to be lost from sight or sidetracked as "black boxes" reacting in a mathematically predictable way to such factors as abundance of food, lack of competition and predatory pressures, etc. Why did the family Cichlidae undergo the most explosive adaptive radiation among lacustrine fishes and not the other successful fish families? Recently Greenwood (1973) has dealt with this question emphasizing the exceptional

"morphopotentiality" of cichlids as an important factor.

In general, adaptive radiations of organisms will not occur until after an evolutionary novelty has reached a certain degree of development (Mayr, 1960; Bock, 1965). Is there a special set of characteristics, i.e., key innovations, in cichlids enabling riverine forms to cope with the demands of the new lacustrine habitats? It is axiomatic that evolutionary adaptation (Bock, 1965) can be measured only in terms of function, regardless of how we employ the term (Schaeffer, 1965). Yet in most theoretical reviews no well documented examples are given and function is either superficially discussed in very broad general terms or inferred from form.

The focus of this paper is on key innovations in cichlids and how they have played a decisive role in giving the family a significant competitive advantage over other fish families in the rapid colonization of African lakes. Using detailed documentation and experimental analysis I will try to give a concrete case history of the emergence of an evolutionary innovation, and subsequently that of a higher level of organization and to discuss the findings in the light of the "modified saltationist theory" as interpreted by Davis (1949, 1964) and Frazzetta (1970) and the synthetic theory as proposed by Simpson (1953), Bock (1959, 1965), and Mayr (1960, 1963).

GENERALIZED PERCOID PHARYNGEAL JAW APPARATUS

In order to evaluate properly the change from the "generalized" to the "specialized" group, I will start with the functional analysis of the pharyngeal jaw apparatus of *Pristolepis fasciatus*, which is considered a generalized percoid (Rosen and Patterson, 1969).

Morphological pattern

Each upper pharyngeal jaw (Fig. 2:UB) is composed of three intimately articulated elements, i.e., the 2nd and 3rd infrapharyn-

gobranchials with corresponding toothplates and the 4th toothplate, which function as one unit. The left and right upper pharyngeal jaws remain independent units. There are neither joints nor simple articulations between skull base and the upper pharyngeal jaws.

The lower pharyngeal jaws (Fig. 2:LB) are also paired each representing the fifth ceratobranchial provided with a corresponding toothplate (Fig. 1:CB5).

Each upper pharyngeal jaw is operated *directly* by (1) a retractor pharyngeus superioris (Fig. 1:RPH; Fig. 2:RP) muscle which originates from the first three vertebrae and inserts on the posterodorsal surface of the upper pharyngeal jaw; (2) two levatores interni (Fig. 1:LI) originating from the anterodorsal corner of the prootic and inserting on the anterodorsal surface of the jaw; and *indirectly* by (3) levator externus 4 (Figs. 1, 2:LE4) originating from the anterodorsal corner of the prootic and inserting on a dorsal process of the 4th epibranchial (Fig. 1:EB4); (4) levator posterior (Figs. 1, 2:LP) originating from the ventral aspect of the pterotic and inserting on the dorsal aspect of the fourth epibranchial just posterior to the insertion of the fourth levator externus; (5) the fifth adductor (Figs. 1, 2:AD5) originating from the posterior rim of the fourth epibranchial and inserting on the superior aspect of the posteromedial corner of the lower pharyngeal jaw.

Each lower pharyngeal jaw is operated *directly* by (1) pharyngocleithralis internus (Figs. 1, 2:PHCI, PCI) originating from the cleithrum and inserting on the inferior aspect of the jaw; (2) pharyngocleithralis externus (Figs. 1, 2:PHCE, PCE) originating from the more distal part of the cleithrum and inserting on the ventrolateral surface of the anterior corner of the jaw; (3) pharyngohyoideus (Figs. 1, 2:PH) running between the anterior tip of the jaw and the superior aspect of the urohyal; and *indirectly* by the fifth adductor (see (5) above).

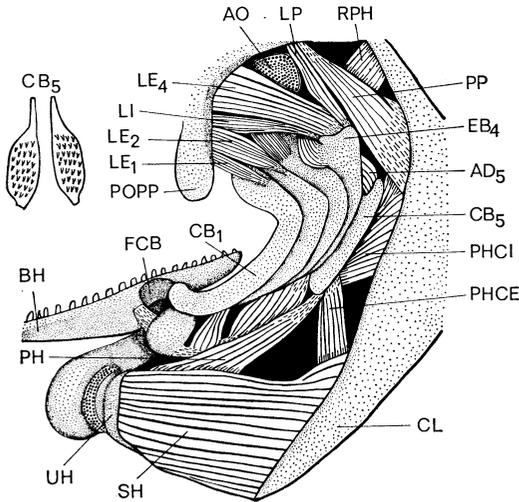


FIG. 1.—Lateral view of branchial apparatus and muscles of *Pristolepis fasciatus*. Opercular, suspensory apparatus, gills, gill rakers, and mucous membrane have been removed. AD5, adductor; AO, adductor operculi; BH, basihyal; CB1, first ceratobranchial; CB5, lower pharyngeal jaw (insert is dorsal view); CL, cleithrum; EB4, fourth epibranchial; FCB, fossa for hyoid ramus; LE1-4, levatores externi 1-4; LI, levator internus; LP, levator posterior; PH, pharyngohyoideus; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; POPP, postorbital process; PP, protractor pectoralis; RPH, retractor pharyngeus superior; SH, sternohyoideus; UH, urohyal.

All generalized percoids exhibit the pattern described above. The salient features are: the connection of the "dorsal" muscles (i.e., levator externus 4 and levator posterior) with the dorsal branchial elements (i.e., epibranchial 4), the absence of an articulation between the upper pharyngeal jaws and skull base and the paired, independent lower pharyngeal jaws.

Functional mechanisms

The sequence of muscle contractions has been analysed electromyographically [using the methods of Osse (1969) and Osse et al. (1972)], while the movements of the pharyngeal jaws have been determined by successive X-ray pictures. Both procedures were performed on unrestrained and un-

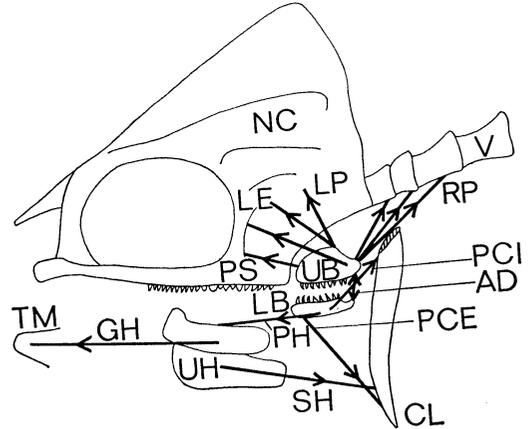


FIG. 2.—Diagram of position and direction of major branchial muscles in the generalized percoid fish *Pristolepis fasciatus*. Ad, adductor; CL, cleithrum; GH, geniohyoideus; LB, lower pharyngeal jaw; LE, levator externus; LP, levator posterior; NC, neurocranium; PCE, pharyngocleithralis externus; PCI, pharyngocleithralis internus; PH, pharyngohyoideus; PS, parasphenoid; RP, retractor pharyngeus superior; SH, sternohyoideus; TM, tip of mandible; UB, upper pharyngeal jaw; UH, urohyal; V, vertebra.

anesthetized *Pristolepis* feeding on live crickets.

As shown in Fig. 3 we can distinguish two phases:

Phase 1 ("retracted-adducted"), with activity in the levator posterior, geniohyoideus anterior, pharyngocleithralis internus (PHAR CL I) and the retractor pharyngeus superior. The effect of the combined activity of these muscles on the pharyngeal jaws (UB, LB) is shown in Fig. 4 with bold lines. Both jaws are retracted and rotated, but occlusion of teeth does not occur. This phase is initiated by the geniohyoideus anterior muscle which pulls the hyoid apparatus (Fig. 4:HY, UH) forwards and up and is immediately followed by the retractor pharyngeus superior, levator posterior and finally the pharyngocleithralis internus muscles.

During *phase 2* ("protracted-abducted") the fourth levator externus (Fig. 3:levator ext 4), pharyngohyoideus and adductor contract first, closely followed by the ster-

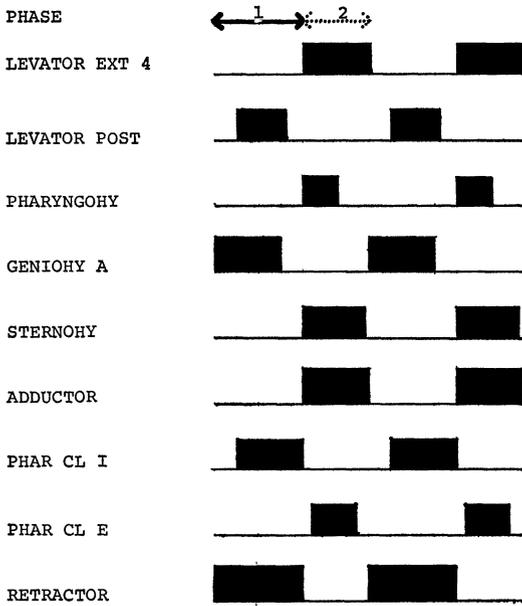


FIG. 3.—Diagram of active periods of branchial and hyoid muscles of unanesthetized and unrestrained *Pristolepis fasciatus* feeding on live crickets. GENIOHY A, geniohyoideus anterior; LEVATOR EXT 4, fourth levator externus; LEVATOR POST, levator posterior; PHAR CL E, pharyngocleithralis externus; PHAR CL I, pharyngocleithralis internus; PHARYNGOHY, pharyngohyoideus; RETRACTOR, retractor pharyngeus superior; STERNOHY, sternohyoideus.

nohyoideus and pharyngocleithralis externus muscles. The effect of the combined activity of these muscles on the jaws is shown in Fig. 4 in broken lines.

An important characteristic of this coordinated pattern is the three pairs of antagonist muscles: levator externus 4—levator posterior, pharyngocleithralis externus—pharyngocleithralis internus, sternohyoideus—geniohyoideus anterior. Paradoxically the *fifth adductor* is only morphologically an adductor. Electromyography of unrestrained and unanesthetized fish shows the exact opposite function: the muscle *abducts* the jaws. The movements of the pharyngeal jaws of *Pristolepis* transport food into the esophagus thus resembling the condition in the nandid fishes (Liem, 1970). Food preparation (or mastication) by pharyn-

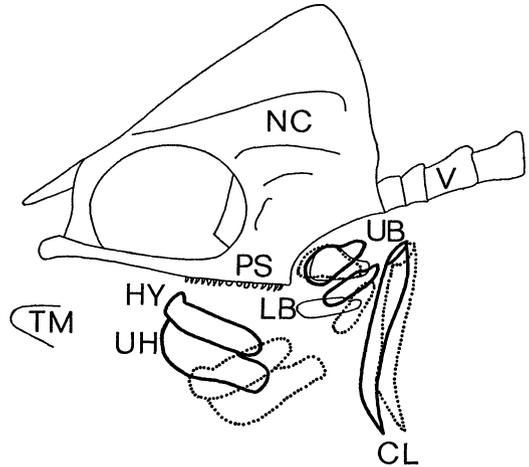


FIG. 4.—Diagram of movements of pharyngeal jaws as revealed by sequence of successive X-ray pictures in the generalized percoid fish *Pristolepis fasciatus*. CL, cleithrum; HY, hyoid; LB, lower pharyngeal jaw; NC, neurocranium; PS, parasphenoid; TM, tip of mandible; UB, upper pharyngeal jaw; UH, urohyal; V, vertebra.

geal jaws does not take place in either *Pristolepis* or other generalized percoids, Cottidae and some Blennidae (Vanden Berghe, 1928).

CICHLID PHARYNGEAL JAW APPARATUS

This description is based on *Haplochromis burtoni*, a generalized African cichlid.

Morphological pattern

The upper pharyngeal jaws are paired and slightly separated (Figs. 5, 6:UB). Each consists of joined 2nd and 3rd infrapharyngobranchials with corresponding toothplates and the fourth toothplate, functioning as a single unit. A distinct dorsal articular process on the superior aspect of the third infrapharyngobranchial (Fig. 13: AS) articulates with a corresponding process, the pharyngeal apophysis, on the skull base (Fig. 9:A). This *basipharyngeal joint* between skull base and upper pharyngeal jaw is synovial, offering controlled mobility. Such a joint is absent in generalized percoids (Fig. 2).

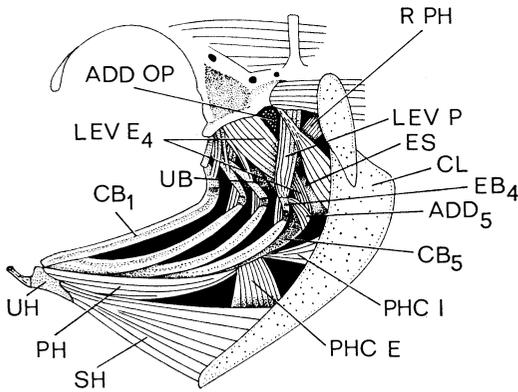


FIG. 5.—Lateral view of branchial apparatus and muscles of *Haplochromis burtoni* (Lake Tanganyika) after removal of opercular, suspensory apparatus, gills, gill rakers and mucous membrane. ADD5, fifth adductor; ADD OP, adductor operculi; CB1, first ceratobranchial; CB5, lower pharyngeal jaw; C, cleithrum; EB4, fourth epibranchial; ES, esophagus; LEV E 4, fourth levator externus; LEV P, levator posterior; PH, pharyngohyoideus; PHC E, pharyngocleithralis externus; PHC I, pharyngocleithralis internus; RPH, retractor pharyngeus superior; SH, sternohyoideus; UB, upper pharyngeal jaw; UH, urohyal.

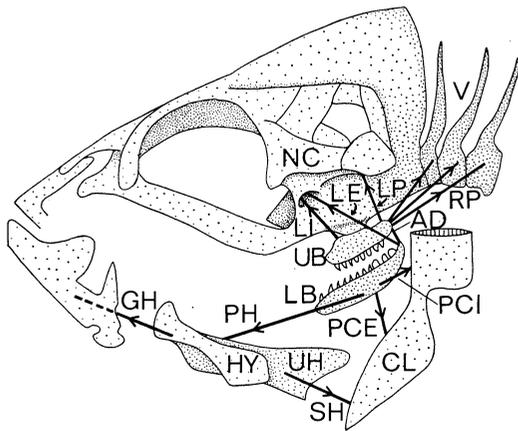


FIG. 6.—Diagram of position and direction of some major branchial muscles in a generalized cichlid fish. AD, adductor; CL, cleithrum; GH, geniohyoideus; HY, hyoid; LB, lower pharyngeal jaw; LE, fourth levator externus; LI, levator internus; LP, levator posterior; NC, neurocranium; PCE, pharyngocleithralis externus; PCI, pharyngocleithralis internus; PH, pharyngohyoideus; RP, retractor pharyngeus superior; SH, sternohyoideus; UB, upper pharyngeal bone; UH, urohyal; V, vertebrae.

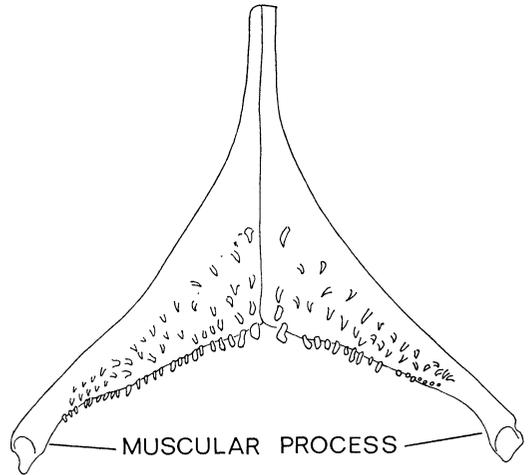


FIG. 7.—Dorsal view of lower pharyngeal jaw of the scale-eating *Plecodus paradoxus* from Lake Tanganyika.

In sharp contrast with the condition in generalized percoids, the lower pharyngeal jaws are suturally united, functioning as a single unit (Fig. 7). Each posterodorsal corner of the jaw is differentiated into a prominent process which serves as an insertion of the fourth levator externus and fifth adductor muscles. I, therefore, will refer to it as the *muscular process* of the lower pharyngeal jaw.

The muscles operating on the lower pharyngeal jaw directly resemble those of *Pristolepis* very closely with the remarkable exception that the fourth levator externus (Figs. 5, 6, 11, 16: LEV E4, LE4), which, although originally a "dorsal gill arch" muscle, bypasses the dorsal fourth epibranchial element to insert on the muscular process of the lower pharyngeal jaw (i.e., the suturally united, ventral fifth ceratobranchials (Figs. 5, 7: CB5)). The fourth levator externus muscle in the Cichlidae has become dissociated from the fourth epibranchial element and, consequently, also from the upper pharyngeal jaw, to assume a new and salient role in operating the lower pharyngeal jaw.

The muscles operating the lower pharyngeal jaw are essentially similar to those of *Pristolepis* but with the important differ-

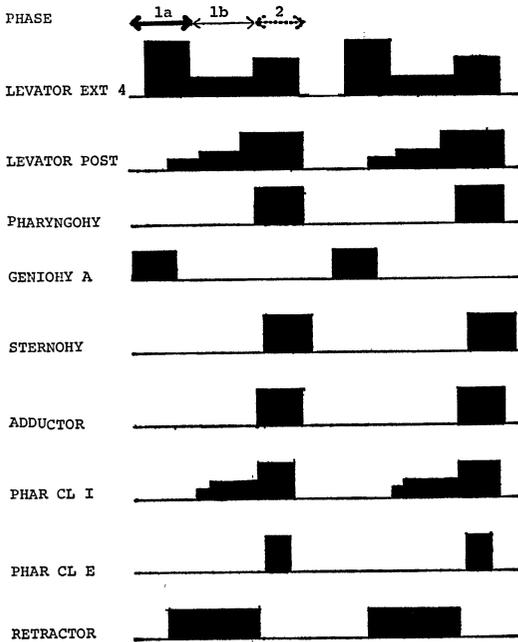


FIG. 8.—Diagram of active periods of muscles of unanesthetized and unrestrained *Haplochromis burtoni* feeding on *Gammarus* sp. Abbreviations as in Fig. 3.

ence of the addition of the fourth levatores externi muscles to the two muscular processes.

All Cichlidae exhibit the specialized morphological pattern described above. The characteristic specializations are: The appearance of two synovial basipharyngeal joints, the sutural connection of the two fifth ceratobranchials to form a single lower pharyngeal jaw provided with two muscular processes, and the shifts of insertions of the fourth levatores externi muscles from the fourth epibranchials to the lower pharyngeal jaw (this is at variance with the observations of Chardon and Vandewalle, 1971; Vandewalle, 1971; Vandewalle, 1972).

Functional mechanisms

The electromyographic recordings have been made in collaboration with Prof. J. W. M. Osse at the University of Leiden, The Netherlands.

With the appearance of the basipharyn-

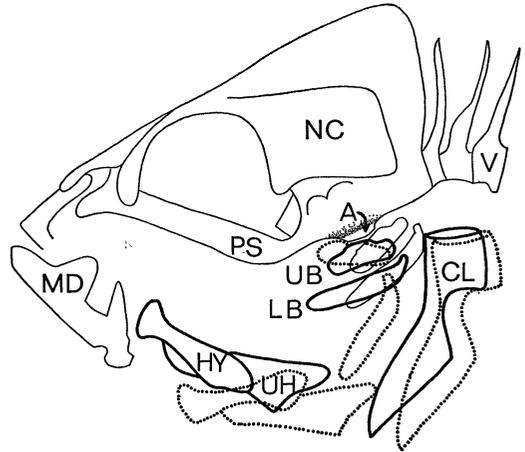


FIG. 9.—Simplified diagram of movements of the pharyngeal jaws of a generalized cichlid fish as revealed by successive X-ray pictures. Bold lines (phase 1a): food preparation (mastication); thin lines (phase 1b): food transport (swallowing, deglutition); broken lines (phase 2): protraction-abduction. A, pharyngeal process (apophysis); CL, cleithrum; HY, hyoid; LB, lower pharyngeal jaw; MD, mandible; NC, neurocranium; PS, parasphenoid; UB, upper pharyngeal jaw; UH, urohyal; V, vertebra.

geal joint, the upper pharyngeal jaw is no longer a "freely-floating" complex (Fig. 6: UB; Fig. 9:A; Fig. 13:AS).

The pattern of muscle contractions in cichlids as revealed by electromyography differs significantly from that of *Pristolepis* (Fig. 8). A third phase (*phase 1a*, food preparation, or mastication) has been added to the two phases found in *Pristolepis* (Figs. 3, 8). This phase is initiated by full contraction of the geniohyoideus anterior, followed by the strongest activity of the fourth levator externus, full activity of the retractor pharyngeus superior towards the end of the phase and weak contraction of the levator posterior. The effect of the combined activity of these muscles during phase 1a is depicted in a simplified diagram in Fig. 9 with bold lines. Both jaws are protracted and strongly adducted. The protraction is carried over from phase 2 (Fig. 9, broken lines) during which the pharyngo-hyoideus (Fig. 6:PH) has pulled the

lower pharyngeal jaw forwards. When the lower jaw is protracted, the strong contraction of the fourth levator externus results in a powerful adduction of the jaws.

In *phase 1b* three muscles are active: moderate contraction of the fourth levator externus, rapidly increasing activity of the levator posterior and full contraction of the retractor pharyngeus superior (Figs. 8, 10). The effect of the combined activity of the three muscles is a pronounced retraction of both upper and lower pharyngeal jaws by respectively strong contraction of the retractor pharyngeus superior and increasing activity of the pharyngocleithralis internus (Fig. 9). The levator posterior (Fig. 6:LP) rotates the upper jaw in such a way that its anterior tip moves down to approach its fellow from the lower jaw (Fig. 9:UB, LB), which rotates upwards as a result of the moderate activity of the fourth levator externus.

Phase 2 is the protracted-abducted condition in which the fourth levator externus, levator posterior, pharyngohyoideus, sternohyoideus, adductor, and pharyngocleithralis internus and externus muscles show considerable activity (Figs. 8, 10). During this phase the retractor pharyngeus superior stops its activity abruptly. The upper and lower pharyngeal jaws are pulled forward by respectively the levatores interni (although I have no electromyographic evidence for this) and the pharyngohyoideus (Fig. 6:LI, PH). The anterior tips of the upper and lower jaws move apart (Fig. 9:UB, LB) by the action of respectively the following groups of muscles: adductor—levator posterior (?), and fourth levator externus—pharyngocleithralis externus and internus.

The pattern of muscle contractions (Figs. 8, 10) associated with the pharyngeal jaws in cichlids can be characterized as follows: (1) The fourth levator externus is active *throughout* all stages of food preparation (mastication) and swallowing (deglutition), performing antagonistic functions in the various phases (Fig. 10); (2) the leva-

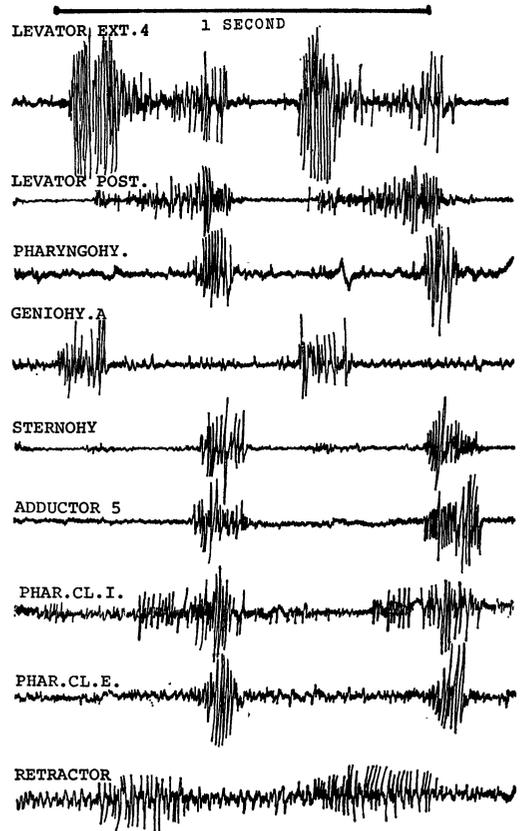


FIG. 10.—Electromyograms of branchial and hyoid muscles of unanesthetized and unrestrained *Haplochromis burtoni* feeding on frozen *Gammarus* sp. Abbreviations as in Fig. 3.

tor posterior is active during most of the three phases except for the initial stage of phase 1a; (3) the pharyngocleithralis internus is active during phases 1b and 2.

Phases 1a and b of cichlids (Fig. 8) represent both temporal and qualitative modifications of phase 1 of generalized percoids (Fig. 3). The ratio in duration of phase 1 and phase 2 in *Pristolepis* is 4:3 (Fig. 3), whereas in *Haplochromis burtoni* the ratio of phase 1a–b and phase 2 has changed to almost 3:1 (Fig. 8). This increase in ratio is caused by the interpolation of an additional interval of food preparation prior to deglutition. The qualitative differences involve the sequences of contraction of three

muscles: (a) The pharyngocleithralis internus is active in phase 1b and 2 (Fig. 8). During phase 1b the muscle performs its original function of retracting the lower pharyngeal jaw (also see Liem, 1970), while in phase 2 it acquires a new function in abducting the lower jaw once it has been pulled back; (b) the levator posterior plays a major role in stabilizing the superior pharyngeal jaws in phase 2, while during phase 1b (deglutition) it rotates the superior pharyngeal jaws (Fig. 9); (c) the role of the fourth levator externus has increased tremendously (Fig. 10), and changes with the shift in position of the lower pharyngeal jaw from an abductor (phase 2), to a rotator (phase 1b), and finally to an adductor (phase 1a).

THE CICHLID PHARYNGEAL JAW APPARATUS AS A KEY INNOVATION

All cichlids, whether riverine or lacustrine, from both the old world tropics and the neotropics, share the functionally integrated, highly specialized pharyngeal jaw apparatus described above. This clearly represents a major adaptive complex. Since this complex is unique among percoids, the Cichlidae can be defined on the basis of this unique evolutionary novelty, which represents strong evidence for the monophyletic origin of the family. The innovation (or novelty) emerged as a new functional and morphological reorganization and subsequent integration of existing branchial muscles, nerves and bones resulting in an ever increasing efficiency of function. The new adaptive complex originated by slight but significant shifts in positions, proportions and fusions of bones and muscles. However, this relatively simple innovation has produced an important change of function.

Let us review the structural and functional reorganization and integration of the cichlid pharyngeal apparatus: the development of the basipharyngeal joints between the cranial base and the upper pharyngeal jaws has furnished efficient Class I and

Class II lever systems to such important muscles as the levatores interni (Fig. 6:LI), levator posterior (LP) and retractor pharyngeus superior (RP), and has cleared the way for many coordinated interactions (including powerful "occlusion") with the lower pharyngeal jaws. Without the basipharyngeal joints the upper jaws are free floating units with limited functional opportunities and no potential mechanism for occlusion and mastication (Liem, 1970). The fusion of the left and right fifth ceratobranchials (Fig. 1:CB5) into a single lower pharyngeal jaw (Fig. 7) provides a significant increase in the control, degree, and kinds of jaw movements, because the resulting synarthrosis will automatically double the number of muscle insertions without increasing the original ancestral number of muscles. In addition to this, another pair of muscles, the fourth external levatores (Figs. 5, 6, 16:LE4), which are originally "dorsal gill arch" muscles, bypass the dorsal element (fourth epibranchial) to insert on the muscular process of the ventral lower pharyngeal jaw. This shift produces an enormous range of possible functions that can be achieved by the total pharyngeal jaw apparatus. The new insertion site of the fourth levator externus makes it possible for the lower pharyngeal jaw to exert a strong adduction ("bite") against the upper one. Besides its new role as a potentially powerful adductor, the modified fourth levator externus is able to move the lower pharyngeal jaw in numerous ways. The lower pharyngeal jaw in cichlids is operated by ten muscles, whereas that of generalized percoids is operated by eight. Concomitantly with the osteological, arthrological and myological modifications, the pattern of sequences of muscle activity during food preparation and swallowing changes considerably (compare Figs. 3, 8).

The new adaptive complex has enabled the Cichlidae to penetrate numerous new adaptive zones, since it provided the organism with a highly efficient and versatile mechanism for food preparation. This in-

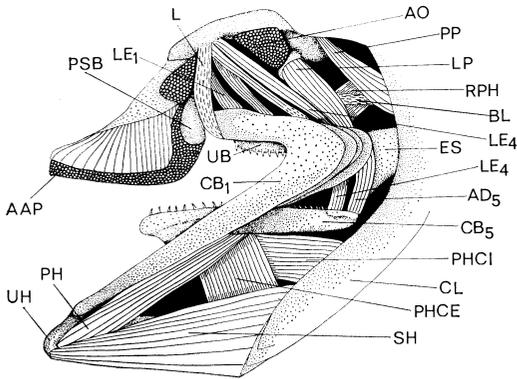


FIG. 11.—Branchial apparatus and muscles of *Cichla ocellaris* (Guyana) after removal of opercular, suspensory apparatus, gills, gill rakers and mucous membrane. AAP, adductor arcus palatini; AD5, fifth adductor; AO, adductor operculi; BL, Baudelot's ligament; CB1, first ceratobranchial; CB5, fifth ceratobranchial (lower pharyngeal jaw); CL, cleithrum; ES, esophagus; L, ligament; LE1, first levator externus; LE4, fourth levator externus; LP, levator posterior; PH, pharyngohyoideus; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PP, protractor pectoralis; PSB, pseudobranch; RPH, retractor pharyngeus superior; SH, sternohyoideus; UB, upper pharyngeal jaw; UH, urohyal.

novation freed the mandibular and premaxillary jaw mechanisms from their dual tasks of food collecting and preparation by eliminating the latter function. Once this adaptive threshold was crossed, the premaxillary and mandibular jaw apparatus could concentrate on one major function only. The release of the restricting influence of a second major function resulted in the emergence of numerous specializations of collecting mechanisms dealing with dramatically diverse foods. Since the appearance of the adaptation of the pharyngeal jaw apparatus is central to the exploitation of new habitats, we can consider this specialization a key innovation (sensu Miller, 1949).

THE ORIGIN OF THE CICHLID PHARYNGEAL JAW ADAPTIVE COMPLEX

The most primitive state of this innovation is found in the neotropical species

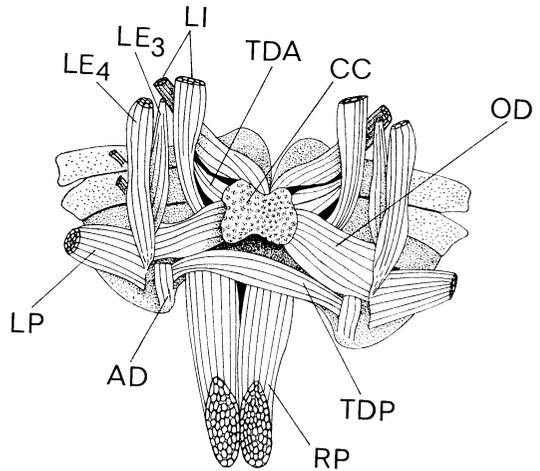


FIG. 12.—Dorsal view of dissected and isolated branchial muscles and apparatus of the generalized perciform *Badis badis*. Gills and mucous membranes have been removed. AD, adductor; CB5, lower pharyngeal jaw (fifth ceratobranchial); CC, cartilaginous cushion; LE3, 4, third and fourth levatores externi; LI, levatores interni; LP, levator posterior; OD, obliquus dorsalis; RP, retractor pharyngeus superior; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior.

Cichla ocellaris (cf. Newsome, 1971). Although this species possesses a fully developed basipharyngeal joint, its lower pharyngeal jaw is composed of separate fifth ceratobranchial elements. The two bones have not formed a complete synarthrosis, and the muscular processes are only weakly developed. The fourth levator externus is moderately developed (Fig. 11:LE4) but it inserts on the lower pharyngeal jaw (CB5), although in a few specimens a lateral slip of the muscle is still attached to the dorsal aspect of the fourth epibranchial. Such an organization of the adaptive complex may be considered intermediate between the primitive state as found in such generalized percoids as *Pristolepis* (Fig. 1) and *Badis badis* (Fig. 12) and the derived state in more advanced cichlids (Figs. 5, 13, 14). The basipharyngeal joint may have evolved initially as a very simple contact between the dorsal surface of the upper pharyngeal jaw and the ventral surface of

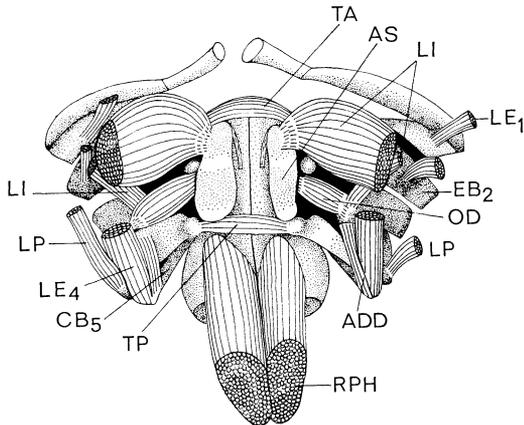


FIG. 13.—Dorsal view of dissected and isolated branchial apparatus and muscles of the scale-eating Lake Tanganyika cichlid *Plecodus paradoxus*. Gills and mucous membranes have been removed. ADD, adductor; AS, articular process of upper pharyngeal jaw; CB5, lower pharyngeal jaw; EB2, second epibranchial; LE1, first levator externus; LE4, fourth levator externus; LI, levator internus; LP, levator posterior; OD, obliquus dorsalis; RPH, retractor pharyngeus superior; TA, transversus dorsalis anterior; TP, transversus dorsalis posterior.

the cranial base. The rubbing and sliding of the two bony surfaces would require a cartilaginous cushion between the two bones as found in the generalized percoids *Badis* (Fig. 12:CC) and *Pristolepis*. It is known (Murray, 1937) that the development of such a simple contact between two bones into an amphiarthrosis and the subsequent change from an amphiarthrosis to a diarthrosis is a relatively simple and rapid ontogenetic process controlled by minor genetic changes.

The shift of the site of insertion of the fourth levator externus from the dorsal fourth epibranchial element to the ventral fifth ceratobranchial may have developed in one of two ways: (1) As found in some specimens of *Cichla ocellaris*, the fourth levator externus may have split into two heads, one inserting on the original site on the fourth epibranchial and the second on the fifth ceratobranchial. The latter hypertrophied under strong selection pres-

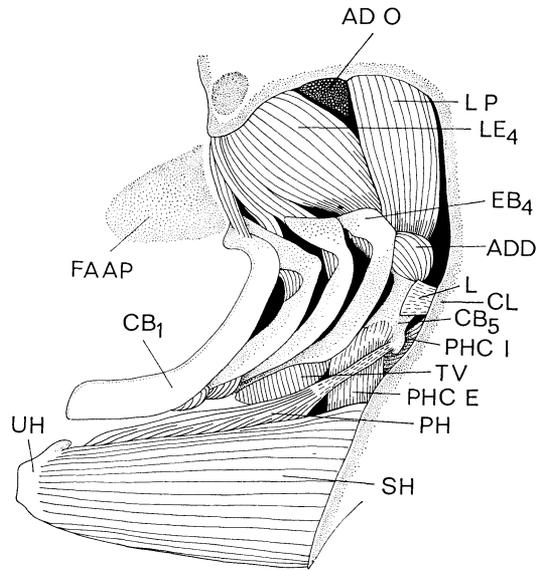


FIG. 14.—Lateral view of branchial apparatus and muscles of *Lamprologus tredocephalus* (mollusc feeder from Lake Tanganyika) after removal of opercular, suspensory apparatus, gills, gill rakers and mucous membrane. ADD5, fifth adductor; ADO, adductor operculi; CB1, first ceratobranchial; CB5, lower pharyngeal jaw; EB4, fourth epibranchial; FAAP, fossa for adductor arcus palatini; L, ligament; LE4, fourth levator externus; LP, levator posterior; PH, pharyngohyoideus; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; SH, sternohyoideus; TV, transversus ventralis; UH, urohyal.

sure, whereas the former's role diminished resulting in a reduction (occasional vestige in *Cichla*) or total loss of the muscle slip. (2) It is known that the levatores arcuum branchialium muscles in teleosts originate from muscle plates which are continuous dorsoventral structures (Edgeworth, 1935). The ventral parts of the muscle plates usually disappear leaving only their dorsal ends as the levatores. It is conceivable that in cichlids, the fourth levator externus retains its continuous dorso-ventral extent throughout its development. Either of the two possible ontogenetic mechanisms may represent the results of relatively simple changes in the genotype.

The levator posterior in generalized per-

coids and *Cichla ocellaris* (Figs. 1, 11:LP) originates from the pterotic anterior to the origin of the protractor pectoralis and has an oblique relationship to the upper pharyngeal jaw complex, which results in a less than 90 degrees angle of pull, so that some of the muscle energy is dissipated. In most cichlids the muscle fiber direction of the levator posterior is at the optimum angle, i.e., perpendicular to the long axis of the upper pharyngeal jaw (Figs. 5, 14:LEV P, LP). This modification is accomplished by a caudal shift in the origin of the levator posterior from a point anterior to one posterior to the origin of the protractor pectoralis.

"Fusion" of the two fifth ceratobranchials by means of a synarthrosis has evolved independently in several phylogenetically unrelated teleost fishes e.g., Anabantidae, some cyprinodonts, *Pogonias*, labroids and embiotocids (Liem, in preparation) indicating that the specialization plays such a highly significant trophic role that it has been exploited by the ever present pressure of selection.

Concomitant with these structural and functional changes, the pattern of nervous coordination of the branchial muscles changes significantly. The diphasic pattern is transformed into a triphasic one (compare Figs. 3 and 8). Such a change seems to have been brought about by the maintenance of the ancestral phase 2 (protraction and abduction) and an increase in relative duration and subsequent subdivision of phase 1 into phases 1a and 1b, respectively dealing with mastication and swallowing. The extension of the ancestral phase 1 may have been realized by the continuous firing of the nerve to the fourth levator externus throughout the feeding cycle, and the earlier firings of the nerves to the levator posterior and pharyngocleithralis internus muscles (Figs. 9, 10). Such changes can occur without major reorganization of the motor, proprioceptive, and sensory centers in the central nervous system.

It is evident that the new adaptive complex took place without the emergence of a truly new structure. An intensification of the masticatory function has led to a transformation of the food transporting pharyngeal apparatus of a generalized percoid into the cichlid adaptive complex dealing with both food transport and preparation. The entire conversion has been accomplished by a modification of preexisting structural elements, which, when functionally integrated, give rise to a new and vastly improved character complex of high selective value. As Mayr (1960) so succinctly stated: "Perhaps most astonishing is the relative slowness of reconstruction that seems to be necessary for successful adaptation to rather drastic shifts of adaptive zones."

EVOLUTIONARY STRATEGIES

The emergence of the pharyngeal jaw apparatus as a key innovation in cichlids has resulted in an astonishingly dramatic episode of proliferation worthy of such snappy metaphors as "explosive evolution," "evolutionary avalanche" and "explosive speciation." For example, current conservative estimates of endemic cichlid species in Lakes Victoria, Malawi and Tanganyika are respectively 165, 200, and 126. Each of these large lakes has its own distinctive cichlid fauna exploiting most available food resources. Endemic cichlids are also well represented in smaller lakes, e.g., Barombi Mbo, a circular crater lake in West Cameroon with a diameter of 2.5 km. housing 11 endemic species (Trewavas et al., 1972). The spectacular diversity is especially manifested in the feeding specializations, which present the pharyngeal jaw apparatus with items as diverse as molluscs, fish scales, insects, whole fishes, higher plants, zooplankton, algae and phytoplankton.

The evolutionary patterns exhibited by the pharyngeal jaw apparatus illustrate most convincingly the ever ready opportunism of evolution. Correlated with the great diversity of food specializations a

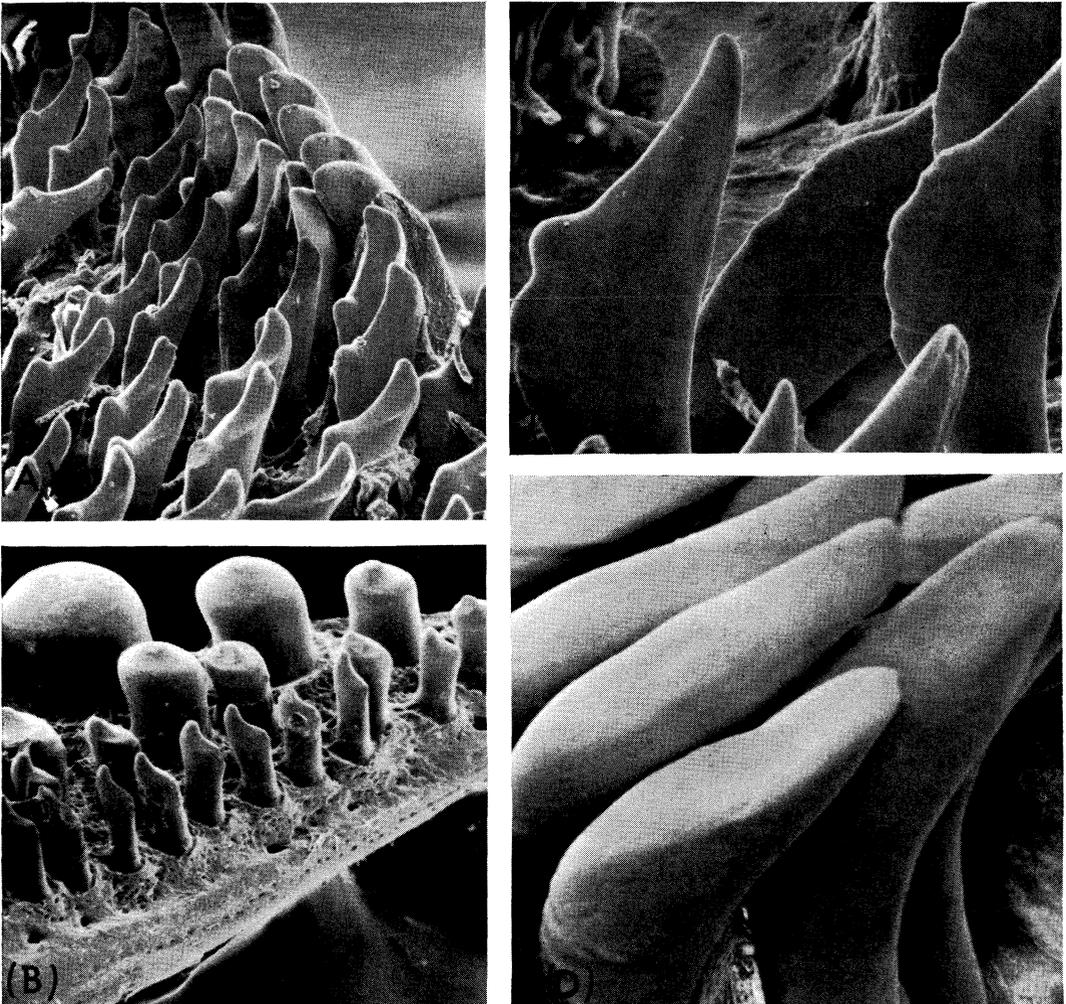


FIG. 15.—Scanning electron micrographs of teeth of lower pharyngeal jaws of Lake Malawi cichlids. A. *Corematodus taeniatus* (scale eater); B. *Haplochromis placodon* (mollusc eater); C. *Ramphochromis macrophthalmus* (fish eater); D. *Labeotropheus fuelleborni* (algae eater).

great number of distinctly different adaptive expressions evolve without changing the basic pattern of integration of the cichlid pharyngeal jaw apparatus. I will discuss some representative examples of adaptive expressions of cichlid pharyngeal jaws.

Adaptive strategies in dentition

The dentition of the pharyngeal jaws show considerable specializations not only among taxa but even in different fields of the same individual jaw.

In the mollusc-eating *Haplochromis placodon* (Fig. 15:B) the greatly enlarged central teeth are able to crush thick hard shells, whereas the (less modified) marginal teeth with the blunt hooklike pattern transport the crushed prey to the esophagus.

In the algae-eating *Labeotropheus fuelleborni* the teeth completely depart from the ancestral condition to form broad flat surfaces which can be used to compact the algal mass to facilitate subsequent swallowing (Fig. 15:D).

In the fish-eating *Ramphochromis macrophthalmus* the sharply-edged anterior margins of the pointed bladelike teeth are distinctly serrated (Fig. 15:C) to rasp flesh from its prey.

In the scale-eating *Corematodus taeniatatus* of Lake Malawi (Fig. 15:A) the teeth accentuate the ancestral condition by developing two "cusps" to enable the jaws to arrange the scales into packets so that they can be transported to the esophagus. An entirely different solution to the same problem is found in the Lake Tanganyika scale-eating species *Plecodus paradoxus* in which the dentition has been reduced to serve primarily as a transporting and manipulating system (Fig. 7).

Adaptive strategies of movements of upper pharyngeal jaws

Adaptive diversity is exhibited in the shape and size of the articular surfaces of the basipharyngeal joints (e.g., Fig. 13:AS). The movements in different adaptive types can be modified by varying not only the size of the articular surfaces but also the shape, i.e., elongate longitudinally or transversely, round or saddle-shaped. Natural selection has produced all possible types. In mollusc feeders, the hypertrophied pharyngeal apophysis also acts as a shock absorber (Greenwood, 1965). Variations in position of the basipharyngeal joints will result in significant changes of the moment arms of the levatores interni, levator posterior, and retractor pharyngeus superior muscles (Fig. 6:LI, LP, RP). All possible combinations between the position of the joint and insertion sites of the three muscles have been fully exploited during cichlid adaptive radiation.

Adaptive strategies of movements of lower pharyngeal jaw

The lower pharyngeal jaw varies in size and shape according to functional demands. Variations are also encountered in the size and shape of the muscular processes and in some cases new processes develop e.g., a

special process for the insertion of the tendon of the pharyngohyoideus (Fig. 14:PH).

In several taxa, the lower pharyngeal jaw becomes firmly anchored to the cleithrum by a strong ligament (Fig. 14:L, CL, CB5). Such a fixation alters the biomechanical properties of the jaw significantly. The ligament in cooperation with some muscles may fix the lower pharyngeal jaw in such a way as to simulate a joint. With the appearance of this functional "joint" the lower pharyngeal jaw becomes a Class 1 lever. This specialization occurs in some of the taxa requiring a powerful "bite" during mastication.

Adaptive strategies of pharyngeal jaw muscles

The muscles operating the upper pharyngeal jaws do not change their relationships to each other, although coordinated shifts in relation to the basipharyngeal joint occur frequently. Both the fourth levator externus and the levator posterior vary in size but retain their long parallel fibered arrangement for which there is strong selection pressure because such an arrangement offers a longer range of movements than pinnate or shorter fibered muscles. In "hard-biting" taxa, the levator posterior is often subdivided into two heads, the anterolateral part having the original insertion on the fourth epibranchial and the posteromedial head inserted on the muscular process of the lower pharyngeal jaw (Fig. 16:LP, LPP).

Numerous functionally determined variations occur in relative numbers of fibers in all branchial muscles except the first three levatores externi.

Significant shifts occur in the position of muscles attaching to the lower pharyngeal jaw. The insertion of the pharyngocleithralis internus may shift posteriorly from a more cranial (Fig. 11:PHCI) to an intermediate (Fig. 5:PHCI) and finally to a more caudal position (Fig. 14:PHCI). The functional consequences are far-reaching: in the anterior position the muscle acts as an efficient abductor with a long power

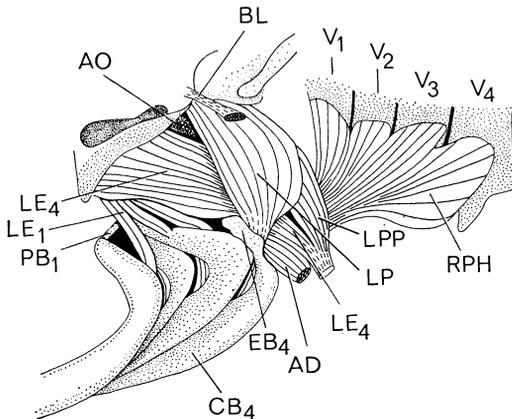


FIG. 16.—Lateral view of some branchial muscles in *Haplochromis vanderhorsti* (Luicha River, East Africa) after removal of lower pharyngeal jaw, which was attached to adductor (AD), fourth levator externus (LE4) and levator posterior (LP). AD, adductor; AO, adductor operculi; BL, Baudelet's ligament; CB4, fourth ceratobranchial; EB4, fourth epibranchial; LE4, fourth levator externus; LP, levator posterior; LPP, posteromedial head of levator posterior; PB1, first pharyngobranchial; RPH, retractor pharyngeus superior; V1–4, vertebrae.

arm, whereas the posterior insertion reverses the function into an adductor of the lower pharyngeal jaw. It is important that the typical timing of activity of this muscle spanning both phase 1b and 2 (as revealed by electromyography in a generalized cichlid [Fig. 8:PHAR CL I]) is remarkably "preadapted" for this complete functional reversal. The evolutionary process has produced the best functional pattern to meet the demands of the specific trophic specialization in each taxon studied.

The insertion of the pharyngochoydeus also shifts from a more anterior (Figs. 5, 11:PH) to a more posterior site (Fig. 14:PH). Without electromyographic data it is premature to evaluate the adaptive significance of this change, but it is conceivable that a posterior insertion incorporates this muscle in the increasingly more important masticatory phase (1a).

The variations in the position of the pharyngocleithralis externus will alter the

power arm and fiber length with subsequent changes in the range of movements.

The versatility of the pharyngeal jaw complex

It is clear from the above examples that the functional integration of the cichlid pharyngeal jaw apparatus is so basic and its potential adaptive versatility so rich that it is maintained throughout the adaptive radiation even though numerous non-disruptive evolutionary changes do take place. Relatively simple, but seemingly endless, evolutionary variations on the basic "cichlid theme" provided prodigious opportunities for eruptive evolution during the exploitation of rich resources of food in the lacustrine environment. The noncichlid pharyngeal jaw apparatus, on the other hand, possesses very limited possibilities of adaptive expressions because its building blocks lack the necessary basic integration and versatility for evolving functional conversions by simple quantum shifts.

CONCLUSIONS AND GENERALIZATIONS

The cichlids possess a key prospective adaptive complex, i.e., the highly integrated pharyngeal jaw apparatus, which has given them a distinct selective advantage during the invasion and subsequent colonization of new lacustrine environments. The invading cichlids successfully occupy contiguous and occasionally overlapping adaptive zones and specialize progressively into diversified sub-zones, ramifying prodigiously and covering a breadth of total adaptation that would have been wholly unpredictable and incredible if we were aware only of the beginnings of the process. This extraordinary success can be attributed to a unique prospective adaptation of maximum potential with a wide range of prospective adaptive zones in the lakes. Ordinarily organisms do not undergo radiation until they possess prospective adaptations.

The preadaptive level of the evolutionary innovation is reflected in a rather advanced state in *Cichla*. The ancestral percoid

pharyngeal jaw apparatus is a mechanism adapted purely for food transport with no provisions for extensive food manipulation, or preparation. Even when the fourth levator externus muscle made the all important shift of its insertion, the original deglutitionary function of the pharyngeal jaw apparatus was not changed. Once this morphological innovation had been established, however, the pharyngeal jaw apparatus became preadapted for a new function, i.e., food manipulation and preparation.

Under influence of new selection forces the novel adaptive complex acquired an extraordinarily distinctive biological role and the Cichlidae emerged as a new percoid family. The functional integration of the distinctive cichlid pharyngeal jaw complex seems so basic that it is rigidly maintained not only throughout the adaptive radiation but also in the many insectivorous *Haplochromis* species in which the fully specialized pharyngeal jaws function only for deglutition (Greenwood, personal communication). Among recent cichlids, only *Cichla* exhibits an intermediate level of integration, since its pharyngeal jaw apparatus seems to have somewhat limited capabilities for food manipulation and mastication, even though the rather weakly developed fourth levator externus has typical cichlid morphological characteristics. During adaptation, under control of the selection forces for food preparation and manipulation, the new adaptive complex is perfected (e.g., in many *Haplochromis* spp.) and becomes further specialized (e.g., in lacustrine cichlids). However, the original function of food transport is rigidly retained throughout the evolutionary process. This study supports Bock's theory (1959) that the emergence of most or all evolutionary novelties involves preadapted structures.

The crucial, primary morphological innovation in the development of the new adaptive type may have been the shift of insertion of the fourth levator externus muscle. As a response to this shift, secondary spe-

cializations, i.e., "fusion" of lower pharyngeal jaws and appearance of basipharyngeal joint, evolved. As discussed above the shift of the fourth levator externus can be accomplished by a very simple change in ontogenetic mechanism. Such a change requires a minor reconstruction of the genotype and will be under strong selection pressure. Although the saltationist theory as originally conceived by Goldschmidt (1940) must be rejected (cf. Simpson, 1953; Mayr, 1963), there is increasing experimental evidence that relatively simple genetic alterations could slightly affect the scheduling or velocity of ontogenetic events, which in turn are capable of producing adult phenotypic changes of rather profound but not monstrous dimensions (e.g., Waddington, 1962; Moss and Young, 1960; Hampé, 1959; Dubrul and Laskin, 1961; Klatt and Oboussier, 1951). Some recent proponents of the synthetic theory reject the possible occurrence of any saltatory changes, falsely maintaining that "saltationists" claim that the first bird quite literally hatched from a reptile egg and that the only way to achieve such a radical change is by polyploidy! A less extreme attitude toward some aspects of the saltationist theory may prove fruitful in our efforts to explain the evolutionary process by which new adaptive types emerge (cf. Frazzetta, 1970; Davis, 1949, 1964; Greenwood, 1973). Based on the data presented in this paper, I propose that the seemingly gradual emergence of the cichlid adaptive complex, i.e., shift of insertion of the fourth levator externus—development of basipharyngeal joint—"fusion" of lower pharyngeal jaws into one unit, took place by rapid saltatory steps under influence of strong selection pressure acting not on a single gene but on the minor reconstruction of the genotype which is involved in the necessary evolutionary changes of the controlling ontogenetic mechanisms. This hypothesis may apply to the evolution of almost all key innovations, and does not involve sudden, immense, "systemic mutations" producing "hopeful monsters" yet

it does incorporate the wealth of ontogenetic raw materials on which natural selection can act as convincingly revealed by many experimental embryologists and morphologists.

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