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COMPARATIVE MORPHOLOGY OF THE FEEDING APPARATUS IN CICHLIDIAN ALGAL FEEDERS OF LAKE TANGANYIKA

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ABSTRACT Feeding apparatus of 11 species of algal feeding cichlid fishes were examined. A set of 14 characters was taken and treated on their state distance for clustering. *Asprotilapia* type, *Petrochromis* type, and *Simochromis* type with three subtypes are recognized. These feeding apparatuses are related to the feeding methods of fishes when they graze on algae from rocks. This grouping is different from Greenwood's (1978) systematic classification based on pharyngeal apophysis of African cichlids.

INTRODUCTION

In Lake Tanganyika more than 20 endemic species of algal feeding cichlid fishes live in rocky shores (Poll, 1956; Marlier, 1959; Matthes, 1960; Brichard, 1975). These fishes are thought to have highly specialized devices for collecting algae from rock (Fryer and Iles, 1972). Recent studies on functional morphology (Osse, 1969; Liem and Osse, 1975) showed that feeding is a dominant function in the head of the fishes, i.e., greatest movement of bony elements and highest muscle activity are devoted to feeding. This conclusion leads to a hypothesis that fishes exploiting the same food resource in the same manner could receive similar influence on their feeding apparatuses. No comparative studies, however, have been carried out on feeding structure in such algal feeders, although there are some comparative studies on those feeding on other trophic groups (Liem and Stewart, 1976; Liem 1979; Stiassny, 1981).

I have been investigating comparatively on such fishes from ecological and morphological points of view at rocky shores of Luhanga and Uvira, located at the north-western end of the lake, since 1979. This paper presents the results of a comparative study on the jaw and suspensorium apparatuses of these fishes.

MATERIALS AND METHODS

The materials used in the present study were adults of 11 species of algal feeding cichlids: *Asprotilapia leptula* (Boulenger), *Limnotilapia dardennei* (Boulenger), *Petrochromis fasciolatus* (Boulenger), *Petrochromis polyodon* (Boulenger), *Petrochromis trewavasae* (Poll), *Pseudosimochromis curvifrons* (Poll), *Simochromis babaulti* (Pellegrin), *S. diagramma* (Günther), *S. marginatus* (Poll), *Telmatochromis temporalis* (Boulenger) and *Tropheus moorei* (Boulenger). All the specimens were collected from rocky shores of Luhanga and Uvira in January 1980.

For analyses, the specimens were fixed in 10% formalin at first, then cleared in solution of 5% H_2O_2 and 1.5% KOH for several hours, and stained with alizarin red S for 5 days for esteological examinations.

The premaxillary ascending process length (apl) and the mandible length (ml) were measured as the distance between the two points a–b and b–c shown respectively in Fig. 1. The angle of the premaxillary ascending process to the dentigerous arm was measured as the angle between *ab* and *bc* as shown in Fig. 1K.

For myological observations, the cleared specimens were stained with alizarin red S as in the former cases but for only 24 hours, and transfered into a Weiger's variation of Lugol's solution for 40 minutes (Bock and Shear, 1970). Then, tendons or ligaments were stained in 1–5% methyl blue for several minutes. For weighing a muscle, all connective tissues were removed in 75% alcohol solution, then water was removed by blotting paper, and the muscle was exposed to free air for 10 minutes.

The terminology of each characters follows to Barel (1976) for osteology, and Liem (1976) and Winterbottom (1974) for myology.

RESULTS

Osteology

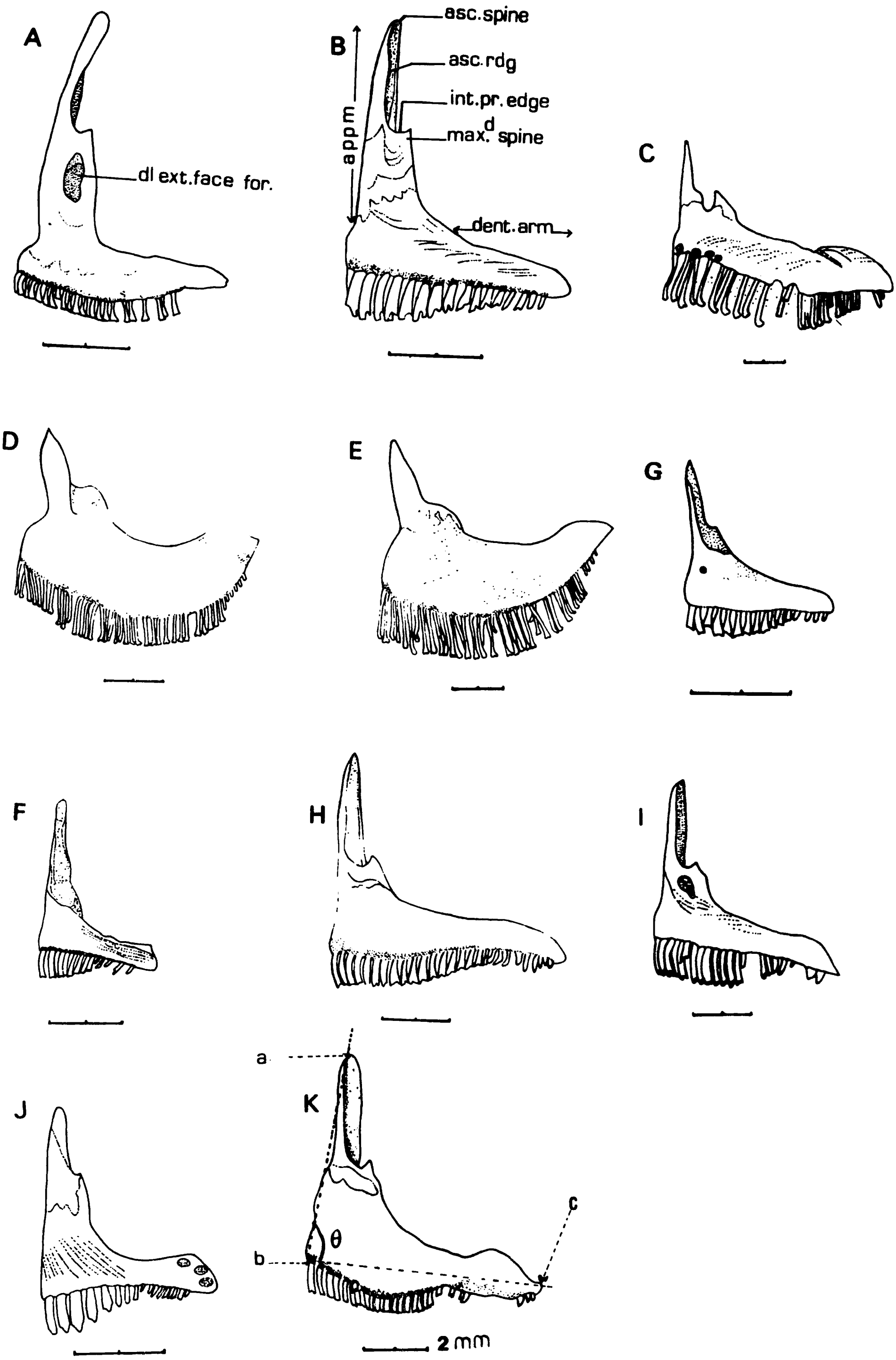
General features of the premaxilla (Table 1, Fig. 1)

Among 11 species, three species of the genus *Petrochromis* have the shortest ascending process and rather long dentigerous arm of the premaxilla. *Petrochromis polyodon* or *P. trewavasae* has a weakly curved interprocess edge, less developed maxillary dorsal spine, large breadth of the ascending process, and rather small angle (60–70°) of the ascending process to the dentigerous arm. These two species are also characterized by the longest and thickest dentigerous arm, which is strongly concave mediocaudally and dorsoventrally, and the rostral end of which is blunt. *P. fasciolatus*, on the other hand, has slightly different characters from *P. polyodon* or *P. trewavasae*: such as deeply curved interprocess edge, developed maxillary dorsal spine, narrow breadth of the ascending process, thin and concave dentigerous arm which is equal to the mandible in length as in many other algal feeding species, and large angle of the ascending process to the dentigerous arm showing about 78–94°.

Asprotilapia leptula has the shortest dentigerous arm and rather long and slightly curved ascending process, and its interprocess edge and maxillary dorsal spine are well developed as in many other algal feeders. The angle of the ascending process to the dentigerous arm is 74–79°.

Limnotilapia dardennei, Pseudosimochromis curviforns, three species of *Simochromis, Telmatochromis temporalis* and *Tropheus moorei* have general features of the premaxilla intermediate between *Petrochromis* and *Asprotilapia*. The relative length of the ascending process falls usually from 3.6 to 4.5, but *T. temporalis* and especially *P. curvifrons* have rather long process: i.e., 2.8–3.7 in relative value like *A. leptula*. Interprocess edge is usually deep, the maxillary dorsal spine is well developed, and the angle of Appm to the dentigerous arm is usually from 80–97°, but 72–87° in *Simochromis diagramma* and *T. moorei*. The relative length of the ascending process against head and of the dentigerous arm against mandible are also fallen between those of *Asprotilapia* and *Petrochromis*. And the dentigerous arm is not concave in most species as in *A. leptula*, but *T. moorei*'s dentigerous arm as well as that of *T. temporalis* is slightly curved.

Fig. 1. Lateral aspect of the left side of upper jaw in 11 species of algal feeding cichlids. K(a, b) shows the measuring points of the ascending process of the premaxilla (appm) length; and ab–bc, the inclination angle of (appm) to the dentigerous arm (dent. arm). int. pr. edge, inter process edge; max. ^{d}spine, maxillad dorsal spine; int. fct. dep, inter facet depression. A, B, C, D, E, F, G, H, I, J and K are respectively: *A. leptula, L. dardennei, P. fasciolatus, P. polyodon, P. trewavasae, P. curvifrons, S. babaulti, S. diagramma, S. marginatus, T. temporalis* and *Tropheus moorei.*


A
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2 mm

Table 1. Features of premaxilla.

	Ratio of head length to ascending process length					Angle of ascending process to basement									Ratio of dentigerous arm to mandible				
Species	X̄	S.D	95% conf. int.	Range	n	X̄	S.D	95% conf. int.	range	n	Inter process edge	Maxillary dorsal spine	Breadth of ascending process	Max.[d] fct.*	X̄	S.D	95% conf. int.	Range.	n
(A) *Asprotilapia leptula*	3.43	0.29	3.06–3.79	3.04–3.85	5	76.0	2.3	73.0–78.9	74–79	5	de	d	b	m	0.78	0.06	0.68–0.89	0.73–0.88	4
(B) *Limnotilapia dardennei*	4.31	0.28	3.97–4.65	4.37–4.58	5	86.0	4.3	81.4–90.5	79–90	5	de	d	b	L	0.92	0.10	0.75–1.09	0.85–1.08	4
(C) *Petrochromis fasciolatus*	5.55	0.26	5.27–5.83	5.47–5.82	6	88.5	5.9	82.2–94.7	78–94	6	de	d	b	m	1.05	0.05	0.91–1.19	1.00–1.11	3
(D) *Petrochromis polyodon*	5.21	0.43	4.75–5.69	4.49–5.64	6	62.6	4.7	56.6–68.5	60–71	5	w	ld	b	m	1.39	0.20	1.05–1.72	1.15–1.65	4
(E) *Petrochromis trewavasae*	5.15	0.38	4.68–5.62	4.70–5.48	5	64.3	4.7	59.3–69.3	60–70	6	w	ld	b	m	1.52	0.07	1.39–1.64	1.45–1.63	4
(F) *Pseudosimochromis curfrons*	3.12	0.13	3.00–3.25	2.88–3.23	7	91.1	4.9	85.9–96.3	82–95	6	de	d	b	sh	0.96	0.07	0.87–1.05	0.80–1.07	4
(G) *Simochromis babaulti*	4.46	0.22	4.23–4.69	4.24–4.85	6	90.5	5.8	84.3–96.6	80–97	6	sde	sd	sm	sh	0.81	0.12	0.61–1.00	0.63–0.90	4
(H) *Simochromis diagramma*	4.10	0.46	3.67–4.51	3.62–4.72	7	75.3	11.0	63.7–86.9	72–87	6	de	d	b	m	1.00	0.06	0.92–1.07	0.92–1.07	5
(I) *Simochromis marginatus*	4.28	0.11	4.11–4.45	4.12–4.36	4	91.8	1.6	87.7–91.8	87–91	5	sde	sd	sm	L	0.88	0.15	0.74–1.12	0.78–1.11	4
(J) *Telmatochromis temporalis*	3.47	0.27	3.19–3.75	3.14–3.70	6	87.0	4.4	81.4–92.5	82–94	5	de	sd	sm	m	1.00	0.14	0.78–1.23	0.82–1.13	4
(K) *Tropheus moorei*	3.72	0.13	3.58–3.86	3.56–3.88	6	91.0	6.7	83.9–98.0	84–102	6	de	d	b	m	1.48	0.19	1.17–1.78	1.27–1.72	4

*maxillad articulation facet w=weak, de=deep, s=slightly, d=developed, ld=less developed, b=big, sm=small, L=longest, m=medium sh=shortest

Internal Topography of Premaxilla (Fig. 2)

Viewing the premaxilla from the internal side, a blunt and hump-like pair of maxillad dorsal articulation facets as well as a wall-like pair of symphyseal articulation facets are found, and a pair of interfacet depression are developed between these facets, in all cichlids examined. From the features of these three anatomical characters, interspecific differences can be established as follows.

The maxillad dorsal articulation facets are different each other in size and shape among the 11 species. *L. dardennei* and *S. marginatus* have longest ones, *A. leptula*, three species of *Petrochromis, S. diagramma, T. temporalis* and *Tropheus moorei* have medium, while *S. babaulti* and *P. curvifrons* have shortest in size. These facets are elongate in *A. leptula*, *L. dardennei*, *S. marginatus*, *S. diagramma* and *T. temporalis*, but ellipsoidal in the remaining species in shape. It may be noticed that asymmetrical features are observed in some species from the internal view. For instance, *A. leptula*, *Petrochromis fasciolatus*, *S. diagramma* and *S. marginatus* have stout maxillad dorsal articulation facet in right and small and rubbed ones in left; but in *P.polyodon* the right maxillad dorsal articulation facet is also rubbed but larger than the left one.

Three species of *Petrochromis* have short symphyseal articulation facets, while the remaining species have rather long ones.

Maxilla (Fig. 3, Table 2)

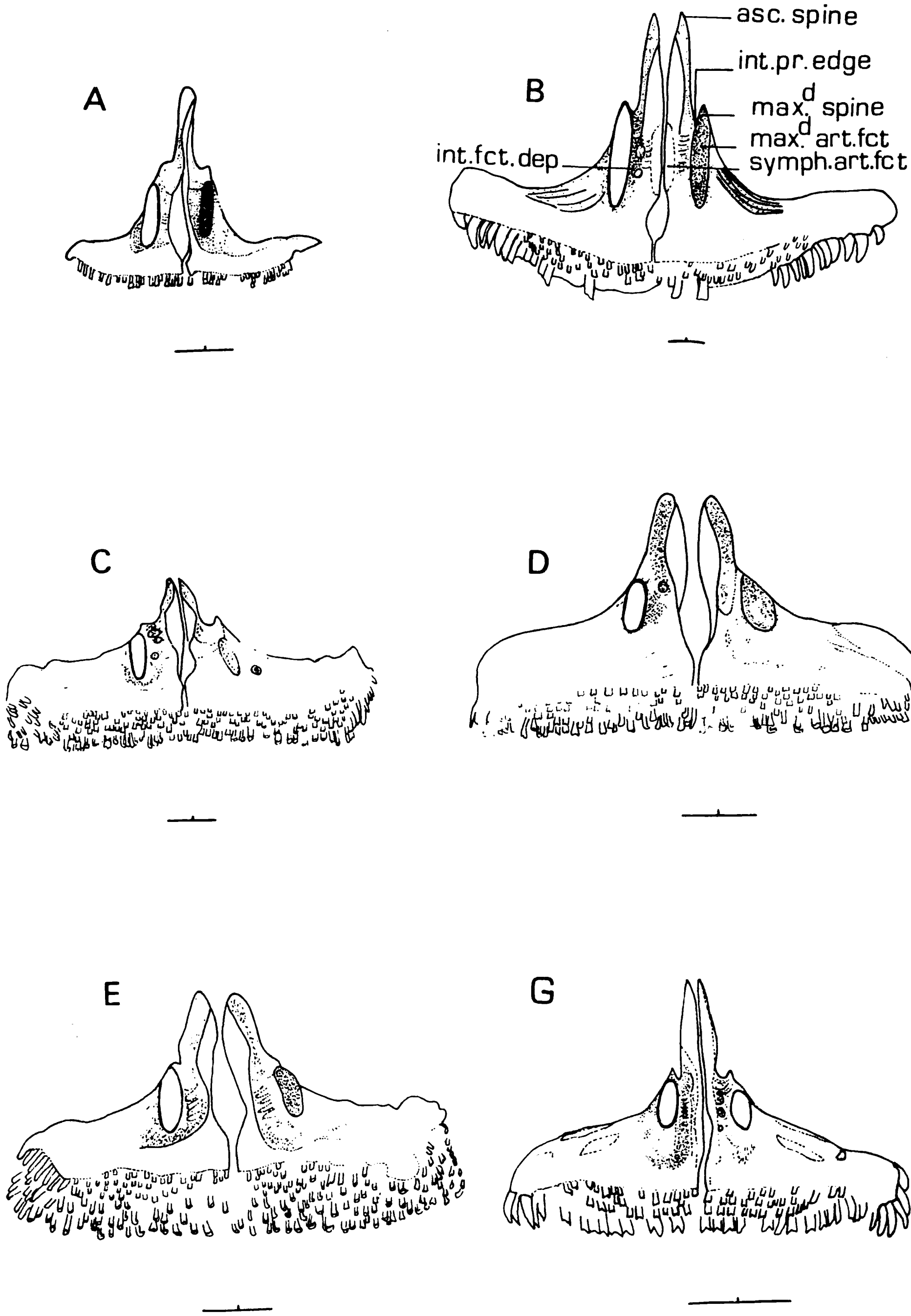
Every maxilla of the 11 species has a flat and enlarged ventral head and two thicker dorsal heads: i.e., the premaxillary condyle in anterior and the cranial condyle in posterior. In most of species examined ventral head is larger than the dorsal ones, and a post-maxillary process, rounded in shape, is situated medially at the posterior margin. In *A. leptula*, however, a rather ventrally situated and strongly projected process, is observed, its maxillary body shows a great concavity in its central part, and the ventral head is smaller than the dorsal ones. The premaxillary condyle and cranial condyle show great variation in size and shape between the species shown in Table 2.

Mandible (Figs. 4 and 5, Table 3)

In the mandible of the 11 species, the angular anterior margin is concave in most species, but only weakly concave in *Petrochromis polyodon* and *P. trewavasae*. The ascending process of the dentary is generally shorter than the ascending process of the angular, except in three species of *Petrochromis* and *Telmatochromis Temporalis* where both ascending process are almost equal in length. Relative size of the coronoid wing to the ventral margin of the dentary is different among the species as follows. In *Asprotilapia* or *L. dardennei* the coronoid

Table 2. Maxilla.

Species	Premaxillary condyle	Cranial condyle
(A) *Asprotilapia leptula*	wide & short	very big & round
(B) *Limnotilapia derdennei*	Small & projecting	small
(C) *Petrochromis fasciolatus*	big & stout	big & rounded
(D) *Petrochromis polyodon*	big & stout	big & rounded
(E) *Petrochromis trewavasae*	big & stout	big & rounded
(F) *Pseudosimochromis curvifrons*	small & short	big & rounded
(G) *Simochromis babaulti*	small & projecting	small
(H) *Simochromis diagramma*	small & projecting	small
(I) *Simochromis marginatus*	small & short	small
(J) *Telmatochromis temporalis*	small & short	small
(K) *Tropheus moorei*	big & short	big & rounded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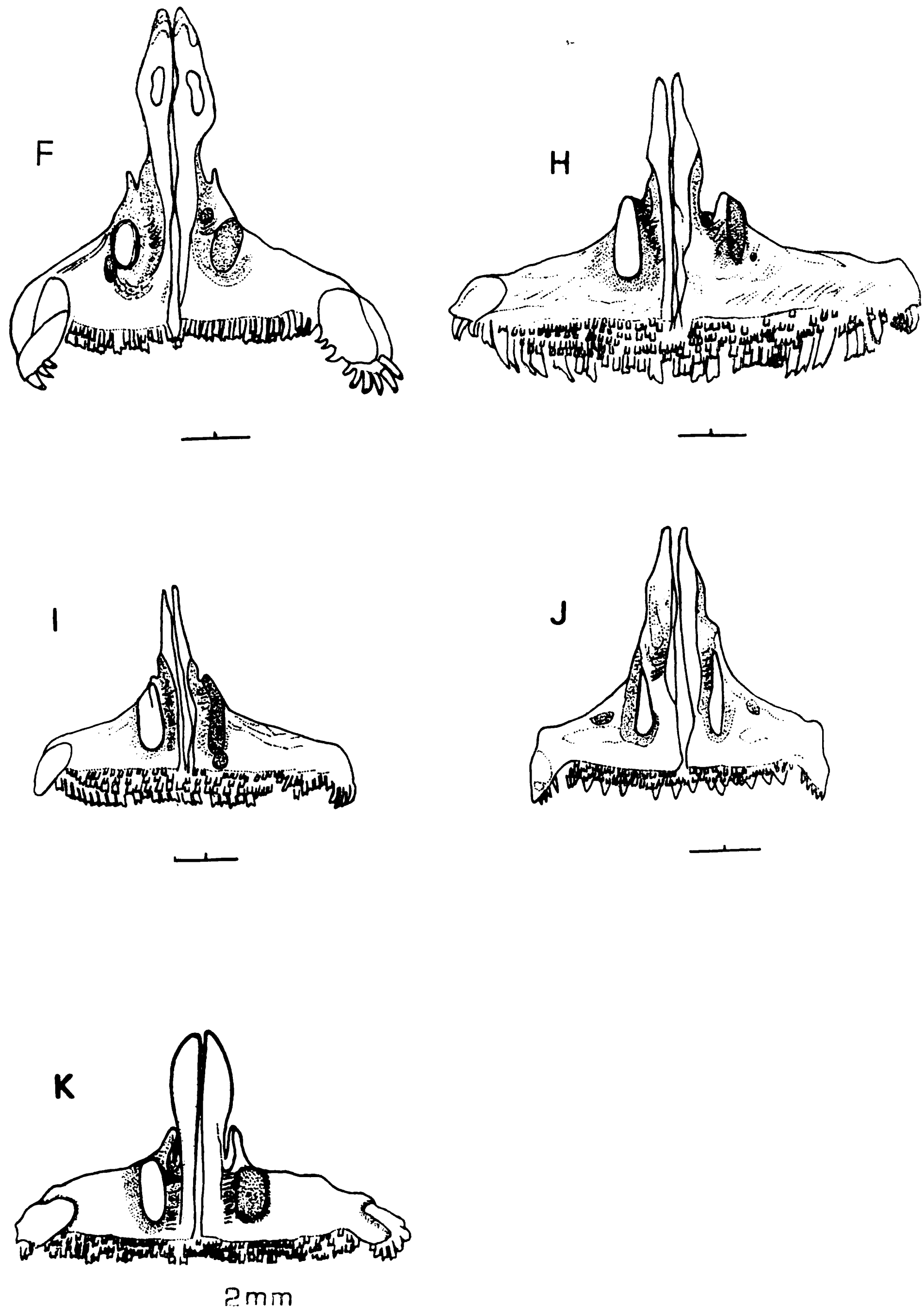


Fig. 2. Internal aspect of the upper jaw in 11 species of cichlids, showing differences in articulation facets shape and size. max. dart, fct, maxillad dorsal articulation facet; symph. art. fct, symphyseal articulation facet. Other label as in Fig. 1.

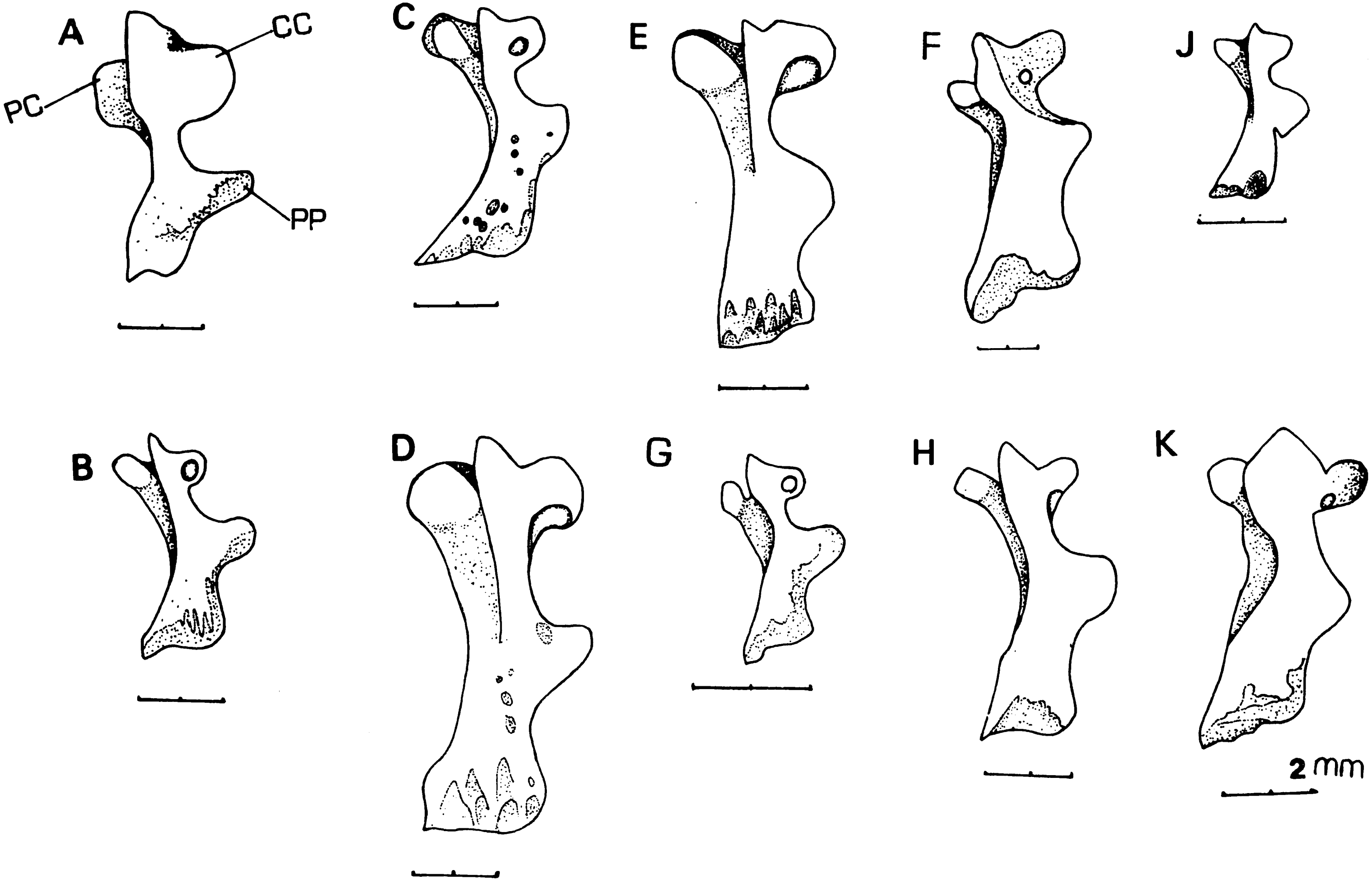


Fig. 3. Laterointernal view of maxilla, showing difference in articulation heads (PC, premaxillary condyle and CC (Capital letter), cranial condyle) region and their medial process (PP, post maxillary process of premaxilla). Label as in Fig. 1.

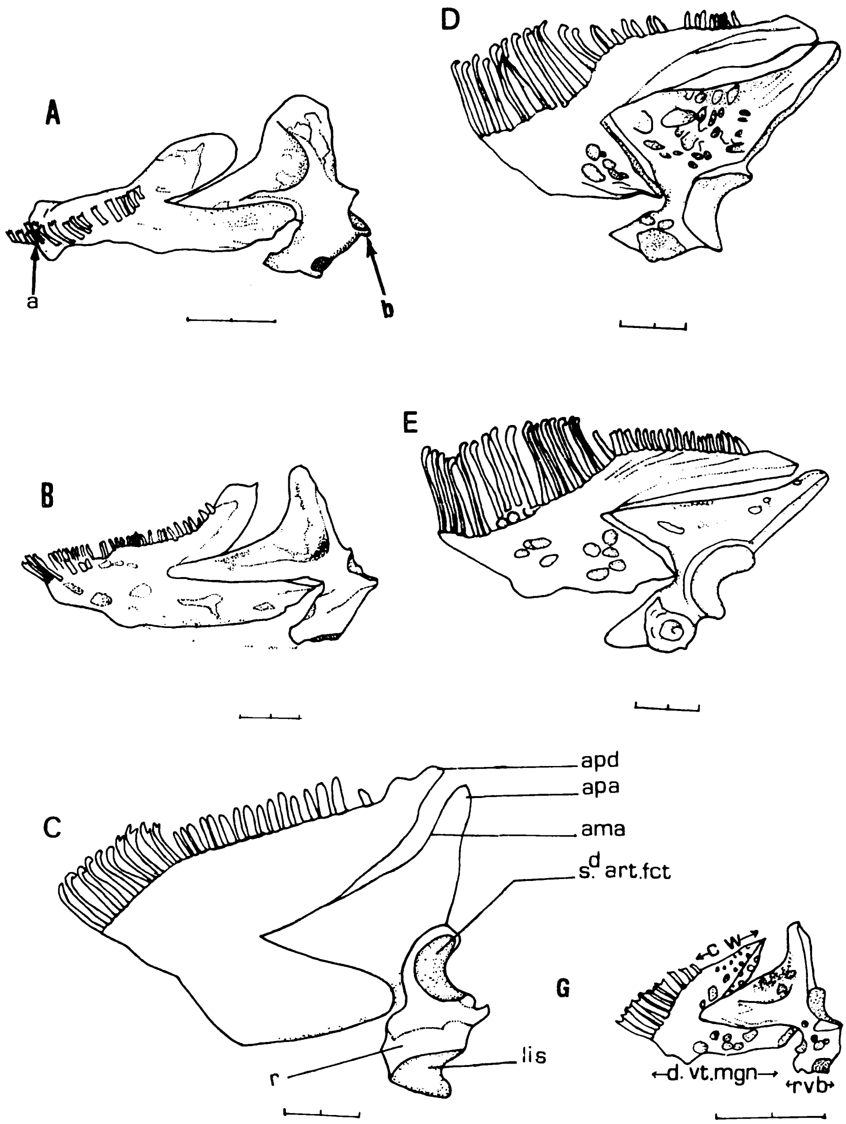
Table 3. General features of the mandible.

	H.L/Mandible length.					H.L/Lim ratio					
Species	$\bar{X}$	S.D	95% conf. int.	Range	n	$\bar{X}$	S.D	95% conf. int.	Range	n	Vm/cw
(A) *Asprotilapia leptula*	3.71	0.46	2.99–4.44	3.13–4.24	4	6.17	0.70	4.43–7.90	5.51–6.90	3	Vm>Cw
(B) *Limnotilapia dardennei*	3.53	0.51	2.90–4.16	3.36–4.10	5	7.61	0.82	6.30–8.92	6.53–8.40	4	Vm>Cw
(C) *Petrochromis fasciolatus*	3.54	0.11	3.37–3.37	3.41–3.67	4	6.60	0.26	5.94–7.26	6.39–6.90	3	Vm<Cw
(D) *Petrochromis polyodon*	4.27	0.34	3.74–4.81	3.96–4.72	3	7.57	0.23	7.19–7.94	7.41–7.92	4	Vm<Cw
(E) *Petrochromis trewavasae*	4.68	0.16	4.43–4.93	4.48–4.87	4	8.85	0.61	7.33–10.38	8.36–9.54	3	Vm<Cw
(F) *Pseudosimoch curvifrons*	3.81	0.17	3.63–3.99	3.64–4.08	6	6.13	0.81	5.26–6.99	5.11–7.11	6	Vm = Cw
(G) *Simochromis babaulti*	3.13	0.37	2.53–3.72	2.58–3.38	4	6.42	1.00	3.93 8.90	5.26–7.04	3	Vm = Cw
(H) *Simochromis diagramma*	3.51	0.18	3.32–3.69	3.29–3.81	6	6.76	0.56	7.74–8.91	6.28–7.13	5	Vm = Cw
(I) *Simochromis marginatus*	3.14	0.01	2.94–3.33	3.02–3.26	4	6.57	0.15	6.20–6.93	6.43–6.72	3	Vm = Cw
(J) *Telmatochromis temporalis*	3.62	0.30	3.25–3.99	3.12–3.89	5	6.33	0.54	4.99–7.67	5.98–6.95	3	Vm = Cw
(K) *Tropheus moorei*	4.86	0.71	3,73–5.98	3.13–5.82	4	6.25	0.43	5.18–7.32	5.81–6.67	3	Vm = Cw

H.L = head length; Vm = ventral margin; Cw = coronoid wing; Lim = interoperculomand ibular ligament length.

wing is shorter than the ventral margin of the dentary, the opposite situation is observed in the three species of *Petrochromis*, and in the other species both are nearly equal in size.

Mandible size to head length is short in *Petrochromis polyodon, P. trewavasae* and *Tropheus moorei*; the ratio ranges from 3.9 to 5.8. *Petrochromis polyodon* and *P. trewavasae* are characterized also by short interoperculomandibular ligament (Lim) on the other hand, *Pseudosimochromis curvifrons, A. leptula, Telmatochromis temporalis, L. dardennei. Petrochromis fasciolatus* and *S. diagramma* have rather long mandible; and *S. babaulti* and *S. marginatus* have the most longest ones. Except for *L. dardennei*, the interoperculomandibular ligament is large in these last two groups including *Tropheus moorei*, with *S. babaulti* and *S. marginatus* possessing the largest Lim of the groups.



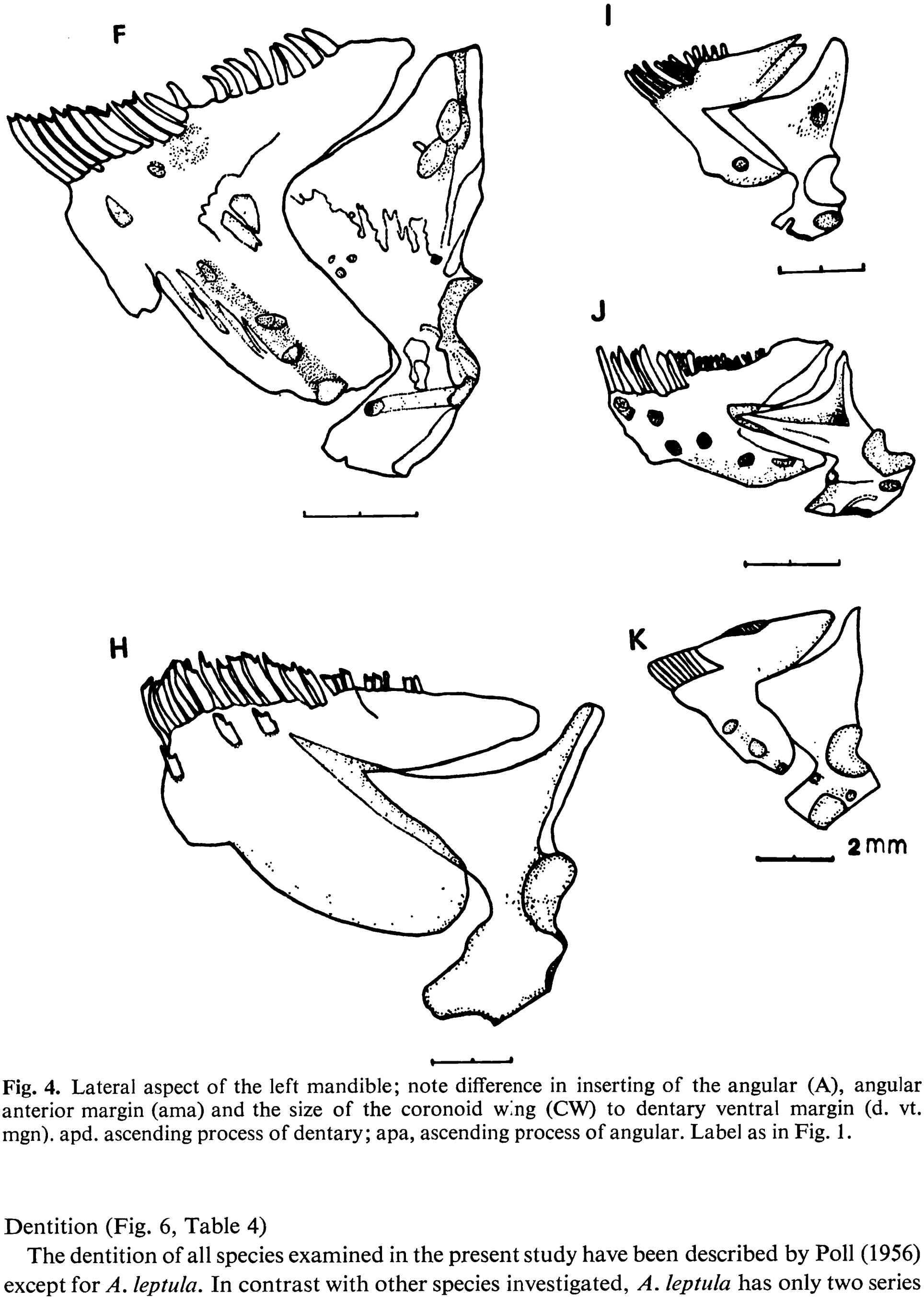


Fig. 4. Lateral aspect of the left mandible; note difference in inserting of the angular (A), angular anterior margin (ama) and the size of the coronoid wing (CW) to dentary ventral margin (d. vt. mgn). apd. ascending process of dentary; apa, ascending process of angular. Label as in Fig. 1.

Dentition (Fig. 6, Table 4)

The dentition of all species examined in the present study have been described by Poll (1956) except for *A. leptula*. In contrast with other species investigated, *A. leptula* has only two series of short tricuspid teeth both on the premaxilla and mandible. No corner teeth are observed. Teeth in outer serie are much taller than inner ones. All teeth have small cusps that are equal in height and the cusps gaps are also less deep. Each tooth is strongly concave lingually from the neck to the crown.

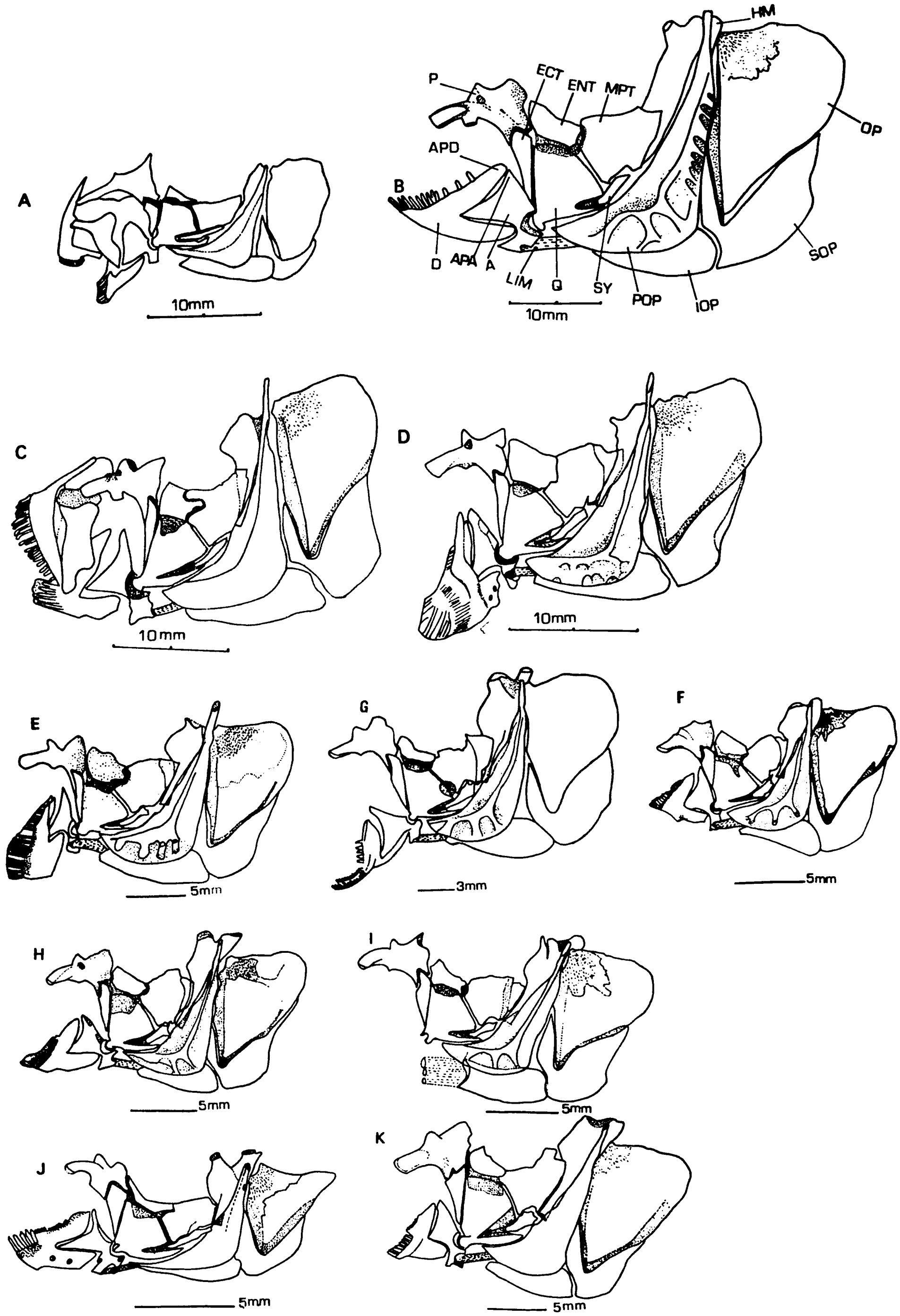


Fig. 5. Lateral aspect of the suspensorium apparatus connected with mandible and opercular apparatus, note joint structure in (P, palatine-; ECT, ectopterygoid-; ENT, entopterygoid-; Q, quadrate-; MPT, metapterygoid). The inserting site of (LIM) in retroarticular (r) is also shown. lis: lim inserting site. Labels as in Fig. 1.

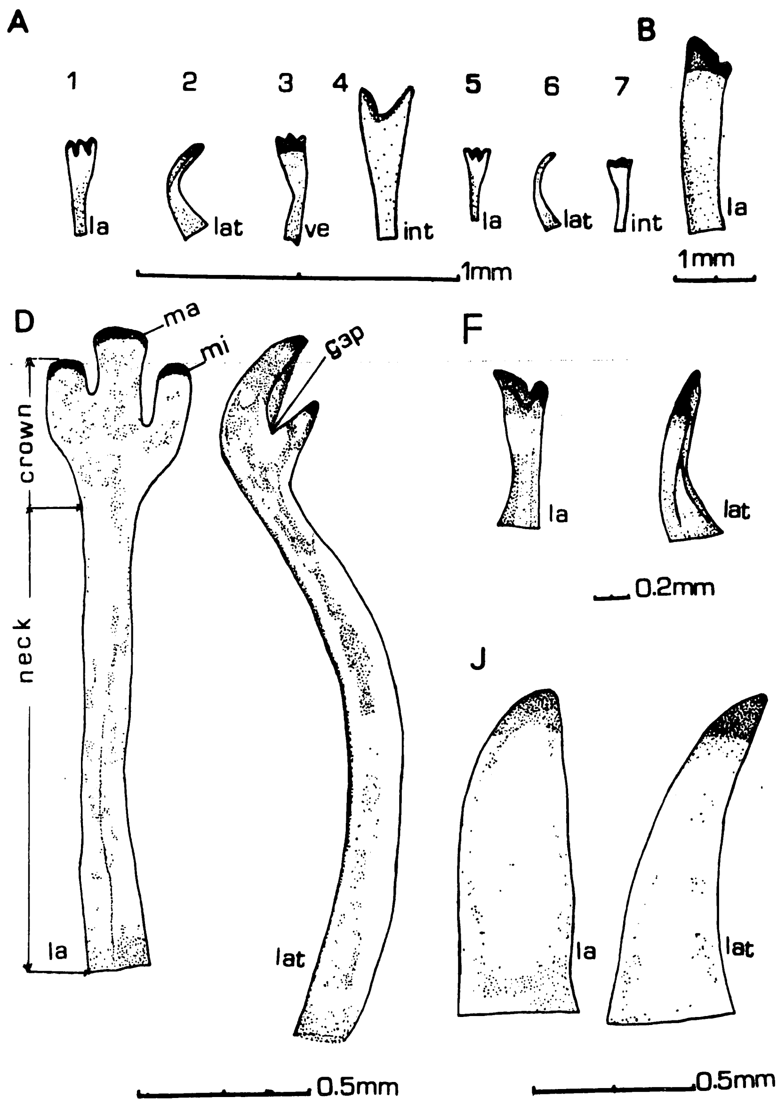


Fig. 6. la, labial; lat, lateral; int, internal; ve, ventral view of teeth in premaxilla. Figures show various tooth structures and teeth shape among algal feeding fishes. A (1–4). outer teeth of premaxilla; A (5–7), inner teeth of premaxilla; B, D, G and J are outer teeth of premaxilla. A, B, D, G, J labels are same as in Fig. 1.

The three species of *Petrochromis* are characterized by large band of long tricuspid teeth that show tooth cuspidation different from other species of algal feeders examined. The cusps gaps are deep but the left and right gaps are different in depth. Within this genus, tooth neck in *P. fasciolatus* is straight, while in the other two species it is more curved labially.

Other species such as *L. dadennei*, *Pseudosimochromis curvifrons*, *Simochromis* and *Tropheus moorei* have bicuspid teeth at their outer series and their cusps gaps are equally deep, except for *L. dardennei*, in which cusps gaps are shallower. And they have sharp conical teeth at the

Table 4. Premaxillary and mandibular dental structure.

Species	Premaxillary teeth type*				
	outer	inn r	corner	teeth serie number	setting pattern
(A) *Asprotilapia leptula*	3	3 (d)	0	2	C
(B) *Limnotilapia dardennei*	2	3 (d)	1	4–5	C (wi)
(C) *Petrochromis fasciolatus*	3	3 (d)	3 (d)	i	C
(D) *Petrochromis polyodon*	3	3 (d)	3 (d)	i	C
(E) *Petrochromis trewavasae*	3	3 (d)	3 (d)	i	C
(F) *Pseudosimochromis curvifrons*	2	3 (d)	1	4–5	C
(G) *Simochromis babaulti*	2	3 (d)	1	4	C
(H) *S. Simochromis diagramma*	2	3 (d)	1	5–6	C
(I) *S. Simochromis marginatus*	2	3 (d)	1	6	C
(J) *Telmatochromis temporalis*	1	3	1	5–6	C
(K) *Tropheus moorei*	2	3 (d)	1	8–10	C

*1, 2, 3: number of cusp; wi: widely setted; d: developed; C: closely setted; i: many

Mandibular teeth type				
outer	inner	corner	teeth serie number	setting pattern
3	3 (d)	0	2	C
2	3 (d)	0	2	C
2 (d)	3 (d)	1	4–5	(wi)
3	3 (d)	3 (d)	i	C
3	3 (d)	3 (d)	i	C
3	3 (d)	3 (d)	i	C
2 (d)	3 (d)	1	4	C
2 (d)	3 (d)	1	4	C
2 (d)	3 (d)	1	5–6	C
2	3 (d)	1	4	C
1	3	1	6	C
2	3 (d)	1	5–6	C

corner.

Telmatochromis temporalis has only conical teeth which are spatulated.

Myology

Jaw Muscles (Figs. 7 and 8, Table 5)

The adductor mandibulae muscle is the largest muscle of the jaw, and it is divided into 4 separable parts called as A_1, A_2, A_3 and A_w. In the 11 species examined the origin and the inserting site of each part are the same as those of other cichlids described by Liem and Osse (1975), Liem and Stewart (1976), Stiassny (1981) and Vandewalle (1972).

These fishes show remarkable differences in weight of the A_1 part comparing with the A_2 or A_3 part. The A_1 part is generally heavier than the A_2 part in all species except in *A. leptula*.

The A_1 tendon length ratio to the head length is also varied: *A. leptula* and *P. fasciolatus* have a long A_1 tendon, whose ratio ranges from 0.16 to 0.23, *Petrochromis polyodon*, *P. trewavasae*, *L. dardennei*, *Pseudosimochromis curvifrons*, *Simochromis* and *Tropheus moorei* show medium ratio ranging from 0.11 to 0.20, while *Telmatochromis temporalis* shows shortest (0.06).

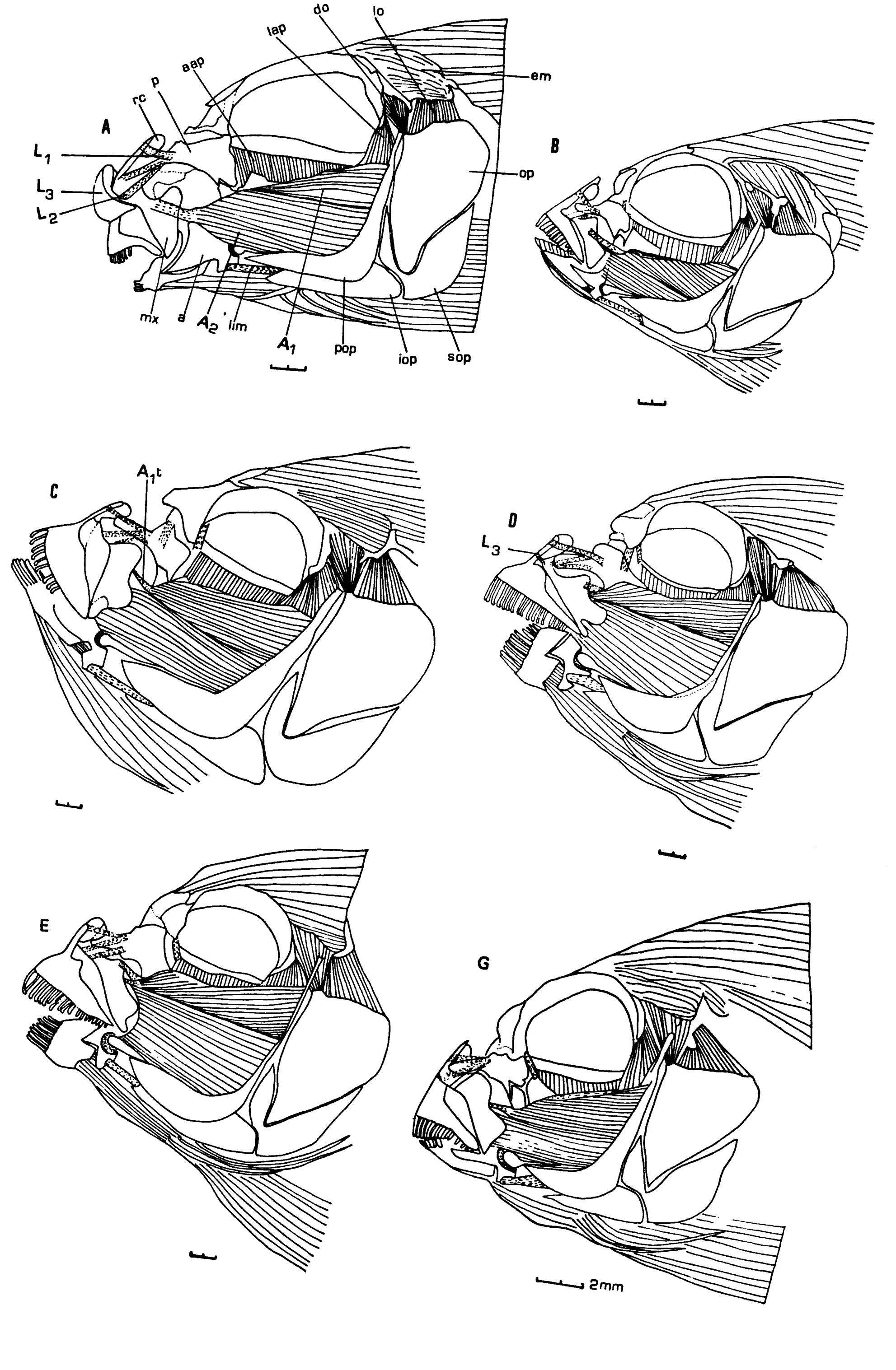
The A_3 part is the smallest of the three parts of adductor muscle, making up to 11.8% in weight, in all species examined. Within the species, *A. leptula, Petrochromis fasciolatus* and *Telmatochromis temporalis* have heavier A_3 part, *Tropheus moorei* has the lightest, and the others are medium.

Table 5. Percentage of adductor mandibulae muscle A_1, A_2 and A_3 parts weight and A_1 tendon length.

Species	A_1 percentage*					A_2 percentage				
	$\bar{X}$	S.D	95% conf. int.	Range	n	$\bar{X}$	S.D	95% conf. int.	Range	n
(A) *Asprotilapia leptula*	23.33	1.18	20.41–26.26	22.58–24.69	3	71.88	2.98	64.49–79.27	69.89–70.45	3
(B) *Limnotilapia dardennei*	57.85	2.20	52.39–63.31	55.67–60.06	3	38.62	7.51	19.97–57.27	30.03–43.94	3
(C) *Petrochromis fasciolatus*	66.73	7.27	57.71–75.75	58.14–74.91	5	25.C0	8.76	14.13–35.88	14.98–35.33	5
(D) *Petrochromis polyodon*	55.32	3.52	49.73–60.92	51.07–59.61	4	40.43	3.09	35.50–45.34	36.94–44.11	4
(E) *Petrochromis trewavasae*	51.08	1.97	47.94–54.22	48.56–52.93	4	43.90	4. 0	37.07–50.74	37.79–45.83	4
(F) *Pseudosimoch curvifrons*	59.59	4.86	51.85–67.33	54.05–65.91	4	36.18	4.85	28.47–43.89	29.54–41.18	4
(G) *Simochromis babaulti*	62.22	3.15	57.21–67.23	58.82–65.96	4	32.36	2.90	27.74–36.98	29.41–36.36	4
(H) *Simochromis diagramma*	55.72	3.85	49.59–61.84	50.52–58.92	4	38.65	2.61	34.50–42.80	35.51–40.99	4
(I) *Simochromis marginatus*	58.20	3.74	48.91–67.49	55.66–62.50	3	37.46	5.39	24.08–50.85	31.25–40.82	3
(J) *Telmatochromis temporalis*	46.62	1.50	44.23–49.01	45.23–48.19	4	44.71	0.74	43.52–45.89	43.96–44.18	4
(K) *Tropheus moorei*	69.78	4.04	63.35–76.20	64.94–73.53	4	28.16	3.41	22.73–33.59	25.27–32.62	4

*The percentage of A_1, A_2 or A_3 was calculated from their summation.

Species	A_3 percentage					A_1 tendon length rat o to H.L				
	$\bar{X}$	S.D	95% conf. int.	Range	n	$\bar{X}$	S.D	95% conf. int.	Range	n
(A)	7.25	0.38	6.31–8.20	6.82–7.53	3	0.207	0.017	0.165–0.250	0.197–0.227	3
(B)	3.53	5.53	10.19–17.26	0.29–9.91	3	0.147	0.013	0.114–0.179	0.132–0.157	3
(C)	8. 7	1.52	6.38–10.15	6.67–10.11	5	0.196	0.030	0.151–0.242	0.159–0.220	5
(D)	4.25	0.79	2.99–5.51	3.44–5.03	4	0.135	0.010	0.124–0.146	0.125–0.150	4
(E)	3.59	0.23	3.01–4.18	3.33–3.78	3	0.164	0.021	0.131–0.198	0.144–0.194	3
(F)	4.23	0.55	3.35–5.10	3.53–4.76	4	0.134	0.006	0.123–0.143	0.127–0.140	4
(G)	5.42	4.37	1.53–12.36	2.13–11.76		0.135	0.020	0.103-0.167	0.107–0.152	4
(H)	5.88	2.49	1.93–9.84	4.17–9.49	4	0.117	0.009	0.102–0.132	0.113–0.130	4
(I)	4.34	1.66	0.20–8.47	3.23–6.25	3	0.152	0.043	0.044–0.259	0.111–0.197	3
(J)	8.67	0.83	7.35–9.99	7.63–9.53	4	0.063	0.011	0.046–0.080	0.053–0.072	4
(K)	2.06	0.96	0.54–3.58	0.74–2.99	4	0.124	0.011	0.107–0.141	0.109–0.134	4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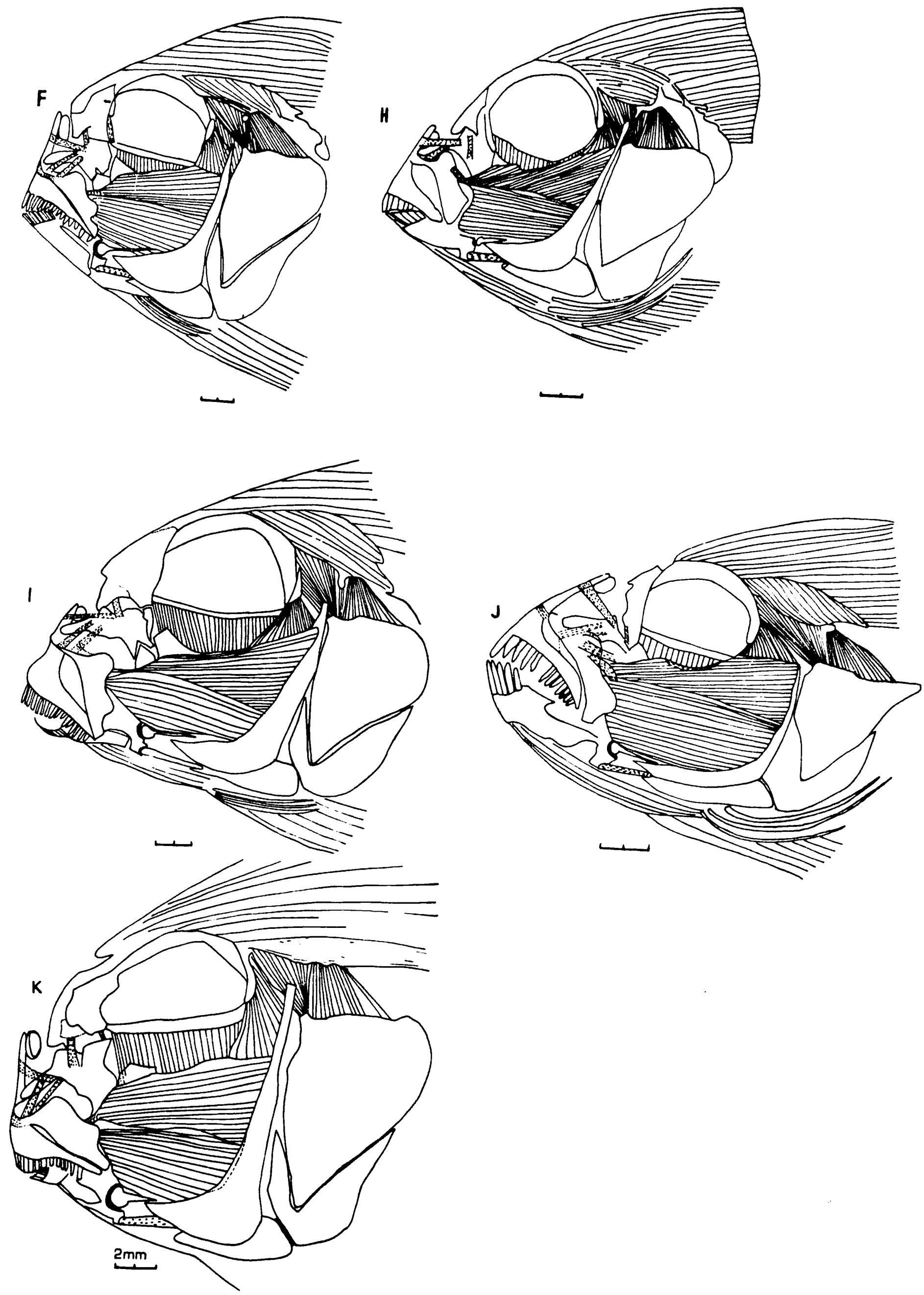


Fig. 7. Lateral aspect of adductor mandibulae A_1, A_2, A_3 parts. A_3 part is located under A_1 and A_2 and not shown in the figures. Note also the shape of the rostral cartilage (rc) in appm. L_3, intermaxillary ligament. Labels as in Fig. 1.

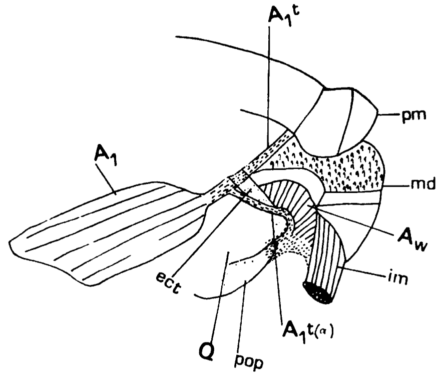
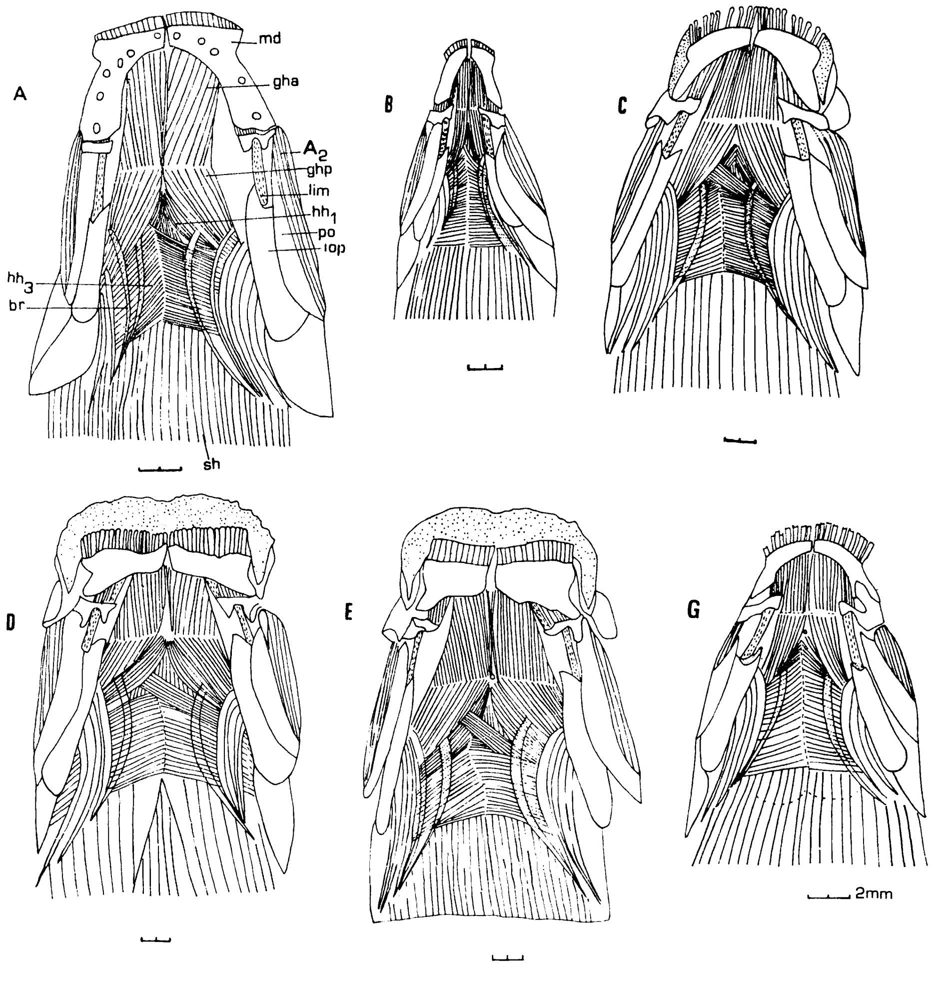


Fig. 8. Lateral aspect of A_1 part with its anterior end divided in two tendons (A_1 t and A_1 t), dorsal aspect of intramandibularis (A_w) and also the dorsal aspect of (im, intermandibularis).



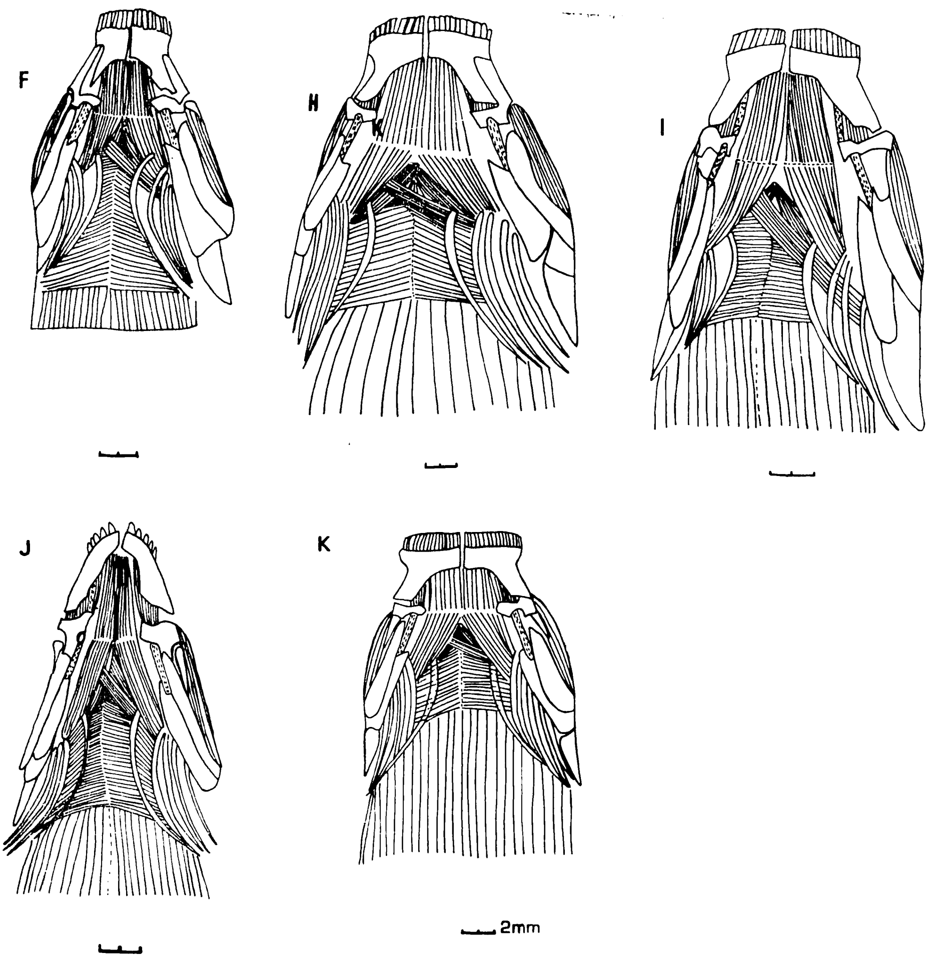


Fig. 9. Ventral aspect of muscles of the head. Gha and ghp length and width are clearly shown. Labels as in Fig. 1.

Table 6. Suspensory apparatus.

Species	En'opterygoid size	Palt. & Ent. joint	Rostral cartilage size	(Ghy size)
(A) *Asprotilapia leptula*	small	not joint	s	L
(B) *Limnotilapia dardennei*	compressed	not joint	s	L
(C) *Petrochromis fasciolatus*	expanded	slightly joint	b	Sh
(D) *Petrochromis polyodon*	expanded	slightly joint	b	Sh
(E) *Petrochromis trewavasae*	expanded	slightly joint	b	Sh
(F) *Pseudosimo curvifrons*	compressed	not joint	s	Sh
(G) *Simochromis babaulti*	compressed	not joint	s	Sh
(H) *Simochromis diagramma*	compressed	not joint	s	Sh
(I) *Simochromis marginatus*	compressed	not joint	s	Sh
(J) *Telmatochromis temporalis*	elongate	well joint	s	L
(K) *Tropheus moorei*	compressed	not joint	s	Sh

Palt. = palatine; Ent. = entopterygoid; Ect. = ectopterygoid; s = small; b = big; L = long; Sh = short; Ghy = geniohyoideus muscles

The Ventral Head Muscles (Fig. 9, Table 6)

The geniohyoideus anterior (gha) and geniohyoideus posterior (ghp) muscles are compound and elongate muscles. Their origin and inserting site are the same as those described in other cichlids by Liem and Osse (1975).

Muscle fibers of the geniohyoideus vary in length in comparison with the mandible length: *Petrochromis*, *Pseudosimochromis*, and *Tropheus moorei* have short muscle fibers, while *Asprotilapia leptula*, *L. dardennei* and *Telmatochromis temporalis* have long muscle fibers of the gha and ghp.

Ligament and Cartilage of the Jaw Apparatus (Fig. 7)

In *Asprotilapia leptula*, the intermaxillary ligament is fused or connected with a massive cartilage as clearly shown in Fig. 7, L3, while in other species no such development was found in this ligament.

The rostral cartilage is small, comparing with the ascending process length, in every species, except in the three species of *Petrochromis*, in which it is large.

DISCUSSION

The 11 species of cichlid fishes treated in this paper are usually classified to 7 genera: *Asprotilapia*, *Limnotilapia*, *Petrochromis*, Pseudosimochromis, *Simochromis*, *Telmatochromis* and *Tropheus*. Greenwood (1978), in his review of the pharyngeal apophyses of African cichlids, re-examined Regan's (1920) classification and recognized 4 types: A) *Haplochromis* type, B) *Tylochromis* type, C) *Tilapia* type and D) *Tropheus* type. According to this classification, *Telmatochromis* is included in type A, *Petrochromis* is in type C, and *Asprotilapia*, *Limnotilapia*, *Pseudosimochromis*, *Simochromis*, *Tropheus* are in type D.

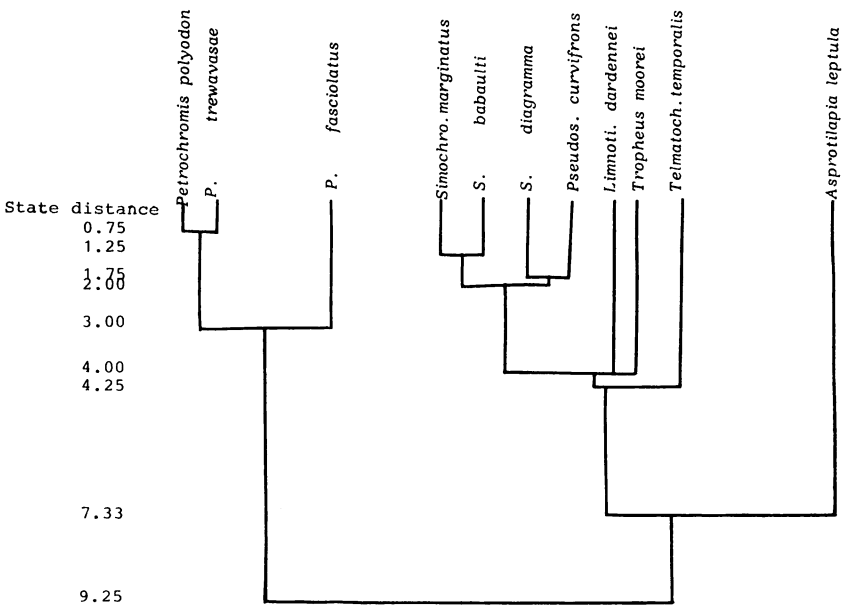


Fig. 10. Phenogram representing the clustering of 11 species of algal feeding cichlids in three types of feeding apparatus, including four subtypes. Their phonetic relationships are depicted with their state distance. Labels as in Fig. 1.

Table 7. Characters state.

Species	Ch. 1	Ch. 2	Ch. 3	Ch. 4	Ch. 5	Ch. 6	Ch. 7	Ch. 8	Ch. 9	Ch. 10	Ch. 11	Ch. 12	Ch. 13	Ch.14
(A) *Asprotilapia leptula*	1	0.5	0.5	0	1	1	1	0	0	0	1	0	1	1
(B) *Limnotilapia dardennei*	0.75	1	1	0.25	0	0.25	0.5	0.33	0.25	0	1	0.75	0.75	0.75
(C) *Petrochromis fasciolatus*	0	1	0.5	1	0.75	0.5	1	1	1	1	0	1	0	1
(D) *Petrochromis polyodon*	0	0	0.5	1	0.75	0	1	1	1	1	0	0.75	0.75	0.5
(E) *Petrochromis trewavasce*	0	0	0.5	1	0.75	0.25	1	1	1	1	0	0.5	0.75	0.75
(F) *Pseudosimochromis curvifrons*	1	1	0	0.75	0	0.5	0.5	0.33	0.5	0	0	0.75	0.5	0.5
(G) *Simochromis babaulti*	0.5	1	0	0.25	0	0.5	0.5	0.33	0.25	0	0	0.75	0.5	0.75
(H) *Simochromis diagramma*	0.5	0.5	0.5	0.75	0	0.25	0.5	0.33	0.5	0	0	0.75	0.5	0.5
(I) *Simochromis marginatus*	0.75	1	0.75	0.25	0	0.5	0.5	0.33	0.5	0	0	0.75	0.5	0.75
(J) *Telmatochromis temporalis*	1	1	0.5	0.5	0	0.5	0	0.33	0.5	0	1	0.25	0.75	0
(K) *Tropheus moorei*	0.75	0.5	0.5	1	0.75	0.5	0.5	0.33	0.75	0	0	1	0.25	0.25

* Ch. 1–Ch. 14 are the same as those reported in the Discussion section

From the results mentioned above, the following 14 characters are chosen for cluster analysis (Sneath and Sokal, 1973): 1) ascending process of premaxillary length to HL, 2) angle of Appm and dentigerous arm, 3) maxillary dorsal facet size and shape, 4) dentigerous arm length to mandible length, 5) premaxillary condyle size, 6) lim length, 7) outer teeth cuspidation, 8) corner teeth cuspidation, 9) teeth series number, 10) rostral cartilage stouthness, 11) geniohyoideus muscles length, 12) A_1 part weight, 13) A_2 part weight, 14) A_1 tendon length. From this analysis three types of feeding apparatuses are grouped as follows (Fig. 10, Table 7). The first type includes only one species, *A. leptula*. The second type includes the three species of the genus *Petrochromis*. This type can be subdivided into *polyodon-trewavasae* subtype and *fasciolatus* subtype. The remaining 7 species comprise the third type, which can be subdivided into the following three subtypes: *Pseudosimochromis-Simochromis*, *Limnotilapia-Tropheus* and *Telmatochromis* subtypes.

In comparison with Greenwood's classification, *Asprotilapia* has feeding apparatus completely different from other species of *Tropheus* type of apophysis. On the other hand, *T. temporalis*, belonging to a different apophyseal type, has feeding apparatus rather similar to most species of *Tropheus* type of apophysis.

In 1979 and 1981, I observed feeding behaviour of the 11 species in the two rocky shores by diving of about 450 hours. Precise results will be published near future, but it is clear that the three types of feeding apparatuses mentioned above are related to their feeding method as follows. *Asprotilapia leptula* continuously "tag" algae on smooth rock surface with a slightly protruded mouth. Three species of the genus *Petrochromis* browse algal film from rock by widely opening both jaws with high degree of upper jaw protrusion. The other species such as *Pseudosimochromis*, *Simochromis*, *Limnotilapia*, *Telmatochromis* and *Tropheus* graze algae on rock surface in a single bite or nip.

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