

Ecological studies on crater lakes in West Cameroon Fishes of Barombi Mbo

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(With 1 plate and 29 figures in the text)

In the West Cameroonian crater lake, Barombi Mbo, and its inflowing stream there are 17 species of fishes, of which 12, including the 11 cichlids, appear to be endemic. We give a systematic account of the endemics, including four new species and two new genera, *Konia* and *Myaka*. The ecology of the lake is described in relation to the feeding biology of the fishes, studied by underwater observation in the lake and the examination of stomach contents. The cichlids in Barombi Mbo probably evolved there from two or three ancestral populations and now show clear ecological separation in their feeding and breeding. The problem of speciation within the lake is of particular interest because of the apparent absence of physical barriers to account for the genetic isolation of incipient species.

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Introduction

Barombi Mbo is a crater lake in West Cameroon, about 35 miles north-north-east of Mount Cameroon at 9°22'E and 4°38'N. Barombi Mbo (from the Barombi word mbo, pronounced mbu, meaning a deep lake) is one of several names for the lake, which is also

known as Barombi Lake, or Kumba Lake from its proximity to the town of Kumba. Tomczek named it Elefanten-see in 1883.

The lake is clear and lies in a small forested crater. The Kake Gorge, to the south-east, carries the outflow which flows via the Kumba River to join the Mungo River. The physical geography and geology of the area around the lake have been described by Gèze (1943).

Trewavas (1962) reviewed the collections of fishes made by previous expeditions and described several new species. In March and April 1970 we visited the lake and in this paper we describe the new species of fishes that we found there, review those already known, and give an account of the ecological and evolutionary relationships of the fishes in Barombi Mbo and its inflowing stream.

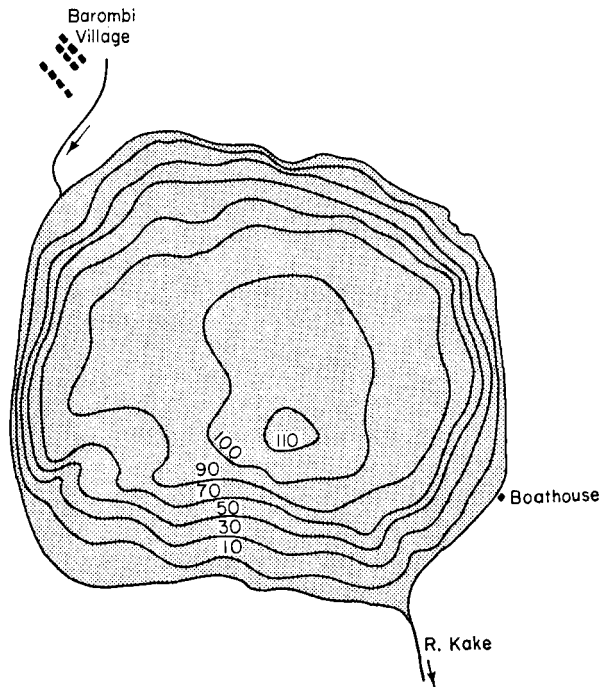


FIG. 1. Bathymetric map of Barombi Mbo (after Hassert, 1912). The isobaths are given in metres.

Systematics of the fishes

ETHELWYNN TREWAVAS

Our plans for work on Barombi Mbo envisaged ecological enquiries based on a fairly well-defined taxonomic situation. In the event there were so many additions and corrections to the earlier account of the fish fauna (Trewavas, 1962) that the fish taxonomist was kept occupied full-time on her speciality.

Briefly, the non-cichlid taxonomy was in the main confirmed, with the addition of a second species of *Clarias*, the widespread *C. walkeri*, to the lake fauna and two other cyprinodonts to that of the feeder stream. Instead of the five cichlid species recognized in 1962, we found that there were 11, all endemic.

In the first place, *Pungu maclareni*, recorded (as *Barombia*) in 1962 as from Lake Barombi Kotto, was found by Thys van den Audenaerde to have been wrongly assigned to that lake and on his personal information the record was transferred in "The Red Book" (Trewavas in Fisher *et al.*, 1969) to Barombi Mbo, where it proves to be abundant.

Our own work on the lake revealed other misapprehensions in the 1962 report. The single specimen listed by me as a possible older individual of *Tilapia eisentrauti* proves to belong to a distinct, unnamed species. The small fishes with enlarged lateral line pores placed by me as young of *Stomatepia mariae* are members of a separate species of *Stomatepia* and a third species of the same genus was introduced to us by the Barombis by the name of "mongo". Lastly it became apparent that we were confusing two species under the name of *T. linnellii* and that the second one had already been described by Holly (1930) as *T. caroli*, a name that I had wrongly placed in the synonymy of *T. linnellii*. The distinction between these two was the only one that gave us any trouble in the field, and the fishermen themselves distinguished *T. caroli* (*fissi*) only in the mature stage.

In this account I give full descriptions of the new species, define some new genera and recapitulate the diagnostic characters of the previously known endemic species, adding any new information about them. A critical account of the non-endemic species is given in a separate paper (Trewavas, in prep.).

Nomenclature

The name *Sarotherodon* Rüppell, 1852, has been used as a subgenus of *Tilapia* by Regan (1920) and recently (1968a) by Thys. Accumulating knowledge, not least of the cichlids of Barombi Mbo, points to its being worthy of full generic rank and I so use it here. This and the recognition of new genera result in the name *Tilapia* disappearing from Barombi Mbo. Regrettably, the name *Barombia* proves to be preoccupied* and I have replaced it by *Pungu*, the Barombi name.

Measurements

The abbreviation SL is the standard length of taxonomic practice, from tip of snout to base of caudal fin, excluding any projecting part of the lower jaw. The depth of the pre-orbital (=lacrima) bone is measured from the middle of its orbital rim to its oral edge, along a line that continues the radius of the eye. Since the two edges of the bone are not parallel the measurement is subject to individual bias, but some of the variation is real and may exist between right and left sides. It is also affected to some extent by allometry, but very little within the size-ranges of our cichlids. The interorbital width is measured between points of dividers pressed against the skin of the tops of the orbits and is little more than the least width of the skull roof between the eyes.

* I am very grateful to Mr G. P. Whitley for pointing this out to me.

List of species of fish from Barombi Mbo and its inflowing stream

Species	Barombi name	Systematics page	Ecology page
Cyprinidae			
<i>Barbus batesii</i> Boulenger	suh, kimbundu	44	78
Clariidae			
<i>Clarias walkeri</i> Günther	nyongo	45	78
<i>Clarias maclareni</i> Trewavas	nyongo	45	78
Cyprinodontidae			
<i>Aphyosemion oeseri</i> (Ahl in Schmidt) (inflow stream only)	—	47	
<i>Epiplatys sexfasciatus</i> Gill	longo katta	47	80
<i>Procatopus similis</i> Ahl (inflow stream only)	lenge	47	80
Cichlidae			
<i>Sarotherodon lohbergeri</i> (Holly)	leka keppe	48	80
<i>S. steinbachi</i> (Trewavas)	kululu	50	80
<i>S. linnellii</i> (Lönnerberg)	kippé, unga	52	81
<i>S. caroli</i> (Holly)	fissi, unga	54	81
<i>Myaka myaka</i> sp. n.	myaka myaka	59	81
<i>Konia eisentrauti</i> (Trewavas)	konye	61	81
<i>K. dikume</i> sp. n.	dikume	63	82
<i>Pungu maclareni</i> (Trewavas)	pungu	66	82
<i>Stomatepia mariae</i> (Holly)	nsess	68	82
<i>S. pindu</i> sp. n.	pindu	70	83
<i>S. mongo</i> sp. n.	mongo	72	83

Of the 17 species now known from the lake and its inflowing stream, 12, including all the 11 cichlids, appear to be endemic. Only *Barbus batesii*, *Clarias walkeri*, *Procatopus similis*, *Aphyosemion oeseri* and *Epiplatys sexfasciatus* are known from elsewhere.

Description of species

CYPRINIDAE

Barbus batesii

Boulenger, 1903: 25, pl. iii fig. 2; 1911: 43, fig. 24; Trewavas, 1962: 152; Trewavas, in prep.

Barbus linnellii Lönnerberg, 1904: 138.

Barombi names: suh, kimbundu (young).

CLARIIDAE

The clariids of Barombi Mbo belong to the subgenus *Clarioides* David of *Clarias*, having all the bones of the side of the head present and fewer than 20 gill-rakers on the lower part of the first arch. There are two species in the lake and (young only) its feeder stream.

Clarias walkeri

(Fig. 3(a))

Günther, 1896: 274, pl. xiv fig. B (Ogowe); Boulenger, 1911, 2: 248, fig. 206 (Ogowe, Gabon, Corisco Is., Benito R., Ja R., Cameroon); Holly, 1927: 198 (R. Sanaga and Yaoundé); Trewavas, 1962: 156, fig. 2 (stream near Barombi Kotto); Thys van den Audenaerde, 1967: 51 (Fernando Poo).

Clarias poensis Boulenger, 1908: 1078, fig. 252; Boulenger, 1911, 2: 244, fig. 203.

Barombi name: nyongo (part).

Clarias maclareni

(Figs 2 and 3(b))

C. maclareni (part., syntypes only) Trewavas, 1962: 157, fig. 3 (lower sketches).

Barombi name: nyongo (part).

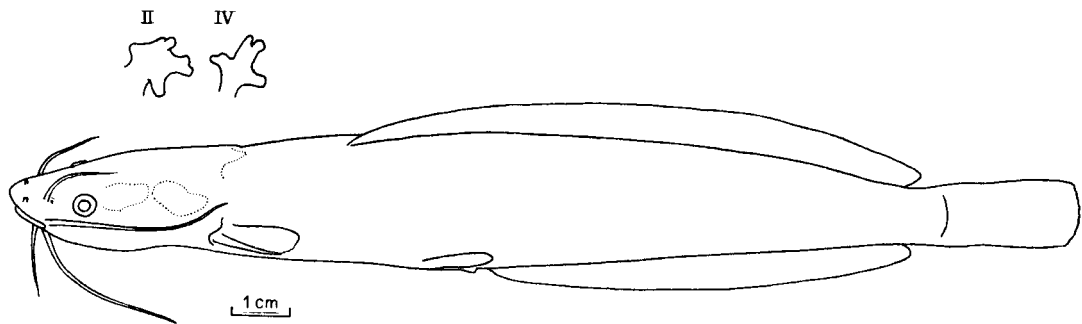


FIG. 2. *Clarias maclareni*, a specimen of 160 mm SL. Dotted lines show the positions of the postorbital and supraperopercular bones. The head is viewed from the left and a little above. Above, suprabranchial trees.

C. walkeri is the common *Clarias* of Cameroun and is reported from the Ogowe to the northwestern Cameroons, River Logone and Fernando Poo. Records from farther west are not well supported (e.g. a doubtful report in Trewavas & Irvine, 1947) and Daget & Iltis (1965) did not find it in the Ivory Coast. A single specimen in the British Museum (Natural History) from Sierra Leone so labelled is indeed very much like *C. walkeri*, although the suprabranchial tree of epibranchial II is less developed than in *C. walkeri* of the same size.

C. maclareni is peculiar to Barombi Mbo, its only close relation being the form from Lake Soden to be described by Griffith (in prep.). Other West African clariids in the British Museum (Natural History) with the bones of the side of the head loosely connected have small eyes and less reduced suprabranchial trees than *C. maclareni*.

The fishermen did not distinguish between *C. walkeri* and *C. maclareni*, but the species are fairly easily distinguished at sight by the size of the eye, smaller in *C. walkeri*. Determination can be confirmed by examining the suprabranchial trees and the bones of the

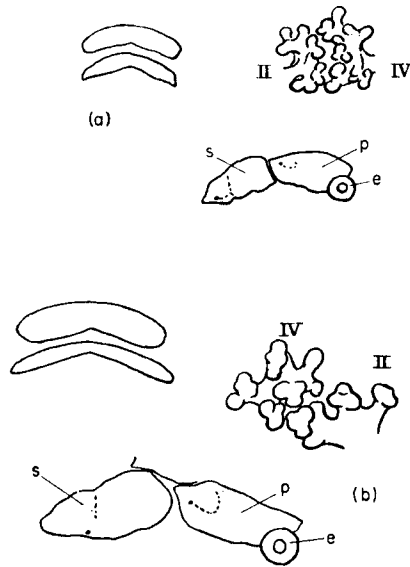


FIG. 3. (a) *Clarias walkeri*, holotype of 151 mm SL, shape of premaxillary and vomerine tooth-patches, supra-branchial trees of left side and postorbital and suprapreopercular bones of right side. (b) The same for the holotype of *C. maclareni*, a specimen of SL 222 mm. From Trewavas, 1962. e, Eye; p, postorbital; s, suprapreopercular.

side of the head, especially if specimens of the same size are compared (Table I and Figs 2 and 3). These two features remain the most reliable distinguishing characters.

The vomerine teeth form a continuous band at all sizes examined and in *C. maclareni* the band is narrower in the middle. The width proves to be variable in *C. walkeri*, so that the width of the band is not a very reliable distinguishing feature. The nature of the union of the bones of the side of the head usually provides a contrast between the two species within the lake basin, but in some *C. walkeri* from the River Wowe and the River Kumba the postorbital and suprapreopercular meet tangentially or are separated by fibrous tissue. The gill-raker count in *C. maclareni*, 9–13 on the lower part of the first arch, also provides no contrast with *C. walkeri*.

TABLE I
Distinctions between Clarias walkeri and C. maclareni

	<i>C. maclareni</i> N=15	<i>C. walkeri</i> N=15 (9 from Mbo, 6 from elsewhere)
Standard length (mm)	114.5–222.5	107–319
Diameter of eye		
As % length of head	9.5–11.8	6.5–9.5
As % interocular width	20.0–25.0	13.0–19.5
Suprabranchial trees	Relatively simple	Elaborate
Union of postorbital and suprapreopercular	Tangential or not quite meeting	Sutural or tangential

The poor development of the suprabranchial trees in *C. maclareni* may be related to lacustrine life, where there is no need to have recourse to air-breathing (cf. the endemic clariids of Lake Malawi, Greenwood, 1961) and perhaps the bigger eyes are more efficient aids to the pursuit of mid-water prey like dikume and myaka myaka (see p. 80) than the barbels with their organs of touch and chemical sense on which most clariids seem to place greater reliance. Unfortunately we did not note the species from whose stomachs these frequenters of deeper waters were recorded.

One specimen of *C. maclareni* had no eyes, and in another the right eye was gone. In both cases the skin had healed over the eye sockets, but there was a pit showing that the socket was as big as that for a normal eye. No doubt some predator had removed the missing eyes.

CYPRINODONTIDAE

Aphyosemion oeseri

Panchax oeseri Ahl in Schmidt, 1928: 165, fig. on p. 166 (Fernando Poo).

Panchax vexillifer Meinken, 1929: 255, fig. ("Westküste Afrikas").

Aphyosemion santa-isabellae Scheel, 1968b: 332, fig. 1 (Fernando Poo).

Aphyosemion santaisabellae; Foersch, 1971: 20, 4 figs.

Aphyosemion oeseri; Trewavas, in prep.

No Barombi name known.

Epiplatys sexfasciatus

Gill, 1862: 136 (Gaboou River); Trewavas, 1962: 159 (Lake Kotto and Barombi Mbo); Scheel, 1968a: 383, figs; Trewavas, in prep.

Haplochilus infra fasciatus Günther, 1866: 313 (Old Calabar); Lönnberg, 1903: 39 (River at Sanye, near Lake Kotto).

Barombi name: longo katta.

Procatopus similis

Ahl, 1927: 79 ("Logobaba, Kamerun"); Trewavas, in prep.

Barombi name: lenge.

CICHLIDAE

Structure of the ovaries

We found eggs and young in the mouths of parents of only one species, *Sarotherodon linnellii*, in which the mother was the brooding parent in all of the eight instances.

In two cichlid species we found no certainly ripe eggs, *Myaka myaka* and *Konia dikume*, but in all the others (*S. caroli* from previously collected specimens only) we found one or more females with large, green, oval eggs nearly ready to be shed.

Many other ovaries were in the stage described as "starting", in which distinct oocytes could be seen with the dissecting microscope. The oocytes ranged from minute, colourless transparent ones to cream-coloured or yellow spheres from 0.5 to 3.0 mm diameter. In some there was a fairly smooth gradation in sizes, but usually there were two or three size-groups, possibly representing two or three future spawning-cycles.

As well as the oocytes there were amorphous bodies coloured bright rust-red or yellow. As these are generally fewer, smaller or absent in ripe ovaries we think they may be nutrient bodies developed in some of the follicles at the expense of the oocyte. They are apparently the same as bodies described by Bretschneider & Duyvené de Wit (1947) and Hoar (1957) in *Rhodeus* as "preovulation corpora lutea" or "corpora atretica". As there is no evidence for a hormonal function nor any close analogy with the corpora lutea of mammals we do not use the former term, and although the latter may be more appropriate too little is known about the development of the bodies in our species for us to feel happy in using it. We refer to them as "amorphous bodies".

The surface of eggs from the mouth of *S. linnellii* bears sparsely distributed bunches of filaments, like those figured for *S. galilaeus* by Kraft & Peters (1963). Examination with the electron scanning microscope of ripe ovarian eggs of *S. lohbergeri*, *St. pindu* and *Pungu* revealed no filaments, but no conclusion can be drawn from this until discharged eggs can be compared.

TABLE II
Vertebral numbers and long diameter of largest ovarian eggs in Cichlidae of Barombi Mbo

	Vertebrae					Diameter of eggs (mm)
	27	28	29	30	31	
<i>Sarotherodon steinbachi</i>			7	8	1	3.6
<i>S. lohbergeri</i>			4			4.5
<i>S. linnellii</i>			15			5-5.5
<i>S. caroli</i>			3	1		5-5.5
<i>K. eisentrauti</i>			5			4
<i>K. dikume</i>			5			?
<i>Pungu maclareni</i>			7			4
<i>Myaka myaka</i>			1	6		?
<i>Stomatepia mariae</i>	1	6				4
<i>S. pindu</i>		9	2			4
<i>S. mongo</i>		7				4.5-5

Testes

Although we handled many ripe and ripening females, we found no males with very large testes such as I have seen for instance in the males of mouth-brooding species in Lake Malawi. I have followed this observation with no quantitative or histological data, but it seems worth while recording it in view of the fact that Heinrich (1967: 724-725) records otherwise unpublished data of Peters showing that in *Sarotherodon melanotheron* ("heudeloti") and *S. galilaeus* the weight of the testis is relatively lower than in *S. niloticus* and *S. mossambicus*, one of a number of characters distinguishing these two pairs of species from each other.

Sarotherodon lohbergeri

(Figs 4 and 5)

Tilapia lohbergeri Holly, 1930: 203, pl. ii fig. 10; Trewavas, 1962: 171, fig. 7. Holotype: 89+23 mm, Vienna Mus. 13951, coll. Haberer, "Cameroun".

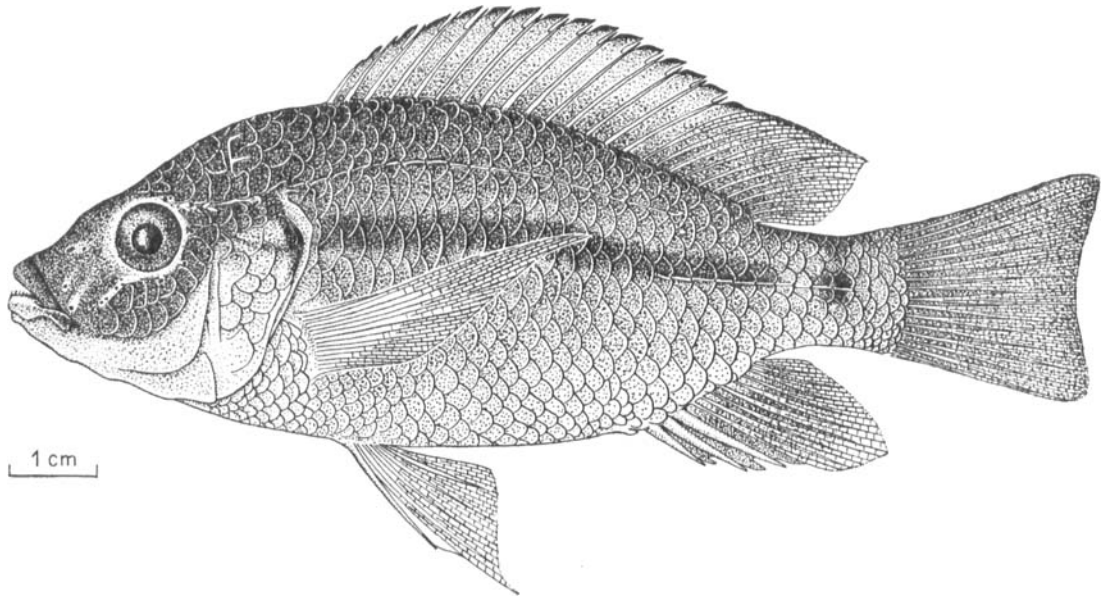


FIG. 4. *Sarotherodon lohbergeri*, a specimen of SL 162 mm.

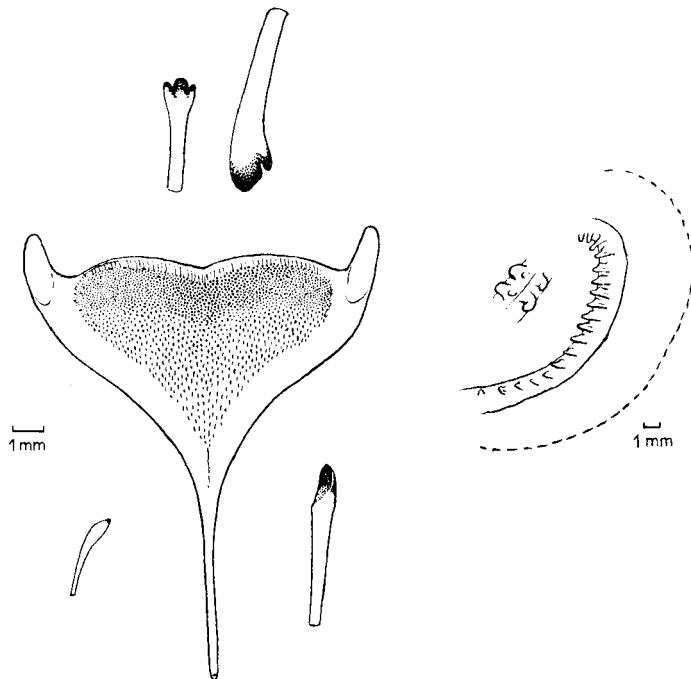


FIG. 5. *Sarotherodon lohbergeri*, inner and outer jaw teeth; lower pharyngeal bone and isolated anterior and posterior teeth; first gill-arch and oral view of two inner and two outer gill-rakers; the inner rakers have a subsidiary tubercle. In part from Trewavas, 1962.

Barombi name: leka keppe.

This species is easily recognized in life and when freshly caught by the prominent black band extending from the opercular spot to the caudal peduncle. When preserved there is also an upper band between the dorsal fin and the upper lateral line. At all times it is distinguished from *K. eisentrauti* and *S. steinbachi* by the acute snout and the terminal mouth with rather thick lips. The young of about 30 mm SL have pearly iridescent bodies with no stripe (but the stripe may appear in preserved young) and their pelvic fins and the anterior edge of the anal are orange to vermilion.

Closer examination reveals the characteristic movable teeth of the jaws, in four to seven rows in adults and already three or four rows in young of 27–34 mm. The shafts are slender and the expanded crowns are spoon-shaped with a lateral notch in the outer row, tricuspid in the inner rows. This dentition corresponds to the method of feeding described on page 80 and has evolved several times in African Cichlidae—in *Tilapia mariae*, in the subspecies of *S. nilotica* in Lake Rudolf, in *Neotilapia* (Lake Tanganyika), *Petrochromis* and *Petrotilapia*. These are unrelated to *S. lohbergeri* and to each other; in some, but not in *S. lohbergeri*, the outer teeth may become tricuspid, either in the adult or throughout life. In most of them the pharyngeal teeth are fine, unicuspid and close-set on broad tooth plates, as they are in *S. lohbergeri* (Fig. 5).

The intestine of a fish of 86 mm SL measures 410 mm, 4·8 times the standard length.

A fish of 78 mm SL contained green ovarian eggs of 4·5 mm long diameter, 13 in the right ovary, 27 in the left. Two of 73·5 mm and 83 mm had eggs of 4·0–4·2 mm; in the 73·5 mm fish there was a total of 46 eggs, 23 in each ovary. Many ovaries contained yellow and rust-red amorphous bodies as well as small oocytes of two sizes, the larger cream-coloured and up to 2·5 mm diameter. At 3·0–3·5 mm the oocytes were already turning green.

We observed no mating or parental behaviour, but eggs of this size must surely be incubated in the mouth. This is supported by the evidence of Dr Pasqual (quoted by Trewavas, 1962) that in aquaria they are mouth-brooders; he had the impression that both parents carried the larvae in this way. Biparental care is consonant with the lack of external differences between the sexes.

The species in the River Kumba

Two young Tilapias of 24·5 and 30 mm SL were caught by Dr R. H. L. Disney in narrow-meshed traps in the River Kumba at Buea Road bridge, just below the town of Kumba. These agreed very well with young *S. lohbergeri* in colour, having in life no black markings (no tilapia-mark), but vermilion pelvic fins, anterior edge of anal and lower edge of caudal; there were three rows of teeth in the jaws and the numbers of dorsal rays (XVI 11 and XVII 10) and gill-rakers (respectively 14 and 16 on the lower part of the first arch) are within the ranges of *S. lohbergeri*. The significance of this find is discussed on page 85.

Sarotherodon steinbachi

(Figs 6 and 7)

Tilapia steinbachi Trewavas, 1962: 178, fig. 10, 11.

Holotype and paratype: BMNH 1961.10.18.40–41, respectively 113 and 90 mm SL, collected by Professor Eisentraut's expeditions.

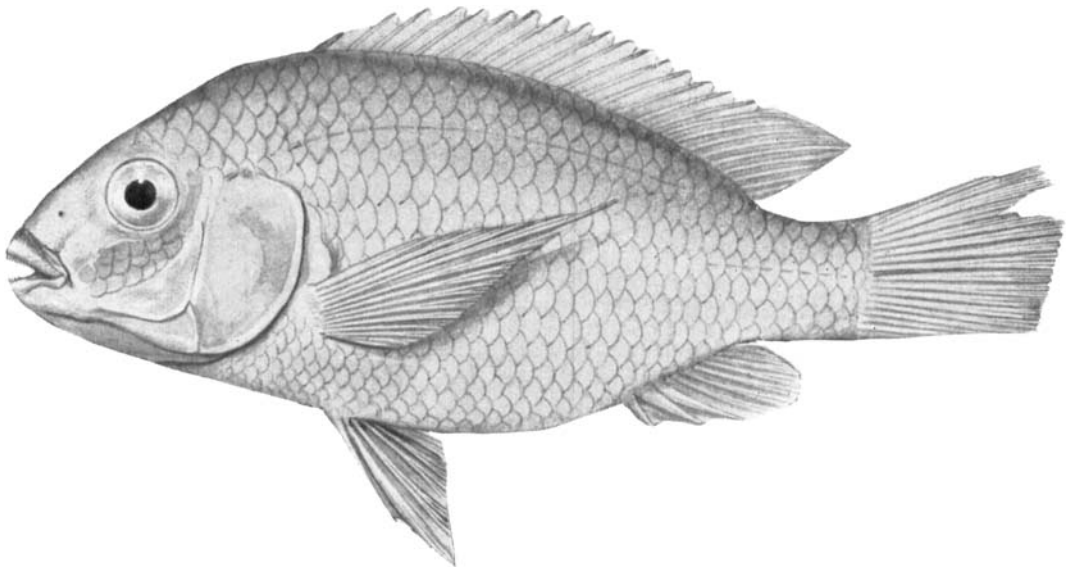


FIG. 6. *Sarotherodon steinbachi*, holotype.

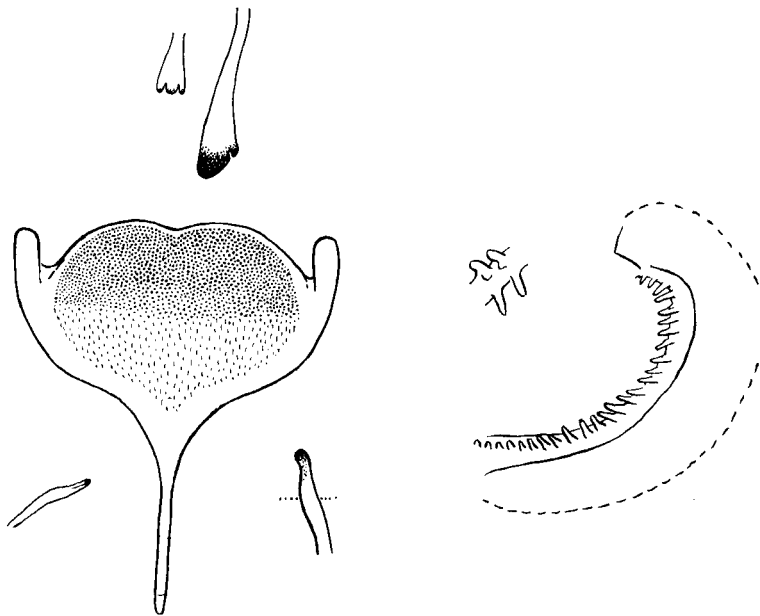


FIG. 7. *Sarotherodon steinbachi*. Inner and outer jaw teeth and lower pharyngeal bone with two of its teeth; first gill-arch and oral view of two inner and two outer gill-rakers. In part from Trewavas, 1962.

Barombi name: kululu.

When alive or freshly caught this species had no black band along the body or at most a very vague one, but this vague band is present in most preserved specimens. There is no tilapia-mark at the sizes seen, except in the smallest, a fish of 39.5 mm SL, in which it is grey and rather ill-defined. We found no sexual differentiation in colour.

Kululu is recognisable by the very small mouth and rather abruptly decurved snout profile, the Roman-nose-like appearance being produced by the projecting premaxillary pedicels, so placed in using the upper jaw to rake bottom deposits into the mouth.

Further diagnostic features are the very small teeth of the jaws, usually in three, rarely two or four series; the short gill-rakers, 18–23 on the lower part of the first arch; and the massive pharyngeal bones, whose length (including the anterior blade) is nearly half that of the head (45.0–49.5%) in adults. The condition of the slender pharyngeal teeth of the type as described in 1962 proves to be characteristic, the complete brown-tipped ones being interspersed with shorter teeth whose brown tips are worn off. The cause of this, deduced from the stomach contents of the types, is confirmed by the observations of Professor Green and Dr Corbet (p. 81). In the young fish of 39.5 mm this wear had not started.

The intestine, coiled seven to nine times, measures 350–460 mm in two fishes of 75 and 77 mm SL, 4.7–6.0 times the standard length.

Green ovarian eggs in a fish of 84 mm SL measured 3.6 × 3.0 mm. With them were small white oocytes but no red and yellow amorphous bodies; they were probably nearly ready to be shed. The eggs are already green when the long diameter is 2.6 mm and the ovaries then contain several coloured amorphous bodies.

We have no information on mating or parental behaviour.

Sarotherodon linnellii (Lönnerberg) and *Sarotherodon caroli* (Holly)

Barombi names: kippé, unga and fissi, unga, respectively.

In 1962 I regarded these as one species, but experience at the lakeside, attention to the opinions of the Barombi fishermen and subsequent analysis of about 40 specimens of each have persuaded me that there are two and that the two scientific names already available apply to them respectively. They are distinguished as follows.

Sarotherodon linnellii

(Figs 8, 9(a)–(c) and 11(b))

Tilapia (Gephyrochromis) linnellii Lönnerberg, 1903: 42.

Tilapia linnellii; Boulenger, 1915: 159, fig. 104.

Tilapia linnellii (in part); Trewavas, 1962: 174, figs 8, 9.

(1) An intense black tilapia-mark present on the dorsal fin in the young from the stage when they are still in the maternal mouth until they reach a SL of about 100 mm, after which it becomes vaguer in outline and fainter; it may be absent altogether above SL about 120 mm or may still be recognisable at SL 150 mm.

(2) Dorsal spines (XIV) XV or XVI, mode XV. Modal formula XV 12 (Table III).

(3) Gill-rakers on lower part of anterior arch 15–18, mode 17 (Table III).

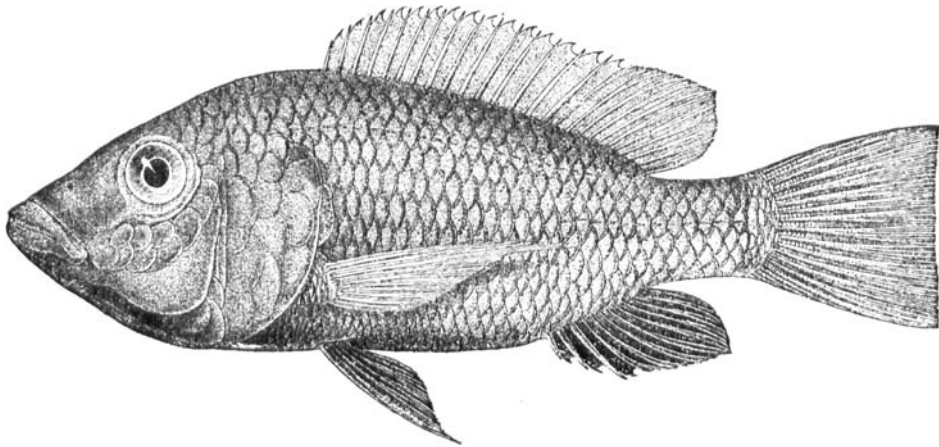


FIG. 8. *Sarotherodon linnellii*, one of the syntypes, a kippé, (from Boulenger, 1915, fig. 104).

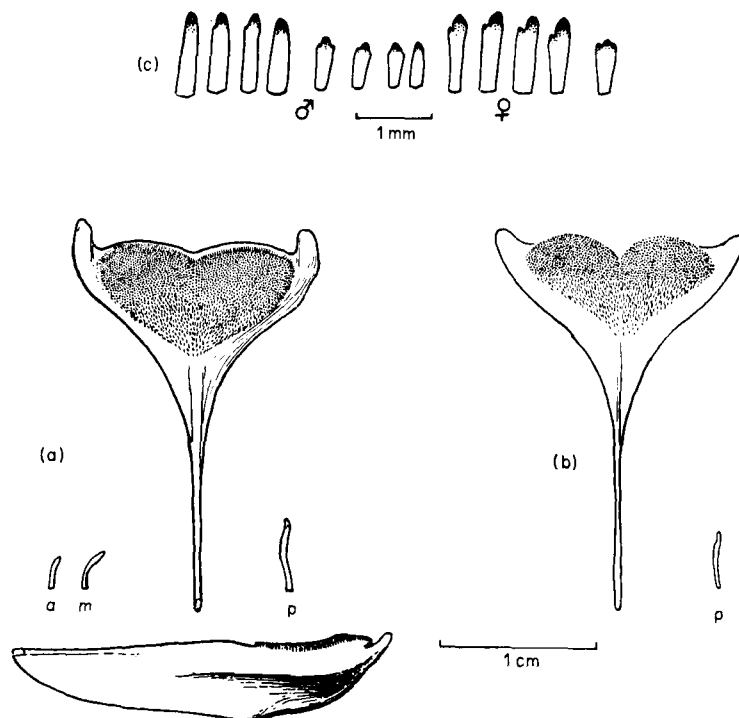


FIG. 9. Lower pharyngeal bones of, (a) *S. linnellii* of SL 150 mm and, (b) *S. caroli* of SL 143 mm with a posterior tooth (p) of each and anterior (a) and middle (m) teeth of *S. linnellii*. (c) Outer and inner jaw teeth of male and female *S. linnellii*.

- (4) Diameter of eye in young of 60–91 mm SL 28–31 % of length of head.
 (5) Blade of lower pharyngeal bone in young of 64–83 mm SL 0·8–1·8 times median length of dentigerous area, in bigger fishes more than twice as long.
 (6) Teeth of jaws and pharynx very small, but always a little bigger than in *S. caroli* of the same size.
 (7) Breeding males green.

TABLE III
Frequencies of meristic numbers in Sarotherodon linnellii and S. caroli

	<i>S. linnellii</i>	<i>S. caroli</i>
Dorsal formula		
XIV 12	1	—
XV 11	13	3
XVI 10	1	1
XV 12	23	13
XVI 11	3	17
XVI 12	—	4
Dorsal spines		
XIV	1	—
XV	36	16
XVI	4	22
Dorsal totals		
26	15	4
27	26	30
28	—	4
Soft anal rays		
8	1	—
9	17	9
10	13	16
11	2	4
Vertebrae		
29	15	3
30	—	1
Gill-rakers on lower part of arch		
15	3	—
16	13	—
17	21·5	2 (juveniles)
18	3·5	11·5
19	—	13·5
20	—	10

Sarotherodon caroli

(Figs 9(b), 10 and 11(a))

Tilapia caroli Holly, 1930: 204, pl. ii fig. 11.

Tilapia linnellii (in part, not of Lönnberg); Trewavas, 1962: 174.

- (1) No tilapia-mark on dorsal fin, at least at SL 62 mm and over.
 (2) Dorsal spines XV or XVI, mode XVI. Modal formula XVI 11.

- (3) Gill-rakers on lower part of anterior arch 18–20 (rarely 17 in juveniles), mode 19 (Table III).
- (4) Diameter of eye in young of 62–99 mm SL 21·5–27·6 % of length of head.
- (5) Blade of lower pharyngeal bone always more than twice the median length of the dentigerous area, at least at SL 62 mm and over.
- (6) Teeth of jaws and pharynx even smaller than those of *S. linnellii* of the same size.
- (7) Breeding (or spent?) males grey with black or dirty grey smudges.

Teeth of jaws

In both species the young have bicuspid outer and tricuspid inner teeth, and females retain the cusps in the inner and in all but a few posterior teeth of the outermost series. But in sexually active males the outer teeth become replaced by unicuspid and in some of the larger males some or all of the inner teeth are unicuspid, the anterior as large as the outer.

In *S. linnellii* the unicuspid replacement teeth are usually fewer than the bicuspid of a female of the same size, as the following figures show.

Upper outer teeth in 10 females of SL 135–150 mm: 90–116.

Upper outer teeth in 10 males of SL 139–163 mm: 70–86.

The change to unicuspid teeth was less complete in the males of *S. caroli* at our disposal than in those of *S. linnellii*. In most specimens, at least some outer teeth retained a shoulder representing the minor cusp, and the numbers were not reduced. Thus of seven females of SL 95–145 mm, one had only 80 teeth in the outer series of the upper jaw, but some gaps; the others had 100–124; of 15 males, 6 had 80–96 and the rest 100–118. In *S. caroli* too we have none with unicuspid inner teeth.

In both species the teeth are small, but they are smaller in *S. caroli* and slightly more numerous.

Lower pharyngeal bone (Fig. 9)

In 1962 I recorded that although the blade of the lower pharyngeal bone in the adult (94–148 mm SL) is 2·4–2·8 times the median length of the dentigerous area, in the young of 50–59 mm these lengths are about equal.

The first indication that we were dealing with two species came from young of an intermediate size, 62–85 mm. Some of these had no tilapia-mark and in them the blade of the pharyngeal was of the same relative length as in the adult. This pointed to the taxonomic importance of the tilapia-mark in small individuals of these species and we then found different modal numbers of gill-rakers and fin rays associated with the presence or absence of the tilapia-mark and used these, especially the gill-raker counts, to separate adults in which the tilapia-mark was no longer a reliable guide.

The pharyngeal proportions distinguishing the two species are:

blade/dentigerous area at SL 64–95 mm	
in <i>S. linnellii</i> :	0·8–1·8 [10]
in <i>S. caroli</i> :	2·1–3·0 [8]
at SL 102–147 mm	
in <i>S. linnellii</i> :	2·0–2·5 [12]
in <i>S. caroli</i> :	2·3–2·8 [12]

[In square brackets are the numbers of specimens used.]

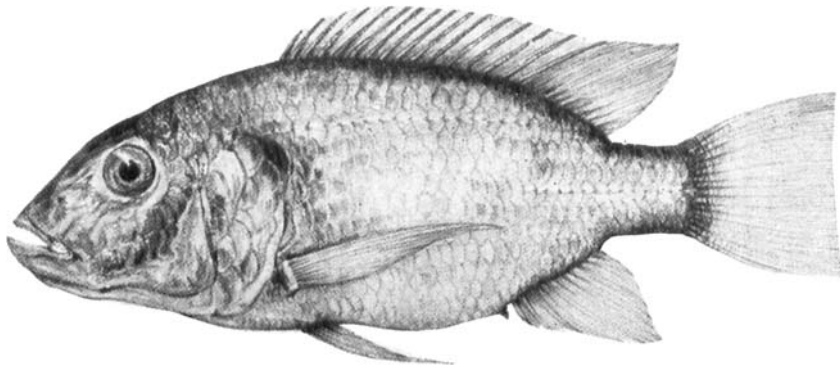


FIG. 10. *Sarotherodon caroli*, holotype, (from Holly, 1930, pl. ii, fig. 11).

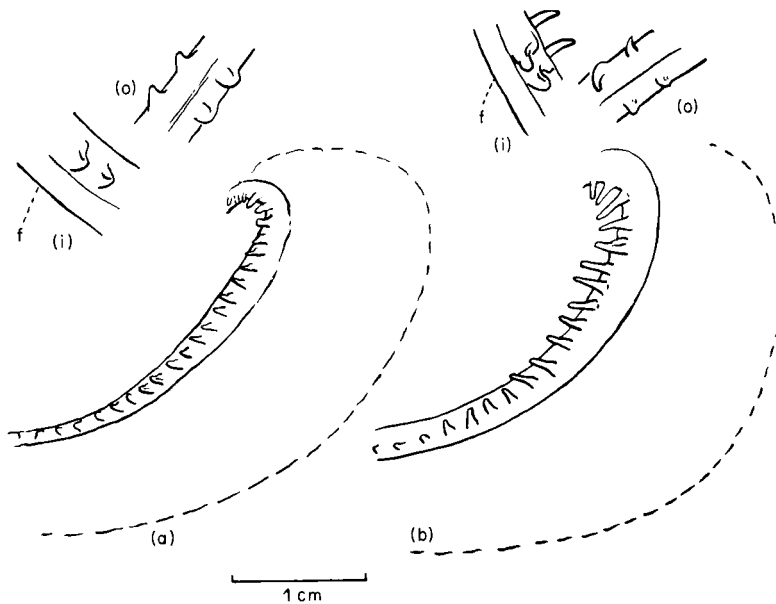


FIG. 11. Gill-rakers of first arch in, (a) *S. caroli* of SL 130 mm and, (b) *S. linnellii* of 135 mm. A broken line shows the outline of the gill. (i) Inner (posterior) view of an upper part of ceratobranchial. (o) Oral view of a lower portion: f, Line of attachment of gill-filaments.

This difference is more marked in young than in adults. In both species the pharyngeal teeth are very slender and the posterior ones, are densely crowded, but in specimens of the same size they are smaller and denser in *S. caroli* and the triangular area of the bone has a great space bare of teeth (Fig. 9(b)).

These differences are too subtle to be used alone for diagnosis but are confirmatory when used with the more obvious ones.

Functionally the higher number of gill-rakers and the longer pharyngeal blade in *S. caroli* are parts of the means by which the capacity of the pharynx is enlarged. The addi-

tional gill-rakers do not make a more efficient filter because they are spaced along a longer arch. They are in fact shorter than those of *S. linnellii* (Fig. 11) and as Greenwood (1953) showed for *S. esculenta* filtering is a function to which tilapiine gill-rakers are poorly adapted. The rakers of all the arches interlock to form a fairly solid floor to the pharynx when the arches are adducted. When the pharynx is expanded water and the fine plankton that forms most of the food of these species (see p. 81) can pass freely between the arches and the minute food organisms are captured in mucus, helped perhaps by the micro-branchiospines that are present as usual along three of the arches.

In addition to allowing a large volume of water to be passed through it, it may be that the functional significance of the enlarged pharynx is the retention of the young in the maternal mouth to a larger size than in most species. I make this suggestion by analogy with *S. lidole* of Lake Malawi, which in its large head and long pharyngeal blade parallels *S. caroli* so closely, and which harbours young to a total length of 40–60 mm.

Barombi names

The Barombis used three names for these two species: unga, fissi and kippé. Individuals in breeding colours they distinguished as fissi (*S. caroli*) or kippé (*S. linnellii*); and juveniles of both species, which look very much alike except for the tilapia-mark, they classified together as unga.

The name kippé was used for fishes usually with a large amount of brassy yellow or yellow-green in the lower half of the head and body and with the body tapering away from the back of the head to the tail. Some of these had intense black areas ventrally from the tip of the lower jaw backwards to the anal fin; in others this area remained brassy. Both shape and colour were taken into account in applying the name kippé. Most of these, and all with the most brilliant colour, proved to be males in some stage of sexual activity with at least the outer teeth unicuspid. But a few were females, one with eggs in the mouth; these had a more silvery general colour with a little greenish iridescence on the preorbital, and it was mainly the shape that caused them to be classed as kippé. Only the largest of these "female kippé" had a few of the outer teeth unicuspid. We are not sure whether the fishermen regarded kippé as a phase of unga or as a separate species.

The male kippé, when preserved, were a good match for the type of *S. linnellii* and in their meristic characters and pharyngeal dentition we could find no reason to regard them as specifically distinct from the silver-grey female unga, including those brooding eggs or young. Confirmation of this (and of the variability of the tilapia-mark at breeding sizes) comes from Dr Corbet's observation of a green kippé with a tilapia-mark courting a grey fish without a tilapia-mark.

One "young kippé" of SL 105 mm proved, however, to have the meristic characters of *S. caroli*; its testes were still small.

On dissection most of the kippé proved to have little food in the gut and much fat among the viscera.

The name fissi began to be used more frequently towards the end of the second week of our visit and was then applied to males of about 130 mm SL upwards, mainly caught in nets, grey in colour with irregular dark grey or black smudges on the lower parts of the head and body and with the snout and dorsum black. We were not sure whether the testes were ripening or recently spent. These fishes had the characters of *S. caroli*.

Although we offered special inducement, no one was able to find a female fissi for us. The females of *S. caroli* in our collection were all juveniles, not recognised by the Barombis as fissi.

On returning to the British Museum (Natural History) I found that in Maclaren's collection made in September, 1948, there are three females of *S. caroli*, one of them, 141 mm in SL, with ovarian eggs 5.5 mm in long diameter.

Breeding

The data in the preceding paragraphs suggest that the form of isolation that now keeps these two extremely similar species apart is a difference in the time (and place?) of breeding, possibly reinforced by a different breeding colouration in the male. This need not involve a rigid annual breeding season, but simply a non-synchronisation of breeding and feeding cycles between the two species. A ripe female *S. linnellii* was collected by Dr C. A. Wright in November 1963, and although specimens of *S. caroli* were present in his collection too their gonads were in an earlier phase.

In both species right and left gonads are about equal in size; the eggs are large, 5.0–5.5 mm in long diameter, and oval. In *S. linnellii* they are green (colour unknown in *S. caroli*). In the right ovary of *S. caroli* of 141 mm SL there were 29 ripe eggs, in that of a *S. linnellii* of 140 mm 35; two *S. linnellii* of 150 and 155.5 mm SL had respectively 68 and 62 ripe eggs in the right ovary. These figures are not enough to establish a specific difference in fecundity.

The surface of the egg bears bunches of minute filaments similar to those figured for *S. galilaeus* by Kraft & Peters (1963, fig. 26(e)).

Our collection includes eight brooding *S. linnellii* of SL 118–163 mm, all females, three of them with young in the mouth, the rest with developing eggs. The young measured 13.5–13.7 mm in SL and 17 mm in total length and already had a large black tilapia-mark. The ovaries of brooding females contained opaque, cream-coloured oocytes of 0.7–2.0 mm and smaller translucent oocytes, as well as rust-red and yellow bodies of irregular shape. Fat-bodies among the viscera were unusually large. We deduce that two or more breeding cycles would have followed the one just in its last phase.

As recorded on page 81, unga exhibiting territorial and courting behaviour were common near the shore and we deduce that whereas adult *S. linnellii* feed in mid-water offshore, they come inshore to mate and brood the young.

The largest *S. caroli* in our collections is a male of SL 148.5 mm; we have females nearly as long. Of *S. linnellii* the largest mature male is one of the syntypes, 163 mm in SL, and we have females up to the same size. In addition we had a large unga of SL 185 mm. This was a silver-grey fish with a little green iridescence on the preorbital and the back and with fins of a watery yellow-green colour. It was in good condition with food in the gut and much fat among the viscera. It was apparently male, but the genital papilla was very small and the gonads were as thin as in a juvenile.

This has its parallel among the tilapias of Lake Malawi, where similar large, fat specimens of *S. squamipinnis* were given a special name, *ngongo*, and on examination proved to have minute inactive gonads.

This largest of the unga had all the outer teeth of the jaws bicuspid, evidence that replacement by unicuspid teeth in the active males is a function of breeding condition and not of mere size.

Myaka gen. n.

Type-species: *Myaka myaka* sp. n.

The tautonymous generic and specific names together constitute the Barombi name for this species. We were corrected if we referred to it as "myaka". The "y" is pronounced as a consonant.

Cichlid fishes of small size with 28–29 vertebrae (mode 29), the mesethmoid free from the vomer, with the facet for the upper pharyngeals weakly developed, not including the basioccipital; scales cycloid, with concentric circuli. Teeth of the jaws few, the inner minute and tricuspid, outer with the minor cusp reduced or absent; teeth of the pharynx also reduced in number and size; lower pharyngeal bone with long blade and restricted dentigerous area. Mouth at an angle of about 50° with the horizontal, the lower jaw usually slightly projecting; gill-rakers short, 19–23 on lower part of first arch; intestine about $1\frac{2}{3}$ times the SL. Gonads paired.

Relationship to *S. linnellii* and *S. caroli* is suggested by the shape of the lower pharyngeal (cf. Figs 9 and 13).

A single species, confined to Barombi Mbo.

Myaka myaka sp. n.

(Figs 12 and 13)

Holotype a mature ♂ of 65+14 mm. BMNH 1971.10.20.34.

Paratypes 15 specimens of 44.5–66.5 mm SL. BMNH 1971.10.20.35–49.

Barombi name: myakamyaka.

Proportions as % SL

Depth of body 32.0–35.5; length of head 37.0–44.0; length of pectoral fin 27.0–32.5, of caudal peduncle 14–17 (1.05–1.3 times its own depth).

Proportions as % length of head

Length of snout 27–33, diameter of eye 23–29, depth of preorbital 17.5–22 (usually 19.0–21.5), interorbital width 26–31, length of lower jaw 33–39, usually 35–37 (33 is the percentage of a very long head, 39 of a short one), length of premaxillary pedicels 22–26, length of lower pharyngeal bone 33.3–37.5, its width 24.5–26.5.

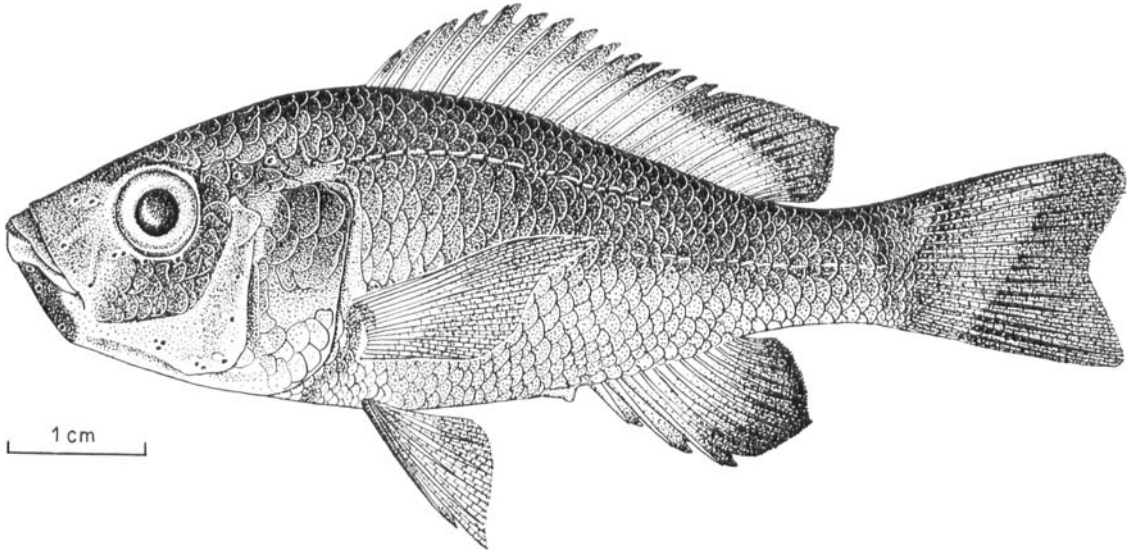
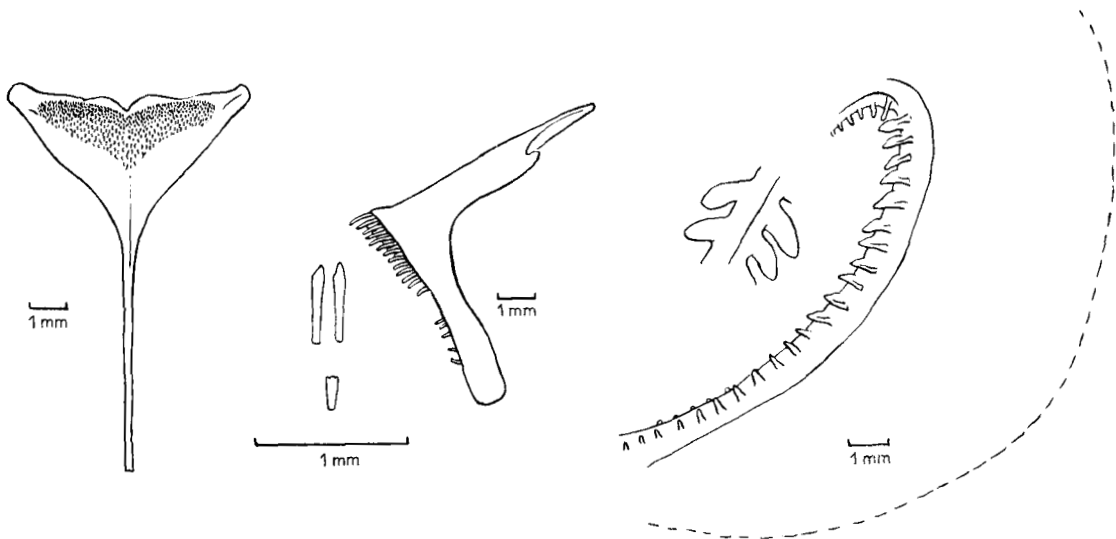
Pharyngeal teeth very weak, confined to a short posterior area whose length is contained 3.5–5.3 times in the length of the blade.

Teeth of jaws very small, in two series, the inner tricuspid, outer either simple or with a very small minor cusp; when simple either truncate, so probably simple by wear, or conical or near conical apparently by replacement; anterior teeth directed forwards, with a gap at the symphysis; 24–42 teeth in outer series of upper jaw.

Gill-rakers short, (3–6)+(0–1)+(19–23) on the anterior arch. Microbranchiospines present on outer sides of 2nd, 3rd and 4th arches.

Scales 29–37 in the lateral line series, 4–5 from origin of dorsal fin to lateral line, 16–19 around caudal peduncle. When, as in several, there are more than 31 or 32 in the l.l. series this is because the rows above and including the lateral line are irregular.

Dorsal with 25–27 rays, usually 26 or 27. Formulae XV 10 (f.2), XIV 12 (f.3), XV 11 (f.5) or XV 12 (f.7).

FIG. 12. *Myaka myaka*, holotype.FIG. 13. *Myaka myaka*, dentition of jaws, lower pharyngeal bone and gill-rakers of first arch, with oral view of two inner and two outer rakers from the upper part of the ceratobranchial.

Anal III 8 (f.1), III 9 (f.18) or III 10 (f.7).

Pelvics reaching anus or genital papilla.

Colour watery grey or greenish grey, usually with yellow pelvic fins. No tilapia-mark.

Size. Known only at the size-range of the paratypes.

Breeding

The holotype was the only male seen by us with advanced gonads. The testis was 1.7 mm wide, but its anterior third was narrower. It was feeding and there were fat-bodies

among the viscera; there was more black pigment about the head and body than in any other. In the females the ovaries were all very short, at the hind end of the abdomen, and contained very few oocytes and some amorphous bodies. In a fish of 60 mm SL, examined when preserved, the right ovary contained a single, not quite spherical, orange-coloured body that may have been a nearly ripe egg; two similar bodies were in the left ovary and both ovaries contained a few much smaller oocytes.

I think it possible that in this species the eggs are smaller and fewer than in other cichlids of Barombi Mbo. The fact that in several there was little material in the gut, the viscera were packed with fat and the genital papilla was swollen suggests that they were preparing to breed or recently spent. If this interpretation is correct *Myaka myaka* is a species of low individual fecundity. Nothing is known about its parental habits.

Konia gen. n.

Type species: *Tilapia eisentrauti* Trewavas = *Konia eisentrauti*.

Konia from the Barombi name of the type species—konye.

Resembling *Tilapia* and *Sarotherodon* in having the apophysis on the base of the skull for the upper pharyngeals formed from the parasphenoid alone a ventral apophysis on the 3rd vertebra, cycloid scales with concentric circuli and in the outer bicuspid and inner tricuspid teeth of the jaws; but differing from them in the narrower interorbital space (23.5–28.3 % length of head), the shorter intestine ($1\frac{1}{4}$ – $1\frac{1}{2}$ times the SL of the fish) corresponding to a more carnivorous diet, and the absence of a “tilapia-mark” at the junction of spinous and soft parts of the dorsal fin.

It resembles the genus *Sarotherodon* in having the mesethmoid free from the vomer, in the large eggs (4 mm diameter in the type species) presumably brooded in the mouth of one or both parents, fine pharyngeal teeth, the lower on a bone whose anterior blade is 0.7–1.5 times the length of the toothed area, and gill-rakers numbering 14–17 on the lower part of the first arch.

Vertebrae 29.

Within *Sarotherodon* it resembles none so much as *S. lohbergeri*, its companion in Barombi Mbo, but this, in addition to having a *Sarotherodon*-like interorbital width and a long intestine, has a very distinct dentition.

Konia eisentrauti

(Figs 14 and 15)

Tilapia eisentrauti Trewavas, 1962: 168, fig. 5A, 6A.

T. (Pematolapia) eisentrauti; Thys, 1968: xxviii.

Barombi name: konye.

The “dubious specimen” whose description was appended to that of this species in 1962 is now known to be a dikume (*K. dikume*).

K. eisentrauti is recognised in the field by the evenly decurved profile of the snout descending to a nearly horizontal mouth and by its colour-pattern. This consists of an upper series of black blotches parallel to the dorsal outline and a black band of uneven width extending from the opercular spot to the anterior part of the caudal peduncle; at the posterior end of the peduncle is a vertical blotch meeting its fellow over the top. The

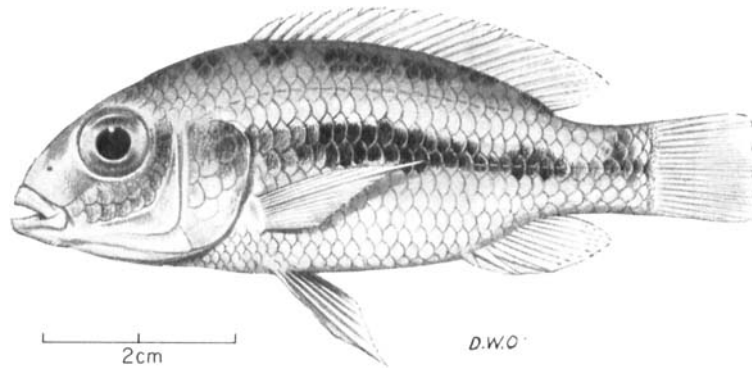


FIG. 14. *Konia eisentrauti*, a paratype of SL 64.5 mm.

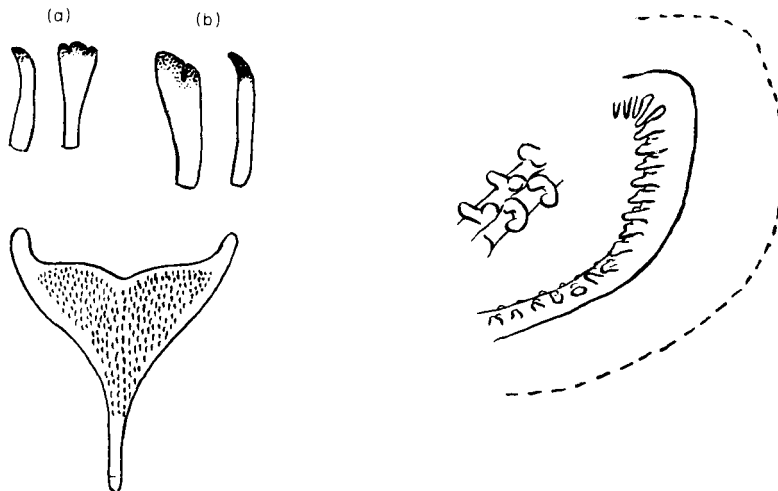


FIG. 15. *Konia eisentrauti*, (a) inner and (b) outer jaw teeth and lower pharyngeal bone of a paratype of SL 62 mm and gill-rakers of first arch in another specimen. Both inner and out gill-rakers have a subsidiary tubercle. In part, from Trewavas, 1962.

fins are colourless (in the smallest the soft dorsal had faint pinkish stripes); there is no tilapia-mark.

Larger individuals have a dark grey snout and back and the upper series of blotches is no longer visible. The colour-pattern is then similar to that of leka keppe (*S. lohbergeri*), but the shape of the snout is distinctive. As in leka, individuals of both sexes with maturing gonads often have the branchiostegal membrane, isthmus and in some chest and lower jaw black. This seems to be related to gonad condition and not to size.

Further distinguishing characters are the three regular rows of teeth (two in the 35.5 mm fish, a few teeth of a fourth in the lower jaw of an 86 mm one), the outer having less slender shafts than in *S. lohbergeri*; the shape of the lower pharyngeal bone (Fig. 15), in which the blade is 0.7–0.95 of the median length of the toothed area; and the narrow interorbital space, 24–27% of the length of head.

In a specimen of 66 mm SL the intestine measured 86 mm 1.43 times the SL.

Our specimens ranged from 35.5 to 86 mm SL. The 86 mm fish was the only male with advanced testes; these were about 2.3 mm wide and looped to fit their increased length into the body-cavity the viscera were packed with ribbons of fat.

The largest ovarian eggs seen by us were in a fish of 54 mm SL; they were green, nearly spherical, with a long diameter of 4 mm. The abdomen was nearly filled with these eggs, of which there were seven in the right ovary, nine in the left. In the interstices between them were a few very small translucent oocytes. Two other females contained green eggs of 3.6–3.7 mm, one a fish of 59.6 mm SL, the other 82 mm. The latter had a total of 58 eggs, 33 in the right ovary, 25 in the left. We deduce that the size of the eggs is fairly constant and the number depends on the size of the mother.

The majority of our specimens had very narrow testes, or ovaries in the stage at which small cream-coloured and smaller translucent oocytes are mixed with red and yellow amorphous bodies. We identified no very young specimens (but perhaps because the mesh of the traps was too wide) and we think that the species was just entering upon a breeding-cycle. Ripe eggs are of a size at which mouth-brooding is the probable mode of parental care, but we found no brooding parents.

Konia dikume sp. n.

(Figs 16 and 17)

Tilapia eisenrauti ("dubious part") Trewavas, 1962: 169, fig. 5B, 6B, c and d.
Barombi name: dikume.

Holotype BMNH 1971.10.20.50, 104.5 mm in SL. Paratypes BMNH 1971.10.20.51–67, 62–111.5 mm SL (17 specimens).

Distinguishing characters

In contrast to *K. eisenrauti* the snout is acute, the mouth at an angle of about 20°–30° with the horizontal, the lower jaw with a slight mental process, its front teeth often projecting beyond those of the upper jaw. When freshly caught no dark markings are to be seen on the body and it can always be recognized by the blood that swells the capillaries, especially at the bases of the fins, and oozes over the surface, staining its silvery colour. Preserved, there appear two to five dark blotches between upper lateral line and dorsal fin and in some a vague dark stripe at the level of the horizontal myoseptum.

The teeth are usually in only two series and the lower pharyngeal bone is very slender, with a relatively longer blade than in *K. eisenrauti*.

Description of the holotypes and paratypes

Proportions as % SL

Depth of body 36.5–40.0; length of head 37.5–40.7; length of pectoral fin 32.0–36.0; last dorsal spine 12.5–16.5; third anal spine 12.0–15.5 (from a little shorter to a little longer than last dorsal); length of caudal peduncle 13.5–16.5 (0.9–1.2 times its own depth).

Proportions as % length of head

Length of snout 31.5–35.0; diameter of eye 27.3–31.8 at SL of 88–112 mm, 31.2–33.3 at SL 62–71 mm; depth of preorbital 19.0–23.0; interorbital width 23.5–28.3; length of lower jaw 33.3–36.7, of premaxillary pedicels 20.0–25.0.

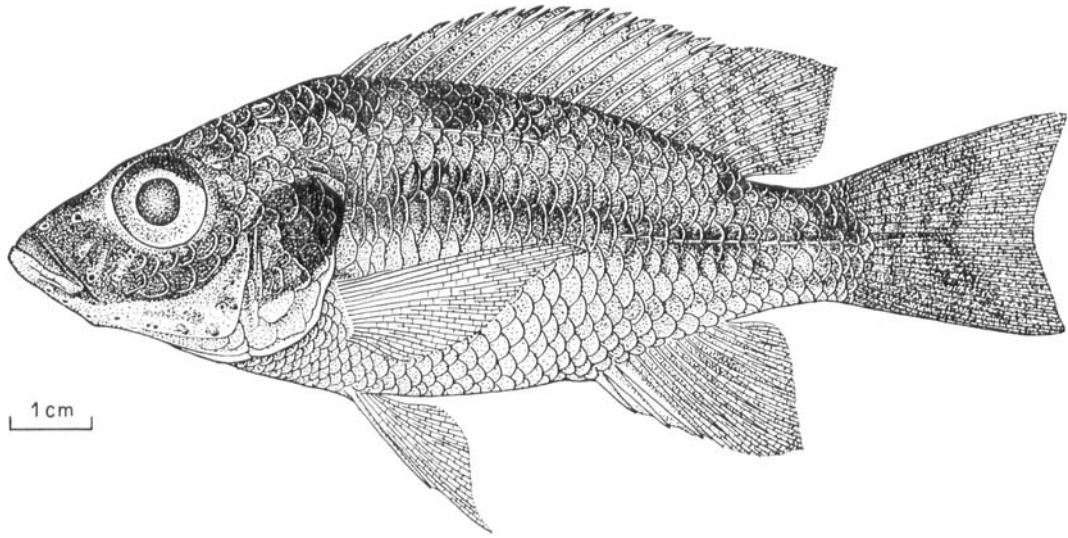


FIG. 16. *Konia dikume*, holotype.

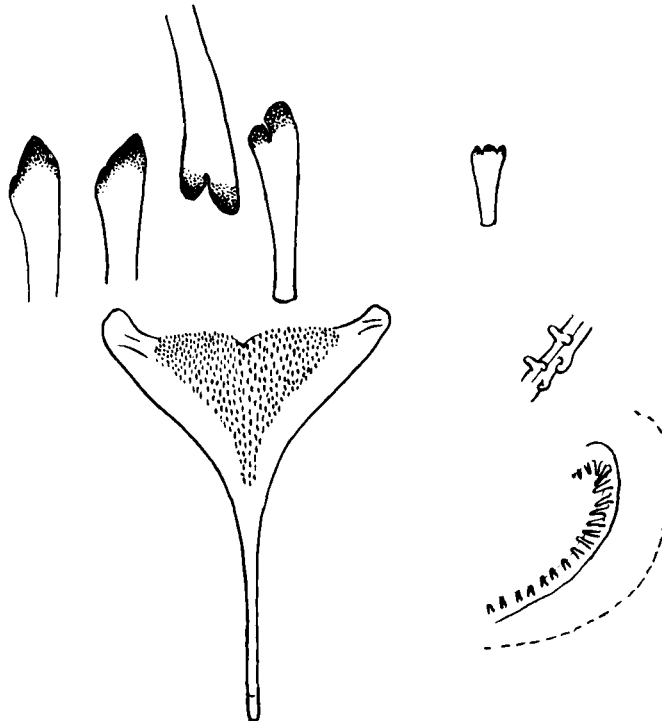


FIG. 17. *Konia dikume*, two lateral teeth of the lower jaw, outer teeth from near midline of upper and lower jaws, an inner tooth, lower pharyngeal bone and outer gill-rakers of first arch in a specimen of SL 109 mm. A section of the arch is drawn in oral view to show that each inner raker has a subsidiary tubercle on the ridge of the arch. In part from Trewavas, 1962.

Length of pharyngeal bone 29.6–30.7, its width 26.0–26.7, the blade up to $1\frac{1}{2}$ times the median length of the toothed area; in young of 62–71 mm SL blade equal to dentigerous area in length and whole bone only 26.3% length of head.

Teeth of jaws in two rows, occasionally with a few teeth forming a third row anteriorly; 45–66 in outer row of upper jaw; outer bicuspid, the two cusps separated by a terminal narrow notch (Fig. 17), in adult 2–4 at end of row with minor cusp reduced or absent; inner tricuspid. Teeth of lower pharyngeal bone very small and slender, not crowded, unicuspid or with minor cusp a mere shoulder.

Gill-rakers on first arch (3–4)+1+(14–16), usually 14–15 on lower part. Microbranchiospines present on outer sides of 2nd, 3rd and 4th arches.

Intestine about $1\frac{1}{4}$ times the SL (a specimen of SL 101 mm).

Scales on cheek in two series, usually expanding to three on the anterior part; in lateral lines series 31 in 14 specimens of the 15 counted, 30 in the other; $3\frac{1}{2}$ –4 between origin of dorsal and lateral line, 16 around caudal peduncle.

Dorsal XV 11 (f.13), XV 12 (f.2) or XVI 11 (f.1).

Anal III 9–10.

Caudal truncate or very slightly emarginate when spread.

Colour. Silvery when freshly caught, with fins tinged watery yellow and snout dark. When preserved, two to five dark blotches between dorsum and upper lateral line and a vague dark band at level of horizontal myoseptum. At 60–70 mm SL preserved specimens with faint traces of 8–10 vertical bars on upper half of body. Dorsal lappets black-tipped. No tilapia-mark.

Most of the many specimens brought to us were of the same size, about 90–110 mm SL, but we saw a few of 60–70 mm. Although absence of smaller ones may be explained by the mesh of the traps and nets used in the deeper waters, the upper size-limit probably represents that of the species, since larger *S. linnellii* and *S. caroli* were caught with the same gear. The narrower-meshed traps set near or at the shore caught few if any of this species.

No ripe individuals were encountered; the males had narrow testes and several females had ovaries at the stage where the largest oocytes were cream-coloured spheres about 1 mm in diameter. In addition there were smaller oocytes and yellow and red amorphous bodies.

Dikume probably spends much of its time at depths of 20 m or more. The freshly-caught fish is suffused with a thin film of bright red blood, the pectoral axil is a red blotch from the swollen and oozing capillaries, the gills are deep red, with gas-bubbles enmeshed among the filaments, the swim-bladder is swollen and all the blood-vessels of the viscera and the lining of the gill-cover are conspicuous and swollen. When the gill-cover of the preserved fish is lifted a perfect impression of the first gill is often seen in the layer of clotted blood lining the operculum.

The occasional *S. linnellii* or *S. caroli* caught with dikume shows no such phenomenon, but they are said to be caught in the upper part of the net.

Pungu nom. n.

Barombia Trewavas, 1962: 184 (preoccupied in Insecta, see p. 43).

Pungu maclareni

(Plate I and Figs 18 and 19)

Barombia maclareni Trewavas, 1962: 184, fig. 14, 15; Trewavas in Fisher *et al.*, 1969: 347, pl. 31 fig. e.

Barombi name: pungu.

Holotype: ♂ 75+17 mm, BMNH 1959.8.18.177. coll. P.I.R. Maclaren (originally wrongly labelled as from Barombi Kotto).

The golden-yellow colour with black blotches is well shown in Plate I. The black markings, although frequently quite irregular, are often arranged along a mid-lateral horizontal band and an upper band parallel to the dorsal outline, like those of *K. eisenbrauti* and *S. lohbergeri* (and many other African cichlids). There is endless variety both in the amount of black and in its arrangement. The contrasting gold that makes this such a conspicuous little fish develops as the fish matures, replacing the more usual silvery background of the young. There is no tilapia-mark.

Even without the distinctive colour pungu would be instantly recognisable by its small terminal mouth and thick lips.

Our specimens ranged from 35 to 100 mm SL. From them something can be learnt of the development of the remarkable dentition, of which that of the holotype (Fig. 18) is typical. The inner teeth have three subequal cusps at all ages, except that from SL 90 to 100 mm two to four teeth in the middle of the lower jaw are larger than the others and have their lateral cusps reduced or absent. There are two inner rows in the lower jaw, one, or one with an incomplete second row, in the upper. The 35 mm fish has only three or four inner teeth in each jaw. The lower outer teeth do not increase in number, being seven or eight from SL 35 mm to 100 mm (one 60 mm fish has only five), but the upper outer increase from 12 at SL 35 mm to 23 at 100 mm. At 35 mm all the outer teeth are notched (except some with the brown crowns worn off). At 53 mm only the two middle upper and six of the eight lower are without trace of a minor cusp. At 100 mm all the outer teeth are simple, including one partly erupted and not yet in use, which shows that at least some of the teeth are simple by replacement, not by wear.

The lower jaw is stout and broad and the jaw-muscles are highly developed, a considerable superficial layer of the A2 part of the adductor mandibulae inserting muscously on the coronoid process (Fig. 19). The proportions of the lower pharyngeal bone and the nature of its teeth are as in the type (Fig. 18).

Microbranchiospines are absent in smaller specimens, but at 65 mm they have developed along the 4th arch and parts of the 2nd and 3rd; in a 95 mm fish there are none on the 2nd arch, a short series (and a corresponding groove) on the 3rd and 4th; in the 100 mm fish there is an interrupted series on the 2nd arch, complete series on the 3rd and 4th.

The intestine in two specimens of 66 and 70 mm SL measured 2.6–2.8 times SL.

The ranges of meristic characters for 11 specimens are as follows:

Gill-rakers (2–3)+(0–1)+(13–16) on the first arch; 13 only in the smallest specimen, 14 in only one.

Scales 29 or 30 in the lateral line series, 14–16 around the caudal peduncle.

Dorsal XV 10 (f.4), XVI 10 (f.5), XVI 11 (f.1) or XVII 10 (f.1). Anal III 8–9.

Vertebrae: 29 (seven specimens).

The largest ovarian eggs were in a fish of 65 mm SL and measured 4×3 mm, six in the

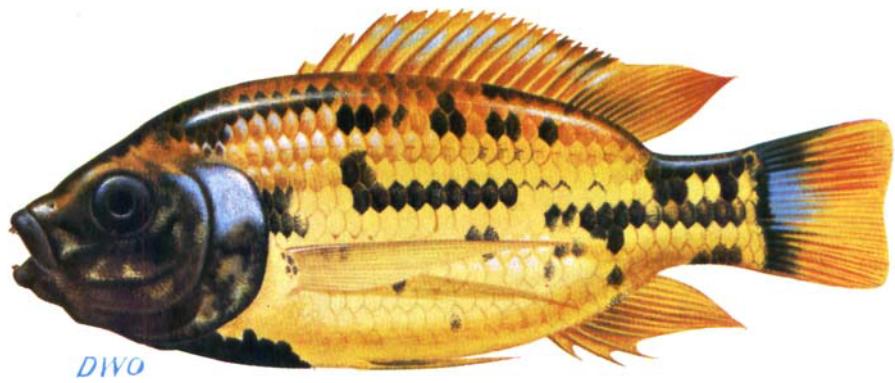


PLATE I. *Pungu maclareni*.

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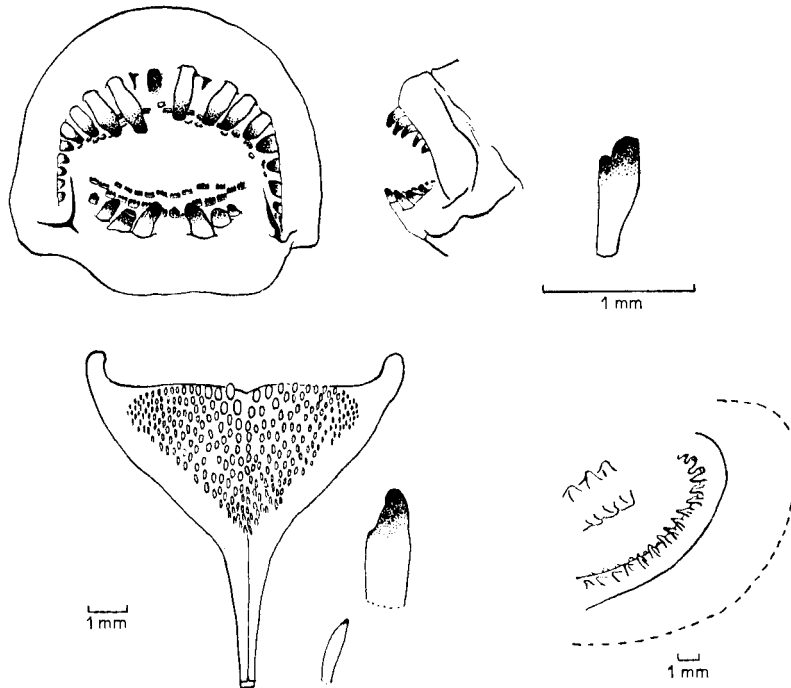


FIG. 18. *Pungu maclareni*, anterior and lateral views of lips and teeth in the holotype, an outer lower tooth in a juvenile of SL 35 mm, lower pharyngeal bone of the holotype and gill-rakers of another specimen. In part from Trewavas, 1962.

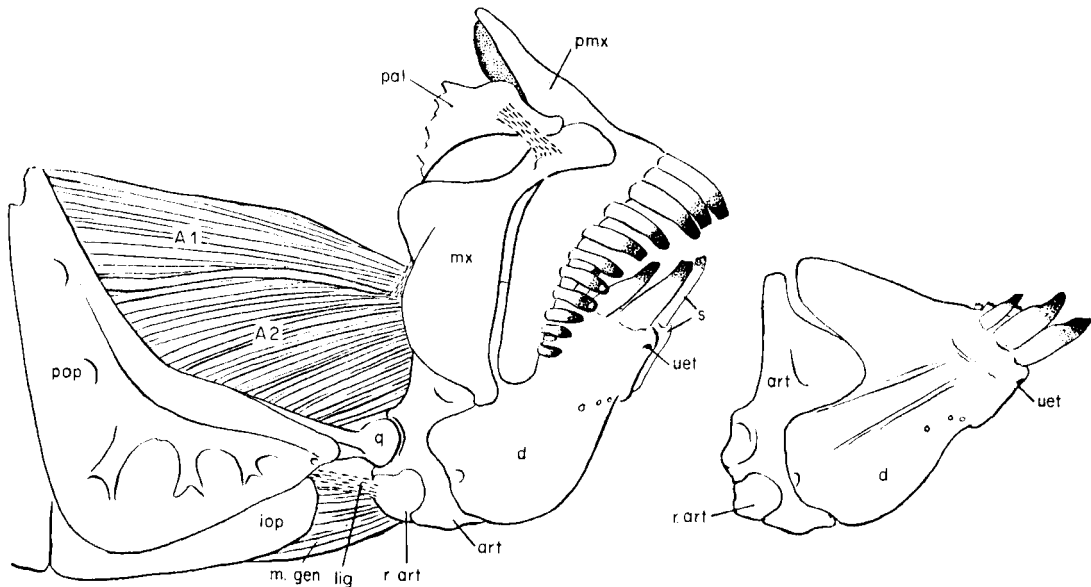


FIG. 19. *Pungu maclareni*, dissection of jaws and their muscles and isolated lower jaw; the upper jaw has slipped forward a little; normally the teeth meet as in Fig. 18. A1 and A2, parts of adductor mandibulae muscle. art, "Articular"; d, dentary; iop, interopercular bone; lig, ligaments; m.gen, geniohyoid muscle; mx, maxilla; pal, palatine; pmx, premaxilla; pop, preopercular; q, quadrate; r.art, retroarticular or "angular"; s, anterior tooth and part of lower jaw of left side; uet, unerupted tooth (probably suppressed right anterior tooth).

right ovary, nine in the left. They were green and lapwing-egg-shaped, with contrast between the widths of the two ends, so were probably nearly ready to be shed. In the same ovaries were small white oocytes of 0.5 mm diameter and some amorphous masses.

We have no information on mating or parental behaviour.

Genus *Stomatepia*

Trewavas, 1962: 181; type species *Paratilapia mariae* Holly, 1930 = *Stomatepia mariae*.

Cichlid fishes with 27–29 vertebrae (mode 28), the third with a pair of apophyses united below, for the attachment of the swim-bladder and the pharyngeal muscles; the apophysis for the upper pharyngeal bones formed by the parasphenoid alone; scales cycloid with concentric circuli; inner teeth of the jaws tricuspid at all ages, outer bicuspid in the young, the small minor cusp becoming minute or obsolete in the adult; lower pharyngeal bone with blade from approximately equal in length to the dentigerous area to nearly twice as long; pharyngeal teeth slender, but not crowded, the lower posterior with minor cusp represented by a shoulder; snout long, cleft of mouth oblique (at 40–50° with the horizontal); gill-rakers 15–21 on lower part of the first arch, slender, the upper slightly expanded distally; a narrow interorbital region (16.0–24.5% of length of head). The mesethmoid is free from the vomer.

Intestine shorter than SL of fish.

Eggs large (4–5 mm in long diameter) and olive-green.

Three species, restricted to Barombi Mbo.

Key to species of *Stomatepia*

- | | |
|---|------------------|
| 1a. Depth of body 25–30.5% of SL; upper jaw 26.8–28.8% length of head | <i>S. mongo</i> |
| 1b. Depth of body 29.5–35.5% SL; upper jaw 28.5–35.2% length of head | 2 |
| 2a. Lateral line cavities of the head enlarged; colour-pattern, if not masked by black, a series of dark blotches along the side; a small, vague tilapia-mark present or absent in the young; usually no micro-branchiospines | <i>S. pindu</i> |
| 2b. Lateral-line cavities of head not enlarged; colour-pattern a continuous dark band along the side; a strong, clear-rimmed tilapia-mark in the young, reduced or absent in adults; microbranchiospines present | <i>S. mariae</i> |

The proportions and meristic characters of the species are summarized in Tables IV and V.

Stomatepia mariae

(Figs 20, 21 and 22)

Paratilapia mariae Holly, 1930: 206, pl. ii fig. 12.

Stomatepia mariae (part.); Trewavas, 1962: 182, fig. 13 (but not 13(a) and (b)).

Barombi name: nsses.

Holotype: ♂ of 109 mm. Vienna Mus. 13950.

From Tables IV and V and Figs 22, 23 and 26 it can be seen that nsses has usually a shorter pectoral fin than pindu and a slightly wider interorbital region than either of the other two species. The range and modal number of the gill-rakers are higher than in *S. pindu* and *S. mongo*. The modal number of dorsal rays is the same as that in *S. mongo* and one higher than in *S. pindu*.

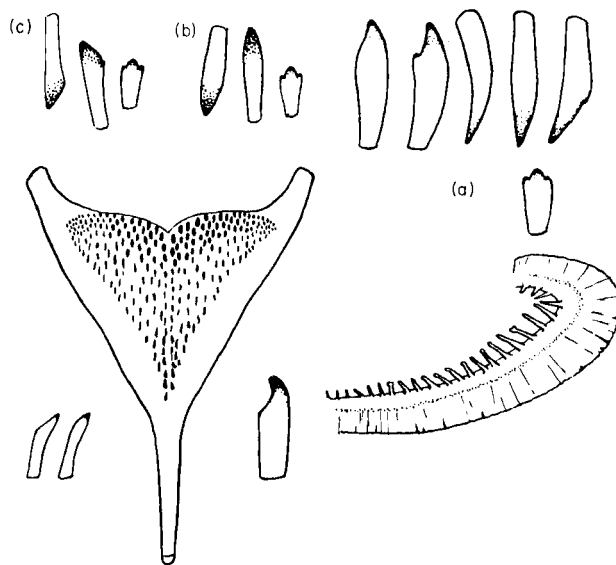


FIG. 20. *Stomatepia mariae*, lower pharyngeal bone and first gill-arch of a specimen of SL 92 mm. (a) Outer jaw teeth and one inner of the same. (b), (c) Outer and inner jaw teeth of two specimens of *S. pindu*, respectively, 58 and 45.5 mm in SL. From Trewavas, 1962.

Microbranchiospines are present on the outer sides of the 2nd, 3rd and 4th arches.

At all sizes it is distinguished from *S. pindu* by the normal, smaller size of the lateral line cavities and by the colour-pattern.

The outer teeth have a small minor cusp up to about 35 mm SL. Above this size they are unicuspid or (a few) with a shoulder representing the minor cusp. The inner remain tricuspid with the middle cusp dominant. There are 40–60 outer teeth in the upper jaw from 50 mm SL upwards, fewer in the young.

We found no black individuals. The colour is silvery grey with some brassy iridescence; a dark grey or black continuous horizontal band extends along the body, usually ending at the anterior end of the caudal peduncle, at the caudal end of which is a dark vertical blotch. Dorsal, caudal and pectoral fins are watery yellow, orange yellow in mature males; pelvic and anal fins may be dusky. In the young there is a large black tilapia-mark; this dwindles with age, but a trace may remain in the adult (Fig. 22).

The largest ovarian eggs were found in fishes of 75–80 mm SL. They were oval, green and about 4 mm in long diameter. In a 75 mm specimen each ovary contained 12 ripe eggs and they took up so much space in the abdomen that one ovary, the left, was almost entirely anterior to the other. In another (80 mm) the eggs, though already green, were not so large (about 3 mm) and the ovaries were side by side. A third specimen (79.5 mm), also with green eggs of 2.9 mm, had 14 in one ovary; the other ovary was smaller.

Ripe or ripening males were bigger, 91.5–109 mm SL.

All specimens with ripe or ripening gonads had large fat-bodies among the viscera.

The smallest specimen caught was captured in a narrow-meshed trap set among the shore vegetation. It measured 19.5 mm and had a conspicuous tilapia-mark.

We saw no mouth-brooding fish but we suppose that such large eggs must be cared for in this way.

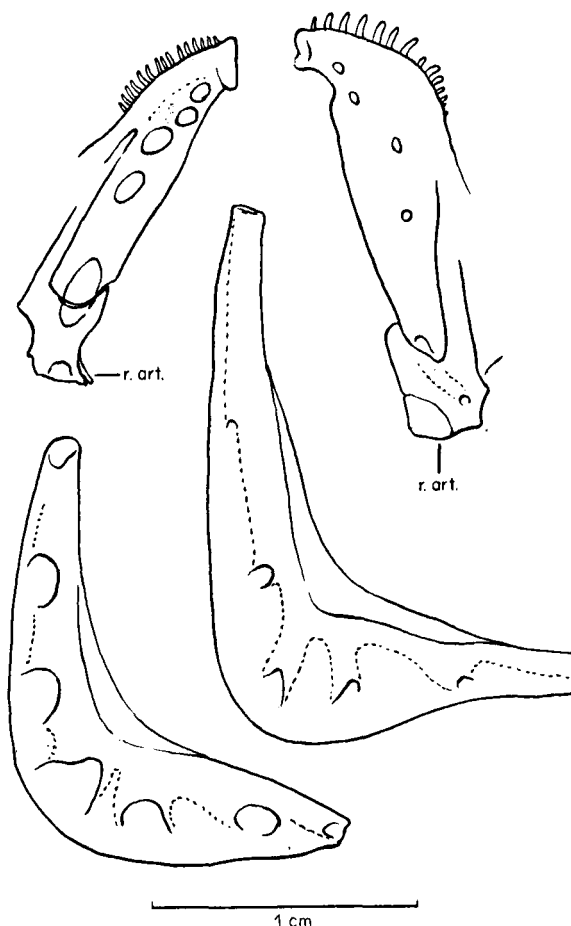


FIG. 21. Lower jaw and preoperculum from, left, *Stomatepia pindu* of SL 88 mm, right, *S. mariae* of SL 107 mm, as examples of lateral line bones of head, in which the canals and bony openings are enlarged in *S. pindu*. The canal in the "articular" of *S. pindu* is so much enlarged that the retroarticular is reduced in comparison with that of *S. mariae*, and the posterior opening in the dentary is extended to involve the articular too. In the drawing the foreshortened coronoid process is omitted.

Stomatepia pindu sp. n.

(Figs 20(b), (c), 21, 23 and 26)

Stomatepia mariae (part., nec Holly); Trewavas, 1962: 182, figs 12, 13(a) and (b).

Barombi name: pindu.

Holotype: ♂ 81.5+20 mm collected in March 1970, BMNH 1971.10.20.1. Paratypes: 21 specimens, 32.5+8 to 91+21 mm, BMNH 1971.10.20.2-22.

The meristic characters and proportions are set out in Tables IV and V.

The teeth are in two series in the young, a third is gradually added and (in one) a few of a fourth. From about 40 mm SL upwards the outer are unicuspid or with the minor cusp reduced to a shoulder, but the inner remain tricuspid, with the middle cusp wider and longer than the lateral; 40-60 in the outer series of the upper jaw at and above 40 mm SL.

Lower pharyngeal as in *S. mariae*, with blade slightly longer than toothed area.

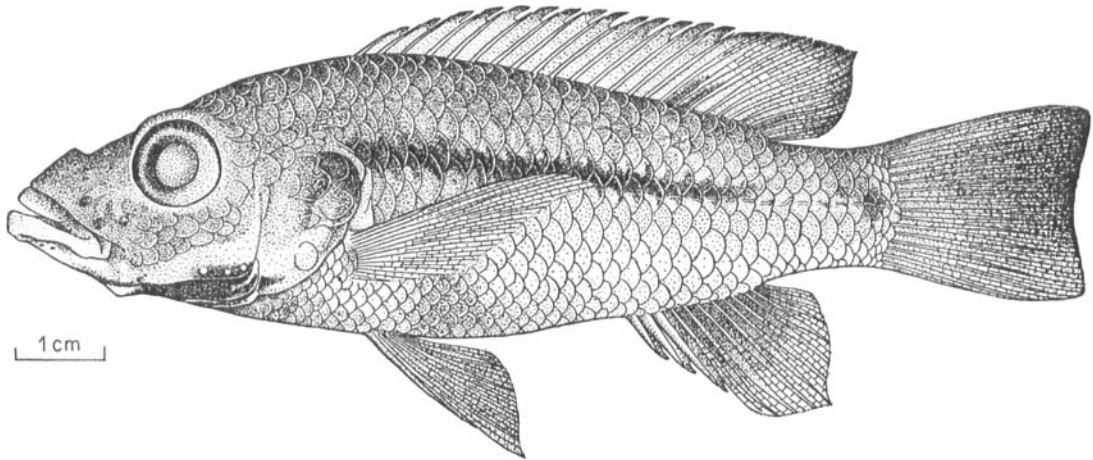


FIG. 22. *Stomatepia mariae* of SL 97 mm.

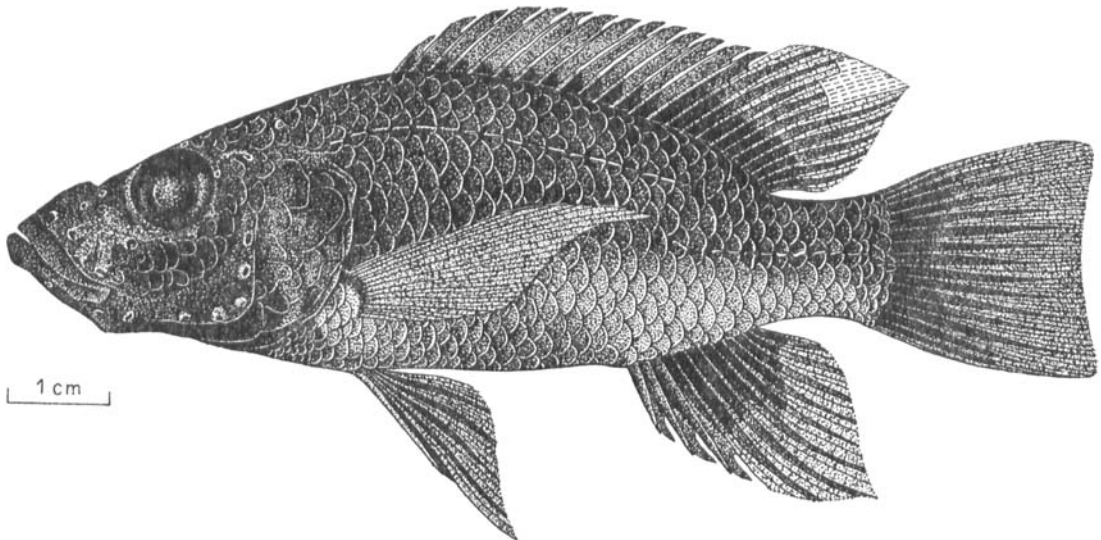


FIG. 23. *Stomatepia pindu*, holotype.

Pindu is deeper-bodied than mongo and usually than nses (*S. mariae*). The depth is 35% SL or more in 10 of 18 in which it was measured, whereas in *S. mariae* only three of 15 were so deep and these were young fish less than 40 mm in SL.

Pindu has a longer pectoral fin than the other two species and in mature fish the dorsal and anal are often produced beyond the base of the caudal.

In contrast to *S. mariae*, there are usually no microbranchiospines. Among 13 specimens examined for this feature they were found in only one and this had incomplete series on the outer sides of arches 2 and 3, none on the fourth.

At all sizes pindu is easily distinguished from *S. mariae* by the enlarged lateral-line cavities of the head (Figs 21 and 23), and the tubules of the lateral line itself are more prominent

too. The colour-pattern is distinctive. Many individuals are totally black, including the fins and in some even the genital papilla. But the black may be restricted to the dorsal side, passing into uneven blotches on the lower parts of the body and fins. Others are grey with a series of dark grey or black blotches along the side (never the continuous band of nesses) and an upper series of blotches above the lateral line (see Trewavas, 1962, fig. 12). In both black and grey individuals there is often a characteristic crimson iridescence on the operculum. One fish when alive had a shining green ground-colour instead of the usual grey and its pelvics were orange.

The most advanced male examined was an all-black fish of 75 mm SL. A female of 68.5 mm had both ovaries full of large (about 4×3 mm), oval, green eggs, eight in the right ovary, seven in the left. This fish had the black pigment in large irregular blotches, darker dorsally, greyer on the lower half of the body. A female of 91 mm with ovaries "starting" was all black except grey zones on caudal and anal fins. It seems, therefore, that the all-black pigmentation has no simple relation to sex and breeding phase, and indeed individuals have been observed to change colour.

The three smallest individuals preserved were pale, two of them with the mid-lateral series of blotches, the third (SL 44 mm) with no dark pattern; and the eight young of the Eisentraut collection (Trewavas, 1962), 41–60 mm in SL, were all, when preserved, grey with the lateral blotch pattern. Some of the latter, up to 50 mm in SL, had a small tilapia-mark. This is less intense than in *S. mariae* of the same size and does not persist into the adult.

Stomatepia mongo sp. n.

(Figs 24 to 26)

Barombi name: mongo.

Holotype: ♀ 93.5+19.5 mm, with ripe ovarian eggs, collected 24.IV.1970. BMNH 1971.10.20.23.

Paratypes: 10 of 79–100 mm SL, collected March–April 1970. BMNH 1971.10.20.24–33.

Meristic characters and proportions are set out in Tables IV and V.

This is a very well characterized species, contrasting with its congeners in the shallow body and long snout. Except the depth of body, most of its proportions are like those of the other two species, but the snout and preorbital bone are a little longer. The lower jaw bears the same relation to the length of head, but the upper jaw is smaller, as shown by the measurement of both the pedicels and the oral edge (Table IV).

As in the other species the inner teeth are tricuspid. The outer have two very unequal cusps or the minor cusp may be reduced to a shoulder or (some teeth of one fish) obsolete. There are 40–64 outer in the upper jaw.

The pharyngeal bone is narrower than in the other two species and its dentigerous area occupies a smaller proportion of the length (Fig. 25).

The lateral-line cavities of the head are somewhat enlarged, but less so than in pindu. The modal number of gill-rakers is lower than in either of the others. Microbranchiospines may be present or absent.

The colour of the body is usually dark grey, counter-shaded, sometimes darker along the side, but without a well-defined pattern of band or spots. Often the pelvic and anal fins are tinged with salmon-pink and the dorsal lappets may be pink or (in males) orange, tipped with black. Some individuals are wholly black as in pindu. There is no tilapia-mark.

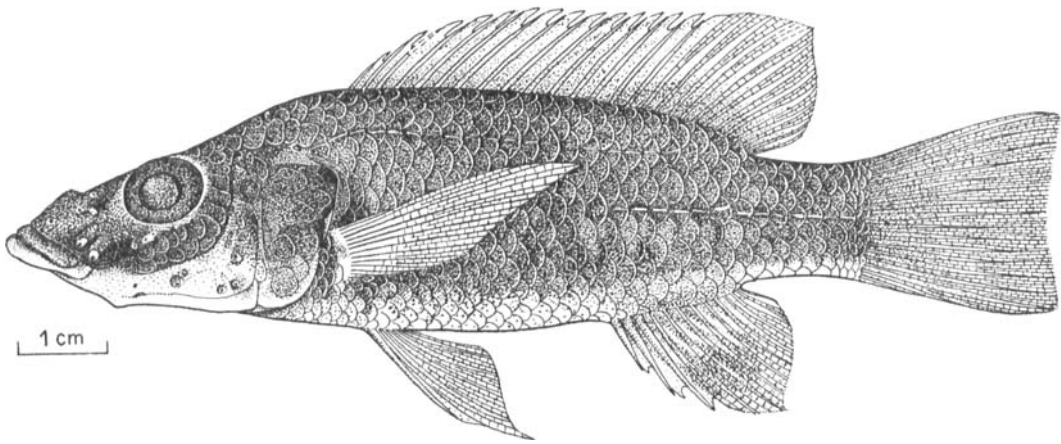


FIG. 24. *Stomatepia mongo*, holotype.

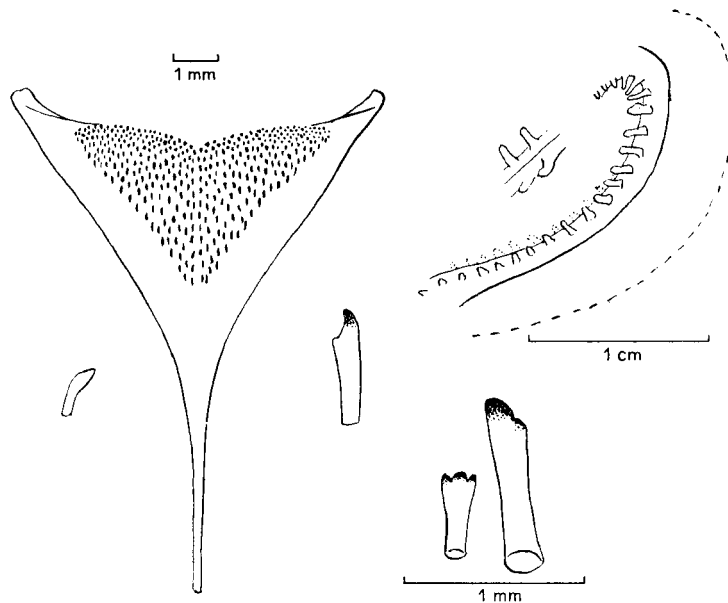


FIG. 25. *Stomatepia mongo*, from a fish of 92 mm. Lower pharyngeal bone and isolated anterior and posterior teeth; left first gill-arch and enlarged oral view of an upper part of the ceratobranchial; and typical inner and outer teeth from the jaws.

Many of the specimens examined had much fat among the viscera, and gonads starting to swell, but one female with cream-coloured oocytes had no fat.

The holotype had ripe, olive green ovarian eggs of long diameter 4.5-5.0 mm as well as some white oocytes of 1 mm. The right ovary contained 18 eggs, the left about 13. In this fish the lower lip is very thick at the symphysis.

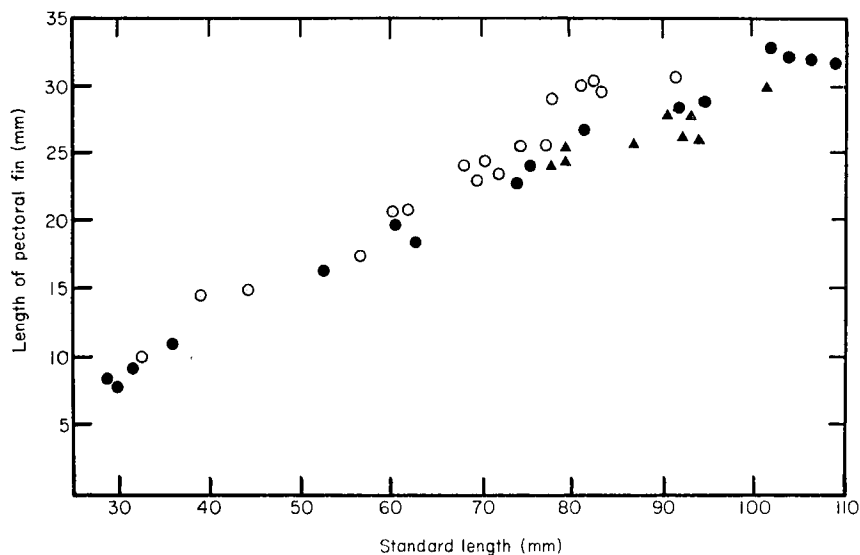


FIG. 26. Length of pectoral fin plotted against standard length: ●, *Stomatepia mariae*; ○, *S. pindu*; ▲, *S. mongo*.

TABLE IV
Proportions in the species of Stomatepia

	<i>mariae</i>	<i>pindu</i>	<i>mongo</i>
SL	29-109	32.5-91	70-101
<i>Proportions as % SL</i>			
Depth of body	29.5-35.4	30.0-37.0	25.3-30.6
Length of head	39.1-43.7	38.6-44.0	38.4-41.4
Length of pectoral	28.0-33.3	32.2-37.0	27.5-32.0
Longest dorsal spine	11.0-15.4	12.3-15.0	12.0-14.0
3rd anal spine	10.0-14.4	12.0-15.0	12.4-14.2
Length of caudal peduncle	13.3-18.0	12.8-15.2	11.0-13.5
<i>Caudal peduncle:</i>			
<i>length/depth</i>	1.0-1.3	0.95-1.2	0.9-1.1
<i>Proportions as % head</i>			
Length of snout	30.5-40.0	31.0-36.6	34.0-39.0
Diameter of eye			
below 70 mm SL	27.8-33.5	25.0-31.4	—
70 mm or more	24.5-29.4	24.0-28.0	23.0-28.5
Depth of preorbital	18.5-24.0	17.8-24.5	20.0-25.2
Interorbital width	18.0-24.5	16.0-20.6	16.0-18.5
Length of lower jaw	38.2-43.5	36.5-42.2	37.6-40.7
Length of premaxillary pedicel			
(at SL 40 mm +)	22.2-26.6	22.6-27.0	19.3-23.4
Length of upper jaw	28.0-32.5	28.5-35.2	26.8-28.8

TABLE V
Frequencies of meristic numbers in the species of Stomatepia
 (for vertebrae see Table II on p. 48)

	<i>S. mariae</i>	<i>S. pindu</i>	<i>S. mongo</i>
Dorsal formula			
XIII 11	—	1	—
XIV 10	1	3	1
XIV 11	3	23	—
XV 10	1	2	2
XV 11	8	2	6
XIV 12	6	—	—
XV 12	—	—	4
XVI 11	—	—	1
Dorsal Spines			
XIII	—	1	—
XIV	10	26	1
XV	9	4	12
XVI	—	—	1
Dorsal totals			
24	1	4	1
25	4	25	2
26	14	2	6
27	—	—	5
Soft anal rays			
8	—	5	4
9	12	22	10
10	7	—	—
Gill-rakers			
15	—	2	1
16	—	3	10
17	—	9	2
18	3-5	12	—
19	8	1	—
20	5-5	2	—
21	3	—	—

We found no mouth-brooding specimens, but probably the eggs are cared for in this way. The species was very rarely caught during our time on the lake, but several specimens turned up in the middle of April in traps. The fishermen were making special efforts to find them for us and in March said that we might expect to find breeding individuals in April. This proved to be the case and it is possible that we were seeing the beginning of an inshore breeding migration.

Ecology of the lake

J. GREEN AND SARAH A. CORBET

Barombi Mbo is roughly circular and about 2.5 km across, with one major outflow through the Kake Gorge at the south-eastern corner and several small inflows, some of them seasonal. The only permanent inflow is near the Barombi village to the north-west. The bottom of the lake descends steeply all around to a maximum depth of 111 m near the middle. Our visit coincided with the end of the dry season, when the water level was probably at its lowest. From markings on rocks and tree trunks projecting out of the water we estimated that the water level fluctuated through about 1 m during the course of a year.

The rim of the crater is heavily forested, and projects up well above the surface of the lake, providing considerable shelter, so that the surface of the lake is generally calm. On only two occasions during five weeks did we observe winds strong enough to produce waves that broke offshore as white horses. The lake is clear, so that underwater observation of fish is easy.

The surface temperature of the lake in March and April was 29°–30°C. We did not have apparatus to measure temperatures in the deep water, but we did suspend a thermometer at a depth of 4 m and then read it *in situ*. When the surface temperature was 29.5°C the temperature at 4 m was 28°C.

The conductivity of the water was low. Measurements made both inshore and in the middle of the lake gave a value of 39 $\mu\text{mho/cm}/20^\circ\text{C}$ in March and April.

The clarity of the water and the low conductivity indicate that Barombi Mbo is not a very productive lake. Vertical hauls with phytoplankton nets through a depth of 100 metres yielded very little plant material. Most of the phytoplankton seems to be too small to be retained by the 180 mesh nets. A high proportion of the stomach contents of the main phytoplankton-eating fishes (unga—*Sarotherodon linnellii* and *S. caroli*) consisted of unicellular green algae with a diameter of about 10 μm or less. Small dinoflagellates were also present in most of these fishes, but were absent from the net samples.

The zooplankton of the open water is also relatively sparse (Green, 1972). For instance the total number of cyclopoids under one square metre is only about one tenth of the number found in Lake Mutanda, the least productive of three lakes in the Kigezi district of Uganda (Green, 1965). The most striking feature of the zooplankton of Barombi Mbo is the total absence of Cladocera.

The bottom of the lake in the deeper regions appears to consist of fine sand and fine organic debris. Our only means of sampling at depth was to allow the plankton nets to drag along the bottom. Such samples yielded very few animals, and were remarkable in lacking chironomid larvae.

Around the shore of the lake, plant material falling into the water from the surrounding forest makes an important contribution to the food supply. The sandy bottom was thickly covered with fallen leaves in some places, and almost clear of them in others. Where the bottom was overlain by dead leaves the invertebrate fauna was more obvious. On the leaves the tubes of chironomid larvae were abundant, and ancyliid limpets (*Ferrissia* sp.) occurred more rarely. Among the leaves were the larvae of caenid and baetid mayflies, as well as ostracods and dragonfly larvae. Small stones provided shelter for a similar group

of invertebrates including mayfly larvae, ostracods and hydracarinae, together with chironomid larvae. In addition, untidy silken webs on stones were found to contain hydropsychid larvae, or sometimes the larvae of the mayfly *Povilla adusta*, which was more typically found in burrows in wood. Peritrichs lived epibiotically on mayfly larvae and chironomid larvae. Epibiotic rotifers were found on the ancyloid gastropod and on mayfly larvae.

The endemic sponge *Corvospongilla thysi* (Brien) covered large areas on the outer surfaces of rocks from near the surface to a depth of at least 3 or 4 m. Another species, *Corvospongilla bohmi* (Hilgendorf), was found in crevices and hollows in rocks and wood over a similar depth range. The rocks and boulders, and the sponges on them, bore a thin coat of aufwuchs and debris derived from the faeces of shore fishes and from material that settled in the water. Fishes were most abundant in these rockier parts of the shore.

The trunks of trees that had fallen into the lake formed an important habitat for invertebrates. The burrowing larvae of *Povilla adusta* were very abundant in suitably old branches and logs. The crevices resulting from their tunnelling harboured numerous other invertebrates, including the larvae of mayflies, caddis, zygopterans and chironomids. Patches of *Corvospongilla thysi* were occasionally found on submerged wood, though it was very much less common on wood than on rock. *Corvospongilla bohmi* was fairly common lining the cavities in wood. Like the rocks the submerged logs and branches carried a thin covering of aufwuchs and debris, and as on the rocks this formed the food of fishes. A crab was once seen breaking up wood as if to extract the invertebrates living in it.

In relatively unshaded regions of the shore there were a few patches of rooted water plants. The least common was *Potamogeton octandrus* which formed loose mats about 5 cm thick on the bottom in water about 0.5–1 m deep. Waterlilies grew in about 0.5–1 m of water and had remarkably few animals, either invertebrates or fishes, associated with them, though their leaves were scored with the oviposition marks of coenagruid dragonflies. Large patches of *Najas pectinata* grew in water 0.5–4.5 m deep. In the shallow parts of its range these plants reached the surface, and the tangle of stems and leaves floating there formed an oviposition site for anisopteran and zygopteran dragonflies. In the deeper part of its range the tops of the plants were about 1 m below the surface of the water. The leaves and stems of *Najas* were densely clothed with epibionts, including gelatinous masses of the blue-green alga *Gloeotrichia*, the diatom *Gomphonema*, the green algae *Spirogyra*, *Bulbochaete* and *Mougeotia*, flosculariacean rotifers and the peritrich *Cothurnia*. Among the leaves of *Najas* were zygopteran larvae, mayfly larvae, ostracods and numerous shrimps (*Caridina*). We did not see fishes feeding on these free-living invertebrates, but large shoals of leka keppe (*S. lohbergeri*) used to graze the epibionts from the leaves and stems of *Najas*.

Animal and plant debris falling onto the surface of the lake contributed to the diets of several species of fishes. *Stomatepia mariae*, *Barbus batesii* and young unga frequently took floating terrestrial insects, and *Epiplatys sexfasciatus* fed almost entirely on these and on emerging mayflies, also taken at the surface. Fruits and seeds, which were often seen floating, were found as the main contents in the stomachs of some *Konia eisentrauti*, *Stomatepia pindu* and *Barbus batesii*. Shoals of *Sarotherodon steinbachi* were often seen dimpling at the surface, and cottony plant hairs, a characteristic component of the flotsam, were often found in their stomachs.

Feeding habits and ecological relationships

The information in this section is derived from two sources: the examination of stomach contents, and observations made underwater in the natural habitat of the fishes. Using a face mask and snorkel, it was possible to observe ten species in the clear water around the edge of Barombi Mbo. Eight of these species were identifiable in the field, but we were unable to distinguish the two species of unga under field conditions. Five other species (*Konia dikume*, *Myaka myaka*, *Stomatepia mongo* and the two species of *Clarias*) were not seen in shallow water, or in dives down to depths of 5 or 6 m; their feeding habits are known only from the stomach contents. Two other species (*Procatopus similis* and *Aphyosemion oeseri*) were found only in the small stream flowing into the northern side of the lake, where no underwater observations could be made.

The main food found in the stomachs of most of the species is shown in the trophic spectrum (Fig. 27) (see Darnell, 1961). In our study the item occupying the greatest volume in a stomach was classified as the main contents, and then any other items were listed. Thus the relative importance of each food is expressed in two ways; as the percentage of fishes with a given item as the main contents; and as the percentage of fishes in which a given item occurred, either as main or as subsidiary contents. Both percentages are shown in the trophic spectrum.

Barbus batesii Suh and kimbundu

Suh is the Barombi name for large *Barbus* and the name kimbundu is applied to smaller specimens with an SL up to about 150 mm. *Barbus* is caught in both the lake and the tributary stream, and we are not certain that all the fishes we dissected came from the lake itself. We were able to watch both large and small *Barbus* swimming near the shore, the smaller ones in water 0.5–1 m deep and the larger ones usually in depths greater than 1 m. We did not see the larger fishes feeding. They swam strongly to and fro, alone or in small groups. Other fishes seemed to avoid them. Small specimens were observed in shallow water vigorously turning over small stones with their snouts, and snapping at the place where the stone had stood. This seems to be an effective technique for catching insect larvae. Several kimbundu collected to feed, together with some *Konia eisentrauti*, around a footprint where the sandy bottom had been disturbed.

In *Barbus* the stomach is not distinct, and whole guts were examined. A high proportion of the fishes contained both mayfly larvae and chironomid larvae. Other arthropod prey included caddis larvae, decapod crustaceans and terrestrial insects. The proportion containing terrestrial insects may be unnaturally high because some of the suh were caught on hooks baited with grasshoppers. Organic debris, sand grains and sponge spicules were probably picked up from the bottom when insect larvae were taken. Some vegetable matter was also found in the guts; one fish had been eating seeds.

Clarias walkeri and *C. maclareni* Nyongo

These two species were not separated in our dissections. Our specimens came from both the tributary stream, where they were caught by women using hand nets, and the lake. In the lake nyongo appeared to have a wide depth distribution; some were caught in traps set close inshore, and some must have entered deeper water, because they had eaten *Chaoborus* larvae, which we did not find in water less than 20 m deep. We never saw nyongo underwater.

The stomachs contained a wide range of food. Insect larvae (mayflies, chironomids and caddis) formed the main food of small and middle-sized individuals. Some of the larger specimens (up to 440 mm SL) had eaten fish, including one *Konia dikume*, one *S. steinbachi*, and one *Myaka myaka*.

Epiplatys sexfasciatus Longo katta

This species swam in small groups close to the surface in inshore waters, but we did not see it feeding. Sometimes the fishes lay just below the surface of the water, but they were also observed keeping station about 20 cm below the surface. The stomach contents were remarkably uniform, with over 89% of the main contents consisting of terrestrial insects including beetles, lepidopterans, caddis and dipteran flies. The other main item was mayflies in the process of emerging. It seemed as if these fishes took nearly all their food at or very close to the surface.

Procatopus similis Lenge

P. similis was found only in the small stream near the Barombi village. The stomach contents consisted entirely of insects, and the majority of these were terrestrial forms, including a high proportion of ants. In spite of its upwardly directed mouth lunge also fed from the bottom; about one third of the stomachs contained mayfly larvae or chironomid larvae.

Sarotherodon lohbergeri Leka keppe

S. lohbergeri was the most abundant fish in shallow water. The main substance in all the stomachs that we examined was organic debris. This was accompanied by other items such as rhizopods (*Arcella*, *Euglypha* and *Diffugia*), bdelloid rotifers, and sedentary diatoms, which indicate that the detritus was picked up from the surface of a plant or a stone. This was supported by field observations. The adults of this species opened their mouths very wide and applied them to the surface of a rock, as though sucking material in. This apparently dislodged any loose organic debris. Young specimens, which have silvery bodies and orange fins, fed by closing their mouths against the surface of the rock and then giving a sideways twist as though wrenching something from the surface. The silver flash produced by this movement in sunlight was a characteristic feature in water less than a metre deep all round the lake. This species also fed by removing the rich aufwuchs from *Najas pectinata*. The fish turned on its side, so that the width of the mouth lay along the axis of the stem. As far as we could see the tissues of the plant were not eaten, but debris on the surface was removed together with filamentous algae or other aufwuchs.

S. lohbergeri has also been observed in shoals at the surface. The upper lip was protruded through the surface film, and small movements were made as if ingesting material from the surface film. These movements may also have been respiratory, but the presence of fine cotton-like plant hairs in the stomachs of some specimens indicated that they had been feeding at the surface. The surface film of the inshore waters was often littered with various plant products, such as seeds, hairs, petals and fallen stamens. The two species which seemed to utilize this source of food to the greatest extent were the present one and *S. steinbachi*.

Sarotherodon steinbachi Kululu

This was one of the easier species to recognise in the field, with a generally pale colour, sometimes with a vague stripe, and a characteristic profile. We saw a single specimen with

a completely black caudal fin among a flock of normally pigmented individuals. The main item in the stomachs was organic debris. A high proportion of the fishes contained sand grains. This agreed with our field observations of feeding. *S. steinbachi* was often seen feeding in shallow sandy areas. The fish would take in a mouthful of sand, and then move the material around in the mouth and spit out the sand, following this with a swallowing movement. After this another mouthful of sand would be taken in. We also observed this species collecting organic debris from the surface of rocks and sponges. The movement appeared to be much more gentle than the corresponding movements of *S. lohbergeri* feeding on the same rock. Shoals at the surface were also observed, apparently ingesting material in a manner similar to that described for *S. lohbergeri*. This would account for the presence of cotton-like plant hairs and adult insects in the stomachs of a few individuals.

Sarotherodon linnellii and *S. caroli* Unga, fissi, kippé

We did not distinguish between these two species in the field or in our early dissections of the stomachs, but dissections of 14 fishes which were positively identified revealed no apparent differences in their stomach contents. The adults of both species ate phytoplankton, but the young included a high proportion of animals in their diet. Specimens with a standard length of 20–70 mm contained mayfly larvae and various terrestrial insects, which were consistently absent from the stomachs of larger specimens. The young unga were abundant close inshore, darting about and feeding in an opportunistic manner, investigating objects at the surface or on the bottom. It was a common experience to find these small fishes removing pieces of dead skin from one's feet and attacking scars on one's legs.

Large unga were observed in very shallow water (0.5–1 m deep), often behaving in a territorial manner, and indulging in mouth fighting. Large fishes seen in deeper water, down to about 5 m, were sometimes in groups of up to six or eight individuals.

Myaka myaka Myakamyaka

This small silvery fish seemed to live in the middle of the lake. We did not see it in shallow water, and only once saw it alive. It was occasionally caught in deep traps and sometimes in nets set far out from the shore. The stomachs contained very fine organic debris and phytoplankton. The organic debris may have been taken from the bottom or from suspension near the bottom, and much of it seemed to be derived from phytoplankton. About a third of the stomachs contained *Chaoborus* larvae, which indicates that *Myaka myaka* feeds in relatively deep water.

Konia eisentrauti Konye

K. eisentrauti was not always easy to distinguish from *S. lohbergeri* in the field. A good lateral profile view was essential. It was not a very abundant species, and our observations on it were rather few. This species included more darkened plant tissues in its diet than did *S. lohbergeri*, and it included a wider range of animals. Several specimens had mayfly larvae as the main contents, and one specimen had eaten large cichlid eggs. The main impression from the stomach contents was that *K. eisentrauti* fed in regions with abundant decaying leaves, catching small invertebrates that it found there. This species normally occurred in small groups, of two to eight individuals. When it fed, *K. eisentrauti* seemed to watch a particular object and snap it up, and then spit out some of the debris that had

been taken in with it. The feeding behaviour resembled that of *S. steinbachi*; but the snapping movement appeared to be directed at some object in the sand (possibly a mayfly larva), whereas the feeding of *S. steinbachi* seemed to be a sorting out of organic material from the sand.

Konia dikume Dikume

K. dikume was abundant in the lake, but we never saw it underwater, probably because it lived in deep water. The fishermen caught *K. dikume* in the deeper parts of gill nets set well away from the shore, or in baskets set deep, and the fishes were always dead when they were brought in. Their stomach contents provided further evidence of a deepwater habitat. The presence of organic debris in most of the stomachs indicated that these fishes often fed near the bottom, where they may also have picked up the sand grains and sponge spicules that were found in some of them. *Chaoborus* larvae, which formed the main contents in many of them, were sometimes mixed with organic debris, and sometimes very clean, as though they had been caught at a time when they were swimming in the plankton. (In plankton hauls taken by day, some of them including material from the bottom, *Chaoborus* larvae were not found in water less than 20 m deep.)

Pungu maclareni Pungu

P. maclareni was abundant in the shallow water near the shore, and was easily recognized underwater by its very thick lips and its pattern of black patches on a background of rich golden yellow. The larger individuals were seen in groups of about ten to thirty feeding over submerged logs or patches of sponge on rocks, usually 1–2 m below the water surface. In the shallower part of its range, *P. maclareni* often fed at rocks in company with *S. lohbergeri*, but on the deeper rocks, 2–3 m below the surface, it fed alone. Typically *P. maclareni* oriented itself head down or on its side as it fed at rock or at wood, moving steadily over the surface taking repeated rasping bites at it. When feeding on sponges it applied its open mouth firmly and briefly to the surface, apparently scraping off chunks with its prominent teeth. Probably the rough surfaces of the sponge and of the submerged wood were rich in detritus and epibiotic organisms that had settled there, and, as well as groups of sponge spicules, the stomachs often contained organic debris, sand grains and benthic and epilithic diatoms. But their diet sometimes included insect larvae, particularly larvae of chironomids and mayflies, which suggested that these fish could vary their feeding habits when the opportunity arose. Further evidence for this was provided by the observation of a *P. maclareni* following a crab which was using its pincers to prise bits off a log tunnelled by larvae of *Povilla*. When the crab removed a piece of wood the fish moved in and picked up something from under the wood as the crab lifted it. Some of the stomachs contained higher plant material, and two of them were packed with the tissues of fruits which must have fallen from a tree into the lake.

Although the larger fish at rocks normally fed only on patches of sponge, a group of about ten small *P. maclareni* (20–30 mm SL) was seen over bare rock in 0.5 m of water. Instead of working regularly over the surface, as the larger fishes did, these young ones would pause as though watching, and then snap at particular objects on the rock.

Stomatepia mariae Nsess

S. mariae lived rather deeper than *S. pindu*, in water about 0.5–1 m deep. They usually swam alone or in groups of two or three, but we have seen larger shoals of up to about 20

fish. When seen underwater they were usually lurking in some sheltered place or cruising slowly around. They were rarely found feeding. Although plant tissues and organic debris formed part of their diet, their stomach contents showed that they are predators. Like *S. pindu*, they often took mayfly larvae and other aquatic arthropods. Unlike *S. pindu*, they frequently visited the surface to take terrestrial insects floating there, and they sometimes preyed on fishes.

Stomatepia pindu Pindu

S. pindu was a common species inshore wherever rocks or submerged logs provided crevices into which the fishes could retreat. They were usually found, in twos and threes, in shallow water, up to about 0.5 m deep, but they have been seen as deep as 3 m. The species was usually recognizable underwater by the dark colouring of even very small fishes; but they could change colour rapidly. When they were pale, sometimes with a row of dark lateral patches, *S. pindu* could be distinguished from *S. mariae* by their humped backs and pointed faces. *S. pindu* is a predator, probably snapping up small aquatic arthropods individually. Those with food in the stomach contained mayfly larvae, caddis larvae, chironomid larvae and decapod crustaceans as well as smaller quantities of organic debris, dark plant tissues and sponge spicules which may have been taken up accidentally together with the prey. Fourteen of the 32 stomachs were empty. We saw adult *S. pindu* feeding only twice. On one occasion, during the daytime, the fish hovered for some minutes as though watching a leaf lying on the bottom; then it moved on and seemed to study two more leaves; and at the fourth leaf, after a period of watching, it suddenly darted down and took up a mouthful of material from under the leaf. It spat out debris and made chewing and swallowing movements. On the other occasion *S. pindu* was seen by torch-light feeding at night. It applied its mouth to a rock and twisted its body as though picking something up. Small *S. pindu* about 15 mm in SL were seen feeding in a similar way, watching and snapping at individual objects on the surface of a rock.

As a predator, *S. pindu* probably spends less time eating than does a scavenger such as *Sarotherodon steinbachi*, but it is surprising that such a common fish was so rarely seen to feed. Possibly it fed in a place or at a time outside the range of our underwater observations, which were confined to well-lit regions in full daylight.

Stomatepia mongo Mongo

S. mongo seemed to live rather deep in the lake. The fishermen caught very few, and these all came from basket traps specially set in several metres of water. Of the nine whose stomachs were examined, six had quite empty guts and the other three contained very little. One contained mayfly larvae and woody tissues; one contained woody tissues only; and one contained scraps of arthropod cuticle. Evidently *S. mongo*, with its large mouth and short gut, takes invertebrate prey.

It is not clear whether *S. mongo* is a rare fish, or simply lives too deep to be caught by the Barombis' basket traps, which are usually set in shallow water.

Predators of the fishes

Two of the species of fish that we examined had eaten other fishes. We were unable to identify the fish eaten by *Stomatepia mariae*, but those eaten by *Clarias* included *S.*

steinbachi, *K. dikume* and *Myaka myaka*. It is probable that *Barbus* also takes fishes, but we did not find any in the few large specimens that we examined.

Both of the two species of snakes found in the lake (*Grayia smythii* and *Natrix anascopus*) have been recorded as eating fishes. The Barombis said that *G. smythii* was often caught in fish traps. One specimen that they showed us was nearly 2 m long.

No crocodiles or turtles were seen in the lake, and the Barombis said that there were none.

The birds around the lake included the following species. The nomenclature follows Mackworth-Praed & Grant (1970).

- Senegal finfoot—*Podica senegalensis*
- Little grebe—*Podiceps ruficollis*
- Long-tailed cormorant—*Phalacrocorax africanus*
- Darter—*Anhinga rufa*
- Grey heron—*Ardea cinerea*
- Pied kingfisher—*Ceryle rudis*
- Malachite kingfisher—*Corythornis cristata*
- Shining-blue kingfisher—*Alcedo quadibrachys*

The Long-tailed cormorant and the Darter are probably the most serious predators, although their populations were not large. We estimate that there were no more than 15 to 20 Long-tailed cormorants and about four Darters on the whole lake. The Pied kingfisher may also be a serious predator, being the commonest of the kingfishers. This species has been reported to confine its attacks to fish less than 10 cm in length (Daget, 1954). A specimen of this kingfisher and a Little grebe were found dead in fish traps which they may have entered in pursuit of fishes.

The Black kite (*Milvus migrans*) was frequently seen patrolling the lake, and once was seen to swoop and remove a fish from the water. This was probably a dead fish thrown out from the nets by the Barombis. The Palm-nut vulture (*Gypohierax angolensis*) was also frequently seen over the lake, but we did not see it take any fishes, although Brown & Amadon (1968) state that it will sometimes snatch live fishes from the water surface.

We did not see any otters in the lake, but an Otter shrew (*Potamogale velox*) was caught in one of the Barombi gill nets. Its stomach was full of broken-up crabs.

Probably the most serious predator on the fishes in the lake is man. The Barombi tribesmen have the sole fishing rights over the lake, and rely for their livelihood on the fishes. Each day they catch about 300 to 500 large unga, which with smaller numbers of *Clarias*, *Barbus* and mos (the prawn *Macrobrachium vollenhovenii*) are sold to "middle men" who carry them to Kumba market. The smaller fishes, such as *P. maclareni*, *S. pindu* and *S. lohbergeri* are kept and eaten by the villagers. It is difficult to estimate the numbers removed for this purpose, but if each person in the village eats five small fishes a day the total number eaten per day may be as high as 1000. The fishing methods of the Barombis on this lake effectively exploit fishes of particular sizes in particular habitats, but the smallest (and largest?) fishes are not caught, and the deeper waters are hardly fished at all.

There are on the lake about five large gill nets, each about 100 m long and 2 m deep, with a stretched mesh of about 5 cm. These nets are set at the surface some distance from the shore in water about 30–60 m deep. They are left out all the time (except when they

are taken up to be washed every four weeks or so) and are examined every morning by the fishermen. These nets catch unga and, in the lower part of the net, *K. dikume*. The mesh is too large to catch *Myaka myaka*, the other pelagic species.

A few shorter gill nets of smaller mesh are set close to the shore, tied to overhanging branches, in water 0.5–2 m deep.

Most of the smaller fishes and some of the marketable unga are caught in basket traps woven from strips of the rachis of the leaves of the raffia palm (Fig. 29). Most of these traps are about 1 m long and 35 cm in diameter, with meshes about 1 cm wide. Smaller traps with finer meshes are sometimes made for special purposes. The large traps are very common all around the edge of the lake. They are usually set on the bottom in shallow water so that the top of the trap just breaks the surface of the water. Sometimes a V-shaped fence is constructed to guide the fishes into the trap. These traps are set without bait, and are left in position for many days at a time. Each fisherman has trapping rights on a particular stretch of the shore and examines his traps daily. The traps catch large unga, which have apparently come inshore to breed, and large numbers of the smaller fishes: *S. lohbergeri*, *P. maclareni*, *K. eisentrauti*, *S. pindu*, *S. mariae*, young *Clarias* and the larger specimens of *E. sexfasciatus*. Sometimes traps of this kind are set deep on a cane rope at depths of 2–3 m or more. It was in deep traps that *S. mongo*, young *K. dikume* and sexually mature *Myaka myaka* were caught.

Other methods of fishing are used near the Barombi village in the lake and in the tributary stream. Boys fish with hook and line for *Clarias* and *Barbus*, and baited hooks are sometimes set in the lake, tied to overhanging vegetation. Women use hand nets of about 2 cm mesh netting on an oval wood frame to scoop for *Clarias* in the muddy pools of the stream. Closely woven circular baskets are used by women and children to dip *P. similis* and *E. sexfasciatus* from the village stream.

Relationships of the fishes of Barombi Mbo

ETHELWYNN TREWAVAS

Fish fauna of the surrounding streams

The streams in the neighbourhood of Barombi Mbo are tributaries of the Mungo River, with the exception of the River Bille, an upper tributary of the Meme. A score of species were caught in these streams by Dr Disney and his staff, using narrow-mesh basket traps and hand nets.

None of the cichlid species of the lake was found either in the feeder stream or in any of the streams of the district, with the exception of two juveniles of *S. lohbergeri*, caught in the part of the Kumba below the town. We understand that there is no barrier to upstream migration of cichlids between the Kake-Kumba confluence and the place where these were caught and it is probable that their parents were washed down from the lake into the Kake and so entered the Kumba.

The only cichlids caught in the streams or the main stream of the Mungo were *Hemichromis fasciatus*, *Chromidotilapia* sp., *C. guntheri* and *Tilapia camerunensis*, none of which is even congeneric with the cichlids of the lake.

Of the six species, all non-cichlids, caught in the feeder stream of Barombi Mbo, five

were also present in other streams, but only four in the lake. Of the two species of *Procatopus* caught in the district the one, *P. similis*, living in the feeder stream was found elsewhere only in the River Kumba of the Mungo tributaries and in the River Bille of the Meme system. These are the two streams nearest to the lake, respectively on its east and west sides, but not communicating with it directly. Of the two species of *Barbus* with parallel-striate scales, only one, *B. batesii*, was caught in the River Kumba, and this is the one present in Barombi Mbo. The only lake-endemic in Barombi Mbo's feeder stream was *Clarias maclareni* (young). *Clarias walkeri* was caught outside the lake basin in the Rivers Kake, Kumba and Wowe and in the Kotto area, where we found no *C. maclareni*. The *Clarias* from Lisoni described by me in 1962 proved to be the representative of a form closely related to *C. maclareni*, but not identical (Griffith, Green & Corbet, in prep.).

In conclusion, we have from the river faunas confirmation of the endemism of the 11 species of cichlids of Barombi Mbo, and no contradiction of the supposed endemism of *C. maclareni*, although its relationship with the form of Lake Soden is confirmed. The cichlid fauna of the upper Mungo and Meme systems provides no species that could be considered a source-species for the Mbo endemics. We must look elsewhere for the relationships of these.

Cichlids of lower zones of rivers of Cameroon

The volcanoes that form the characteristic landscape of West Cameroon are believed to be late Quaternary in date and Mount Cameroon is still active. Their conical shape and little-weathered craters support this view (Gèze, 1943) and the freshwater fish-fauna of Fernando Poo (Thys, 1967) testifies to the recent unity of this volcanic island with the area. The Mungo and Meme are now relatively short rivers. Probably before the volcanic activity rejuvenated their tributaries the cichlids of the lower zone lived farther inland as they do in the Sanaga, and one or more of them might have got into the crater lake, perhaps before all its clan had migrated to the more suitable lowland waters.

We must therefore take into account all the cichlids known from the Mungo and Meme systems including lakes Kotto and Mboandong. Two genera can be excluded as a source for the Mbo cichlids, *Hemichromis* because of the participation of the basioccipital in the apophysis for the upper pharyngeals and the structure of its scales, *Chromidotilapia* because of the "hanging pad" in the pharynx and associated feeding mechanism. *Tilapia* (*Coptodon*) *kottae* Lönnberg, *T. (Pelmatolapia) mariae* Boulenger and *Sarotherodon galilaeus* (Linn.) inhabit the lakes associated with the lower Mungo and Meme. In the brackish water of rivers to the west and south, and probably also of the Mungo and Meme, is *Sarotherodon melanotheron* Rüppell or its subspecies *S. m. nigripinnis* (Guichenot in Dumèril, 1859). Inland, in Rivers Nyong, Ja and Ogowe is the related *S. mvogoi* (Thys).

The extreme trophic adaptations of the Barombi Mbo cichlids must be ignored in looking for relationships, since we have looked in vain for equivalents that are not obvious cases of convergence or at most parallelism.

Groupings among the lake species that suggest multiple origin are:

- (1) *Sarotherodon steinbachi*.
- (2) *S. linnellii*, *S. caroli*, *S. lohbergeri* and *Myaka myaka*.
- (3) *Konia eisentrauti*, giving rise to *K. dikume* and *Stomatepia* (three species).
- (4) *Pungu maclareni*.

As a source group for the first three the genus *Sarotherodon* has the requirements of a mesethmoid free from the vomer (see Trewavas, 1972), a long buccopharynx, 14–24 gill-rakers on the lower part of the first arch and mouth-brooding still in the “experimental” or flexible stage (Kraft & Peters, 1963; Fishelson, 1966; Heinrich, 1967).

(1) *S. steinbachi*, as suggested in 1962, is probably related to *S. galilaeus*. The evidence is, (a) the range of vertebral numbers is as in *S. galilaeus* and higher than in the other Barombi Mbo species (see Table II), (b) the head is shorter, 33.0–36.5% SL, cf. 35.5–48.0 in group 2 and 35.0–40.0 in group 3 and (c) the mouth is smaller; its ratio (lower jaw 26–31% length of head) although nearly the same as in *S. lohbergeri* is measured against a smaller head. Seventeen dorsal spines, its modal number, were not found in any other Mbo species except in one specimen of *S. lohbergeri*, but it is rare too in *S. galilaeus*. It differs from *S. galilaeus* in its small size as well as in its specialized pharyngeal dentition, which could be derived from that of *S. galilaeus* or from *S. lohbergeri*.

(2) *S. linnellii* and *S. caroli* show in their dentition of jaws and pharynx and in the long snout and preorbital bone resemblance to *S. melanotheron*, *S. mvogoi* and *S. schwebischi*, but the massive head is not paralleled by any of these. *S. linnellii* (and perhaps the others) differs from *S. melanotheron* and resembles *S. schwebischi* in being a maternal mouth-brooder.

S. lohbergeri is included with these because of its long head, but the length is not more than it may be in *S. melanotheron*. Alternatively it may be related to the third group, as suggested by the similarity of its colour-pattern to that of *K. eisentrauti*.

Myaka myaka is one of the strangest of the cichlids in the lake. It is the smallest, and has a much less robust appearance than any other. Its long head and big mouth give it the appearance of a miniature *S. linnellii*, but its interorbital width is usually less than even in a small *S. linnellii*. It has reduced both the size and number of the teeth of jaws and pharynx; its scales are small, thin and irregular in arrangement and numbers. Its ovaries are very small. In spite of manifest differences I suggest that it is most nearly related to *S. linnellii* and *S. caroli*, mainly because the long narrow pharyngeal bone is derivable from that of *S. caroli*. If so, the shortness of the intestine is probably secondary, another reduction character.

(3) All the species in the third group have a rather narrow interorbital roof of the skull and a relatively short intestine. The interorbital roof can be narrow in *Tilapia* but not in *Sarotherodon*. The shortness of the intestine may be secondary, but this and other features (relatively short pharyngeal blade, diversity of trophic adaptations) suggest that these may have been derived from a proto-*Sarotherodon*, a tilapiine group with bi- and tri-cuspid teeth, a short epibranchial series of gill-rakers and a rather long ceratobranchial series, still feeding largely on invertebrates, having taken steps towards mouth-brooding.

All further specializations have evolved in the lake.

(4) Thys (1971: 167) has suggested that *Pungu* is related to *Tilapia kottae* and *T. guineensis*, but has not yet given his reasons. In favour of this is the fact that its ethmoid cartilage is very well ossified, the mesethmoid as well as the lateral ethmoid meeting the dorso-lateral wing of the vomer on each side in a brief suture. In this it resembles *T. zillii*, *T. kottae*, *T. camerunensis* and some individuals of *T. guineensis* as well as *T. mariae* and differs from all the other species of Barombi Mbo and all species of *Sarotherodon* that I have examined. It differs from all species of *Tilapia*, including *T. mariae*, in the large eggs, probably mouth-brooded, and from all except *T. mariae* and *T. brevimanus* in the higher

numbers of gill-rakers. Further, the species of *Tilapia* have typically a deep cheek with three or four horizontal rows of scales on it (although *T. kottae* may have only two), whereas *Pungu* has two oblique rows as in *Sarotherodon* and the other Mbo cichlids. Also, *Pungu* has 29 vertebrae and the modal number in *T. mariae* and most species of "*Coptodon*" is 28 (of this group only *T. rendalli* has a mode of 29).

Its relationship presents a baffling problem, since its extreme specialization carries it far from any possible ancestor. Little is known of the variation in ethmoid ossification, the study of which involves a disfiguring of museum specimens justifiable only to a limited extent. Regan (1920) distinguished the subgenus *Coptodon* from subgenus *Tilapia* on this character, but the type species of *Tilapia*, *T. sparronanii*, also has an ethmovomerine union. Preliminary studies suggest that it has a certain taxonomic value and that *T. rendalli* is an exceptional *Tilapia*, in this respect paralleling *Sarotherodon*.

In *Pungu* does the well-ossified ethmoid indicate a close relationship with *Tilapia*, perhaps *T. mariae*, or is it an atavistic convergence, part of the general strengthening of the snout?

Finally, we cannot find outside the lake more than three possible source-species for the Mbo cichlids and we can postulate a fourth (the "proto-*Sarotherodon*"). If this fourth really existed it could have given rise to groups (1) and (2) as well as to the third. The separate origin of *Pungu* is still open to question.

Eye lens proteins

Acting on the advice of my colleague Dr C. A. Wright, I collected lenses from the eyes of a number of cichlids in Cameroon and Ghana. They were dissected from the fresh fish as soon as possible after death and kept chilled until they were delivered at the Museum. For this possibility I have to thank the members of the Helminthiasis Research Unit, Professor D. W. Ewer of Ghana University and the proprietor of the village store at Kuntanasi, near Bosumtwi, for the use of refrigerators. The lenses were transported in a chilled thermos flask.

At the British Museum (Natural History) Mr Ross processed them to produce electrophoretic protein patterns. Without knowing either the geographical or zoological relationships of the species Mr Ross arranged the patterns in three groups. The first comprised eight species of Barombi Mbo, the only ones from that lake that gave successful results. The division between the other two groups seems to me to be more arbitrary. Together they include *Chromidotilapia loembergi* (Lake Kotto), *Tilapia guineensis* (near Accra), *T. discolor* (Lake Bosumtwi), *T. mariae* (Lake Kotto), *Sarotheron melanotheon* (two lagoons in Ghana), *S. multifasciatus* (Bosumtwi) and *S. galilaeus* (Kotto and Nungua reservoir near Accra).

The Barombi Mbo pattern is of nine evenly spaced bands, becoming gradually fainter from the cathode end towards the anode, giving very similar patterns for *K. eisentrauti*, *K. dikume*, *St. pindu* and *Pungu*. That of *S. lohbergeri* is similar but fainter. In *S. steinbachi*, *Myaka myaka* and *S. linnellii* the band immediately at the cathode side of the starting line is stronger than the other three cathode bars and there is a blank at the anode side until three or four fairly well defined bars show up at the anode end. These three species, and especially *S. linnellii*, are the only ones that show some resemblance to any of the outside patterns, namely to that of *S. galilaeus*, in which, however, the densest cathode bar is farther

from the starting line. In all the other external cichlids tested there are two strong bands on the cathode side.

Unfortunately we do not know how to interpret these results. Have they anything to do with relationship or does the chemistry of the environment influence the lens proteins? For relationship we have the close similarity of the patterns of *T. guineensis* and *T. discolor*, whose macrostructure also bespeaks close relationship, but whose environments, respectively a brackish lagoon and a soda lake, are dissimilar. But the patterns of the unrelated *S. melanotheron* and *C. loennbergi* are also very similar, to each other and to *T. guineensis*, the one from the same lagoon as *T. guineensis*, the other from Kotto.

The only legitimate conclusion is that there is something that causes the eye lens proteins of the cichlids of Barombi Mbo to be alike and to differ from those of other cichlids in which they are known, but whether it is genetic similarity or an environmental factor we do not know.

Photographs of the electrophoretic patterns and Mr Ross's account of his methods are available for reference in the Experimental Taxonomy Section of the British Museum (Natural History).

Evolution of the cichlids in Barombi Mbo

ETHELWYNN TREWAVAS, J. GREEN AND SARAH A. CORBET

The 11 species of cichlids in Barombi Mbo thus appear to be endemic and without very close relatives elsewhere. Their evolution within the lake probably began with the initial invasion of the lake by ancestral cichlids followed by their subsequent adaptive radiation which involved, firstly, the initiation of reproductive isolation between units of the ancestral populations, and, secondly, the progressive divergence of the newly-formed species that resulted in their avoidance of competition.

The initial invasions of Barombi Mbo may have been by two to four species (see p. 86). This isolated lake, a crater situated on top of a high volcanic hill, must have been difficult of access for fishes throughout its history, and the first to colonize it will have found themselves in an environment which, though presumably different in major respects from their original home, offered food and space enough to permit a rapid increase in population. It is evident from work on man-made lakes that in such circumstances fish species may change their habits relatively quickly. Petr (1967) has recorded that the schilbeids of the River Volta, *Schilbe mystus* and *Eutropius niloticus*, which in the river were generalized feeders on insects and small invertebrates, have in the Volta Lake become specialists on *Povilla* larvae and are never to be found far from the clumps of rotting wood in which these insects burrow. Loiseau (in press) describes the ready adaptation of *Leptotilapia irvinei*, previously known only from the Volta rapids, to the rocky places in the new lake. Both these changes in habit are such as might eventually result in changed structure. If the first-colonizing cichlids underwent changes of this kind on entering the lake it is scarcely surprising that we can now see no close similarity to the species elsewhere (if they still exist) that provided the pioneers.

Changes of this kind would affect the whole species in its new environment; to explain the early stages of speciation there we must envisage some physical or biological barrier

within the lake capable of producing genetic isolation between the populations that are incipient species. Fryer's (1959) view that incipient species of cichlids in Lake Malawi were kept apart by alternating rocky headlands and sandy bays is not applicable here. None of the species in Barombi Mbo seems to be confined to either rocks or sand, and there are no major discontinuities in the shore-line. Nor can we invoke the separation of basins within the lake by a former low water level, as Greenwood (1951) proposed for Lake Victoria, because the crater of Barombi Mbo is evenly conical. Currents in the lake are gentle, but it is possible that there may at some time have been currents near the out-flow strong enough to prevent the passage of fishes from one side to the other, but only at that point.

Since no major physical barrier exists to account for the initial separation of the populations that became species, the possibility of speciation in the absence of such a barrier deserves very serious consideration.

The divergence of the newly-formed species is paralleled in other organisms: Ayala (1970) has given examples of experiments demonstrating selection for avoidance of competition in sibling species of *Drosophila* resulting in the establishment of greater differences between populations of such species living together than between the same two living apart, and Brown & Wilson (1956) have given instances of this latter phenomenon in wild populations. There is some evidence for selection for the avoidance of competition in Barombi Mbo: our study showed that most of the cichlids are clearly separated from one another in their distribution through space or time, or in their feeding habits.

There is a clear spatial separation between those species that live and feed inshore and those that feed in the deeper water of the open lake, coming inshore only to breed. Within this group of inshore species there is some overlap in diet, but each species selects a main course different from the others.

The main fish foods in the lake are phytoplankton, organic debris, aquatic invertebrates, fishes and adult insects (Fig. 28). The two inshore species of *Sarotherodon* both feed to a large extent on organic debris, but *S. lohbergeri* collects it, together with aufwuchs, from the surfaces of rocks and plants, while *S. steinbachi* collects it mainly from sandy areas. *Pungu maclareni* is the only species in the lake (and perhaps the only freshwater fish) that feeds largely on chunks of living sponge. Its prominent teeth and thick lips may be adaptations to this unusual diet. Insect larvae support a group of predatory inshore fishes which differ from one another in the depths or times at which they feed, the size of their prey, and the relative importance of adult insects in their diets. Young individuals of unga (*Sarotherodon linnellii* and/or *S. caroli*) often feed very close inshore in water too shallow for other fishes, taking flotsam as well as bottom aufwuchs and insect larvae. *Konia eisentrauti* feeds in water about 1–2 m deep, snapping up small invertebrates and sometimes taking the eggs of other fishes. *Stomatepia mariae* takes larger prey than *K. eisentrauti*, including small fishes, and frequently takes adult insects from the surface of the water. *Stomatepia pindu* hunts in a similar way to *K. eisentrauti*, but seems to feed mainly in twilight or at night and so probably encounters a different range of prey. The cyprinodont *Epiplatys sexfasciatus*, feeding at the surface close inshore, makes use of a food source scarcely tapped by the cichlids.

The cichlids in deeper water are silver grey and without markings when alive in contrast to the inshore species which are blotched with black. The significance of such colouration in the camouflage of open-water fishes has been discussed by Denton & Nicol (1965). Those

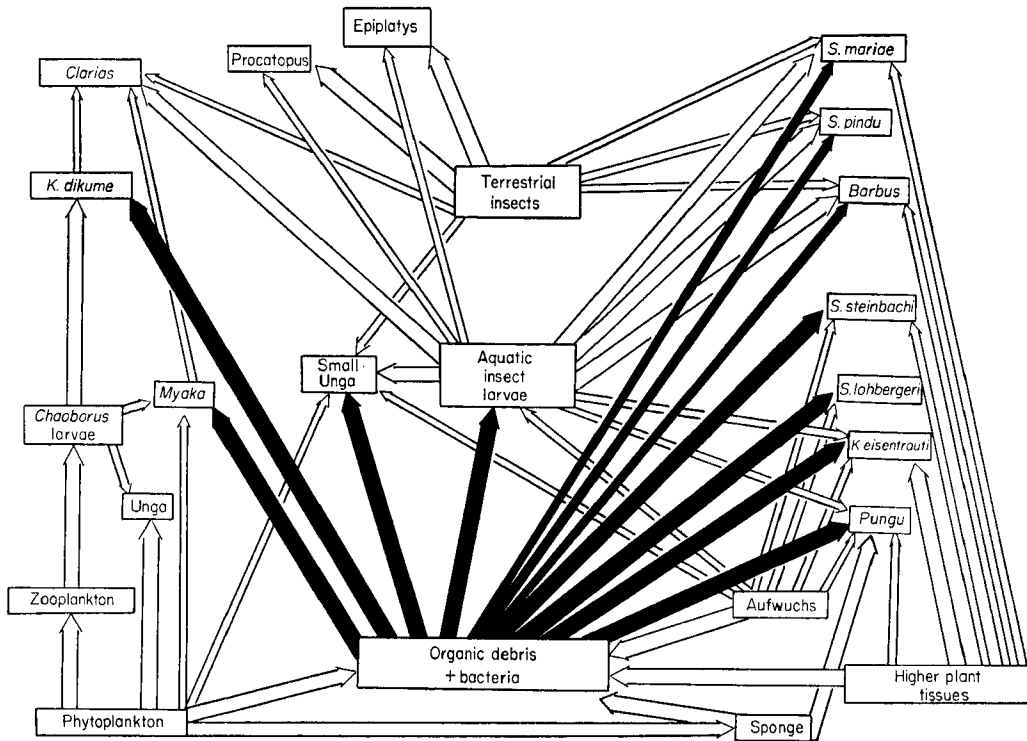


FIG. 28. A food web for the fishes of Barombi Mbo based on the examination of stomach contents. Wide arrows: more than 30% of fishes have the food item as main contents; narrow arrows: fewer than 30% have.

individuals found in breeding condition inshore (of *Sarotherodon linnellii*, *S. caroli* and *Myaka myaka*) showed darker markings resembling those of inshore species. Phytoplankton forms the sole food of adult *S. linnellii* and *S. caroli*, both of which swim a few feet below the surface in mid-lake. *Myaka myaka* probably feeds on dead phytoplankton and other organic debris close to the bottom. No fishes seem to prey directly on the copepods and rotifers in the open water, but these must support the *Chaoborus* larvae which constitute the chief food for *Konia dikume*.

From this survey it is evident that most species of cichlids in the lake differ in their diets so much that no two species are likely to come into direct competition for a scarce item of food. The sibling species *Sarotherodon linnellii* and *S. caroli* provide an interesting exception. They seem to swim at similar depths and they share a diet of phytoplankton; so that if the resource were scarce one might expect severe competition. But Lowe-McConnell (1969), who found three phytoplankton-feeding species of *Tilapia* coexisting in Lake Malawi, has suggested that for such fishes food may not be a limiting resource. More important for cichlids may be the limited space for breeding sites around the shore. If so, competition between these sibling species would be reduced by a difference in breeding seasons. We have some evidence that *S. linnellii* and *S. caroli* do breed at different seasons (p. 58).

We suggest, then, that the stages in the evolution of the cichlids in Barombi Mbo were these. The lake was colonized by two to four cichlid species, (a) an *S. galilaeus*-like form,

(b) a form ancestral also to *S. m. nigripinnis* and *S. mvogoi*, (c) a *Konia eisentrauti*-like form and (d) the ancestor of *Pungu*, feeding respectively on (a) material sifted from fine sand, (b) phytoplankton, detritus and aufwuchs, and (c and d?) invertebrates. The sand-sifter, (a) became more exclusively adapted to that habit; the second form, (b), became divided in response to increased opportunity and competition (especially for limited aufwuchs) into a specialized aufwuchs-feeder (*S. lohbergeri*) and two phytoplankton-feeders; and the invertebrate-feeders, (c), diverged to produce *Konia* with its diet of bottom invertebrates, and the species of *Stomatepia* which avoided competition by feeding at night (*S. pindu*) or in deeper water (*S. mongo*), or by including in their diet waterlogged insects from the surface and even small fishes (*S. mariae*). Driven from the crowded inshore rocks to the deeper water near the middle of the lake, *K. dikume* exploited the dense populations of *Chaoborus*, and *Myaka myaka* (from group b?) fed on detritus near the bottom. The question whether *Pungu* also diverged from group (c) or was highly modified from a separate ancestor has been discussed on p. 87-88.

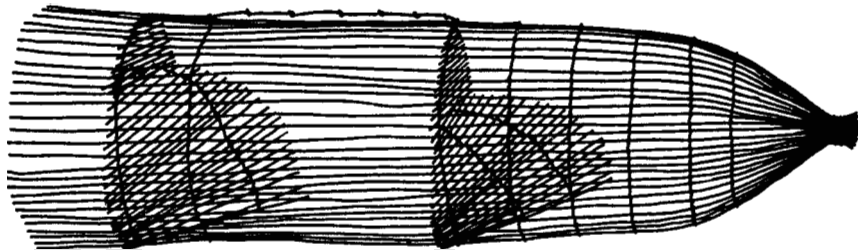


FIG. 29. A basket trap, 110 cm long, from Barombi Mbo.

This impressive ecological separation has clear adaptive advantages for a dense population of fishes exploiting the meagre resources of an oligotrophic lake; but the nature of the factors that initiated speciation within the lake, in the apparent absence of geographical barriers, remains open to speculation.

Comparison with other African lakes

The situation in Barombi Mbo has a double interest from its resemblance in miniature to that in the great Rift Valley lakes, particularly Tanganyika. The scale, both temporal and spatial, is immensely greater in Tanganyika, but this lake has the Malagarazi entering it on the east and an outlet to the Congo on the west, the faunas of the two rivers being related although they have been separated long enough for a degree of divergence to take place. Across these once continuous rivers lies Lake Tanganyika, with a rich fish-fauna consisting mainly of endemic species, especially cichlids, for most of which no obvious source species still exists outside. It has evidently been derived from a very old fauna (old in terms of cichlid time-scale), which may have inhabited the huge shallow lake that is believed to have occupied the central Congo basin. What has happened once in Barombi Mbo has happened again and again in the Great Lakes, giving a multi-tier radiation with convergent adaptations. Fryer has expressed this idea in a diagram (1959: 446). Even in Barombi Mbo we may be seeing the beginning of a second tier in the three species of *Stomatepia* and in *Sarotherodon linnellii* and *S. caroli*.

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Introduction by the Helminthiasis Research Unit ensured us a friendly reception by the Barombi people at the village of Barombi Mbo, who managed to combine a very helpful attitude with a firm reminder that the lake was their property. We welcomed this as a good augury for the conservation of this unique ecosystem. In particular, we thank Joseph Ndokpe Sangwa, who shared his knowledge of the local fishes and told us how to spell their Barombi names. We pay tribute to the memory of the chief, Martin Malleh, who died in 1971.

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